Yoshiaki Kai · Hiroyuki Motomura
Keiichi Matsuura *Editors*

Fish Diversity of Japan

Evolution, Zoogeography, and Conservation

Springer

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Introduction

1

Yoshiaki Kai, Hiroyuki Motomura, and Keiichi Matsuura

Abstract

This chapter provides a brief outline of this book. The Japanese Archipelago, surrounded by two major warm currents and one cold current, is located in the western North Pacific and encompasses several climatic regimes from north to south. Although the land area of Japan is small, the Exclusive Economic Zone (EEZ) of Japan is large and ranks as the sixth largest in the world, including several marginal seas and deep trenches. Together with the various historical factors, Japan has a rich fish species diversity, representing more than 4500 species in 370 families. In order to understand the fish diversity in Japanese waters and its origin, we compile the present information on ichthyofauna, habitat distribution, phylogeography, ecology, morphology, and conservation, as well as the history of ichthyology in Japan. This is the first attempt to review and summarize the studies on fish diversity in Japan by leading current specialists in each field.

Keywords

Ichthyology · Distribution · Phylogeography · Ecology · Morphology · Conservation · Natural history

The Japanese Archipelago, ranging from boreal to subtropical zones, comprises a long chain of islands (ca. 3500 km) located off the eastern coast of Asia. Although the archipelago consists of approximately 6800 islands, the four main continental islands, Hokkaido, Honshu, Shikoku, and Kyushu, cover more than 97% of the total land area (Fig. 1.1). The land area of Japan is small, but the Exclusive Economic Zone (EEZ) of Japan is large and ranks as the sixth largest in the world, including several marginal seas (Sea of Okhotsk, Sea of Japan, and East China Sea) and deep trenches (Izu-Ogasawara, Japan, and Kurile trenches). Two major warm currents (Kuroshio and Tsushima currents) and one cold current (Oyashio Current) flow along the Japanese Archipelago, transporting various kinds of fishes from south or north and forming rich fishing grounds, including the Kuroshio–Oyashio Transition Zone. The archipelago was separated from the continent by the formation of the Sea of Japan during the Miocene, with subsequent deformation through insularity and land-bridge formations,

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resulting from sea-level changes that occurred during the glacial–interglacial oscillations in the Pliocene and Pleistocene (Tada 1994). Owing to such a variety of marine habitats and a complex geological history, Japan has a rich fish species diversity, representing more than 4500 species in 370 families (Motomura 2021).

This rich fish species diversity has attracted the scientists since the late 1700s, and its origin and present status have been continuously studied, resulting in the development of ichthyology in Japan. The intent of this book is to summarize the fish diversity of Japan, compiling the present knowledge of ichthyofauna, habitat distribution, phylogeography, ecology, morphology, and conservation, as well as the history of ichthyology and fish collections in Japan. This is the first attempt to review and summarize studies on the fish diversity of Japan written in English by leading current specialists in each field.

Following this section, the book is organized in five parts. I. Fish Diversity and Ichthyology of Japan; II. Habitat Distribution and Species Diversity; III. Diversity within Species: Phylogeographic Perspective on Japanese Fishes; IV. Morphological and Ecological Diversifications; V. Conservation of Fish Diversity in Japan—comprising 25 chapters in total. Part I (Chaps. 2–4) begins with a review of the fish fauna of Japan and the historical and environmental factors shaped the fish diversity, as well as the history of ichthyology in Japan. Part II (Chaps. 5–9) illustrates the fish diversity in shallow coastal and deep areas, focusing on the current system along the Japanese Archipelago or climatic regimes. Part III (Chaps. 10–12) provides an overview of phylogenetic studies in Japan based on molecular techniques, comprising three chapters for coastal, deep-sea, and freshwater fishes. Because the Japanese Archipelago has a complex geological history as noted above, various patterns of divergences are known in marine and freshwater fishes. Part IV (Chaps. 13–17) describes the recent progress on studies of morphological and ecological diversifications of Japanese fishes, such as the fields of migration, evolutionary development (evo/devo), larval fishes, lateral-line systems, and interspecific hybrids, led by Japanese experts. Part V (Chaps. 18–25) reviews the present status of conservation of Japanese fishes in various habitats, together with the use of "*gyotaku*" for past records, and the adaptation of the Convention on Biological Diversity (CBD) in Japan.

In this book, scientific names generally follow those compiled by Motomura (2021). Major geographic locations, regions, and currents in Japan and adjacent waters are shown in Fig. 1.1, more detailed locations may be provided in each chapter. The current systems around the Japanese Archipelago follow Gamo et al. (2014) and Gallagher et al. (2015). The Ryukyu Islands are herein defined as shown in Fig. 1.1, but sometimes include the Osumi Islands (see Chap. 5).

We hope that this collection of papers, written by leading experts in each of the various fields will provide a stimulating and reliable resource for future research and contribute to the progress of ichthyology of the world.

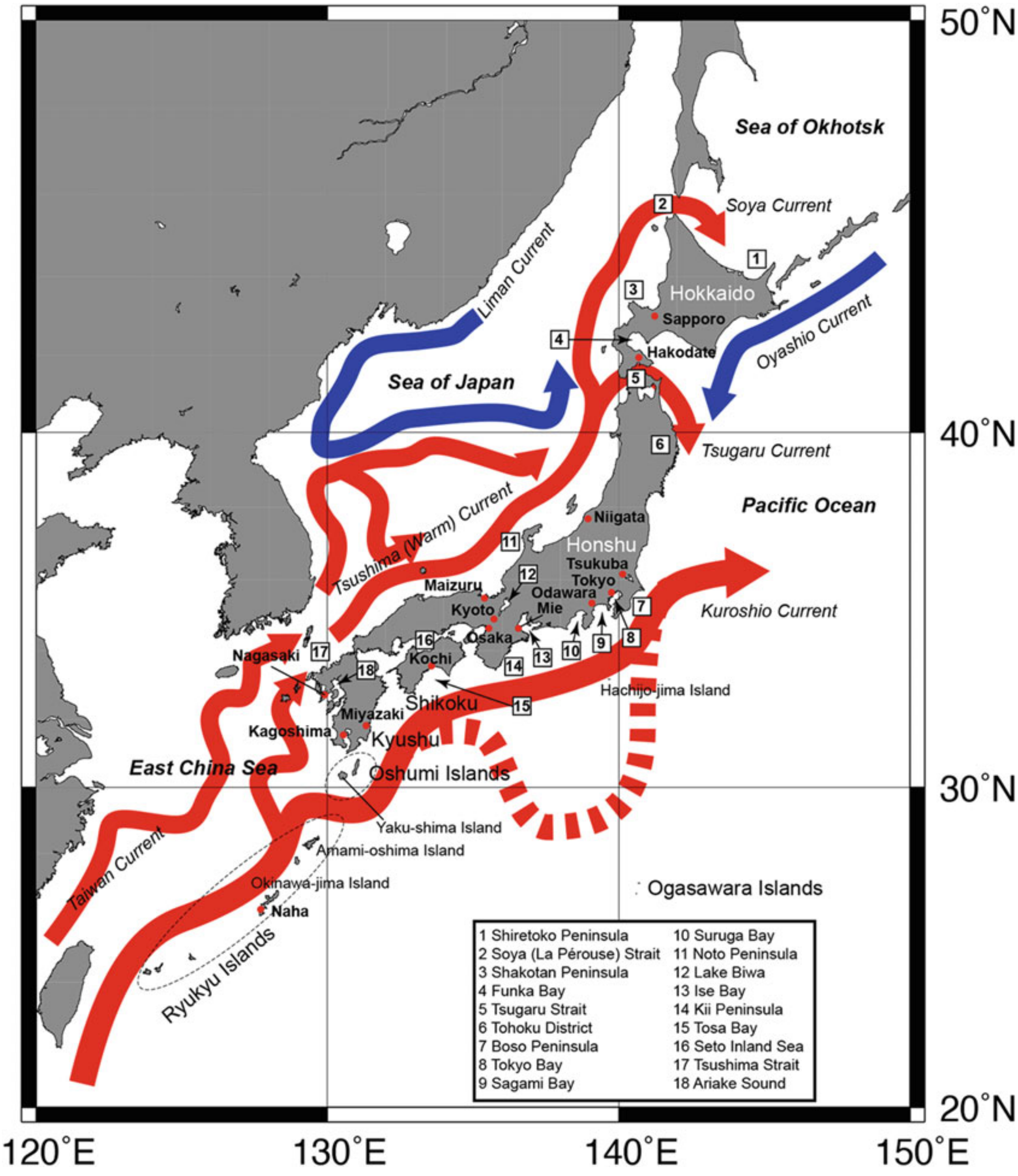

Fig. 1.1 Major geographic locations, regions, and currents in Japan and adjacent waters

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Part I

Fish Diversity and Ichthyology of Japan

Geography, Currents, and Fish Diversity of Japan

2

Hiromitsu Endo and Keiichi Matsuura

Abstract

The Japanese Archipelago has a unique geographic history related to tectonic activities in the western North Pacific Ocean, and it is influenced by two strong currents (the Kuroshio and Oyashio currents). Because it extends for 3000 km from north to south, covering the subboreal to subtropical climatic zones, there are various aquatic environments in seas and freshwaters that have resulted in a high diversity of fish species. We examined the components of Japan's fish diversity and recognized 4476 valid species, which represents 12.5% of the world's ichthyofauna; the top 35 most speciose families include 2571 species (57.4% of Japan's valid species). The top 10 most speciose families are as follows: Gobiidae (469 species), Serranidae (156), Labridae (153), Pomacentridae (111), Apogonidae (102); Cottidae (88), Myctophidae (88), Bleniidae (81), Cyprinidae (78), and Macrouridae (70), with the top five being shallow water marine fish groups from tropical to temperate waters. The two deep sea groups listed, Myctophidae and Macrouridae, indicate that deep trenches and troughs in the seas around Japan provide suitable habitats for deep-sea fishes.

Keywords

Tectonic plate · Current · Fish fauna · Taxonomy · Zoogeography · Japanese Archipelago

2.1 Introduction

Japan is a volcanic island country located in the western North Pacific Ocean and isolated from the eastern Eurasian Continent. It consists of four main islands (Kyushu, Shikoku, Honshu, and Hokkaido), three island chains [the Ryukyu, Izu-Ogasawara (=Bonin), and southern Chishima (Kuril) islands], and many small islands scattered around the main islands. Although Japan is one of the smallest countries in the world for land area, the Japanese Archipelago is somewhat long, extending for 3000 km from north to south and ranging from the subboreal to subtropical climatic zones (Fujikura et al. 2010: Fig. 2.1). Further, Japan faces the Pacific Ocean and its marginal seas, the East China Sea, Sea of Japan, and Okhotsk Sea. There are also small inland seas such as the Seto Inland Sea and Ariake Sound (the largest bay located along the west coast of Kyushu). The land area of Japan is relatively

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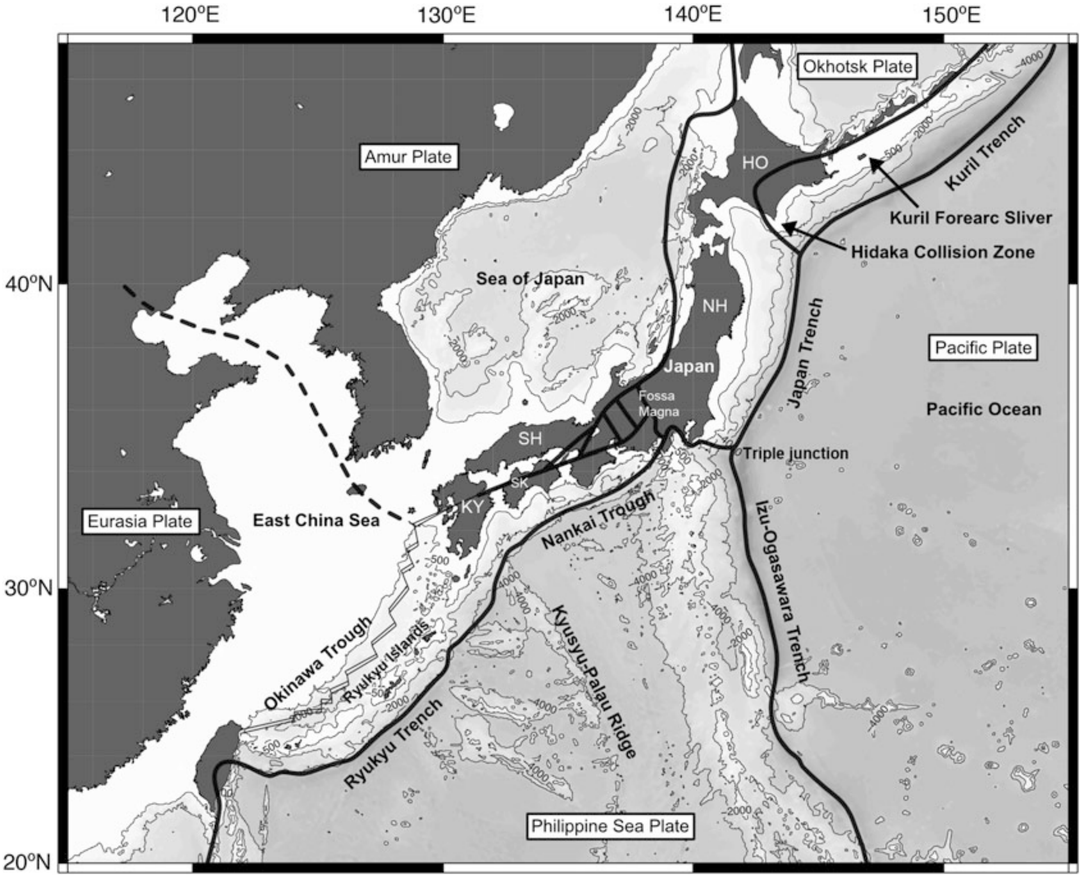

Fig. 2.1 Map of the western North Pacific around Japan showing Japanese Archipelago (*HO* Hokkaido, *NH* northern Honshu, *SH* southern Honshu, *SK* Shikoku, *KY* Kyushu), tectonic plates, trenches, and troughs (modified from Taira 2001: fig. 1c). The map was generated using the Generic Mapping Tools (GMT ver. 4.5.9; see Wessel et al. 2013), with bathymetric data obtained from ETOPO1 (Amante and Eakins 2009)

small (about 5% of Australia's), but it has an enormous water surface area of 4,470,000 km^2, which is composed of inland, coastal, and offshore waters including the Exclusive Economic Zone (EEZ, 4,050,000 km^2) (Japan Coast Guard 2021: Fig. 2.2). Japan's EEZ is the sixth widest for the EEZ area by country and the fourth most expansive for volume in the world (Matsuzawa 2005). This large volume provides extensive habitats for deep-sea fishes in the seas around Japan. Also, two major warm and cold ocean currents (the Kuroshio and Oyashio currents), complicated coastlines, and complex submarine topography affect marine biota around Japan. According to the Census of Marine Life (CoML) project operated worldwide during the years between 2000 and 2010, the diversity of marine biota around Japan is assumed to be the second-highest next to that of Australia and one of the world's marine biodiversity hotspots (Fujikura et al. 2010).

Among 35,898 fish species recognized worldwide (Fricke et al. 2021), 4476 valid species (12.5% of all) were recorded from Japan (Motomura 2021; this study). Although most of them occur in marine and brackish waters (or are diadromous), 152 species inhabit only freshwaters (e.g., Watanabe et al. 2017; Hibino and Tabata 2018). Watanabe et al. (2017) reviewed and discussed the biogeography and

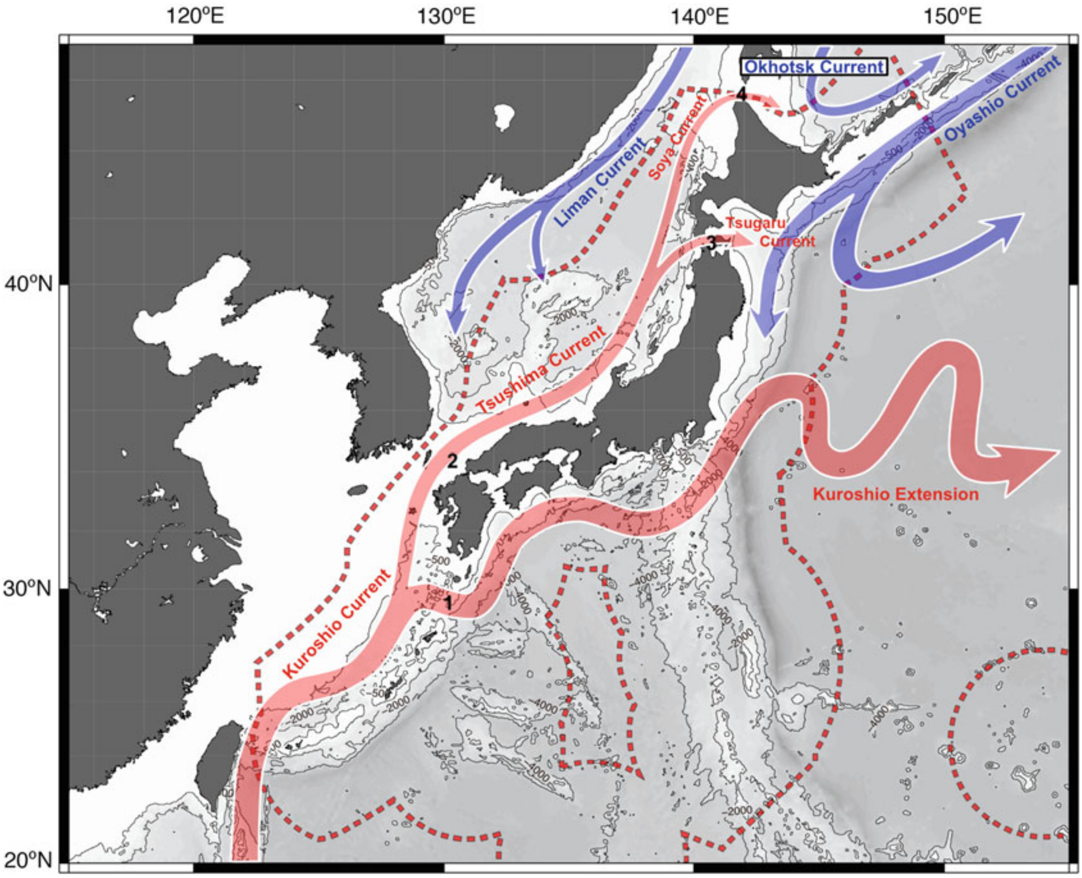

Fig. 2.2 Map of the western North Pacific around Japan showing the Exclusive Economic Zone (*dotted lines*), currents, and straits: *1* Tokara Strait; *2* Tsushima Strait; *3* Tsugaru Strait; and *4* Soya Strait (modified from Nakayama 2020: figs. 2, 3). The map was generated using the Generic Mapping Tools (GMT ver. 4.5.9; see Wessel et al. 2013), with bathymetric data obtained from ETOPO1 (Amante and Eakins 2009)

cryptic diversity of Japanese freshwater fishes. The Japanese fishes inhabit many aquatic environments, from mountain streams to deep-sea trenches and from coral reefs to the frozen sea covered by drift ice in winter (Nakabo 2013). We summarize the historical geography and currents in the Japanese region and the species composition of Japanese fishes by families.

2.2 Geography

The Japanese island arc system consists of four segments: the Kuril Arc, the Honshu Arc [divided into the Northeastern (NE) Japan Arc and Southwestern (SW) Japan Arc], the Ryukyu Arc, and the Izu-Ogasawara (=Bonin) Arc (Taira 2001; Mahony et al. 2011). These arcs are located along the subduction zones of the following tectonic plates (Taira 2001): the Pacific Plate and Okhotsk Plate (a small western part of the North American Plate); the Pacific Plate and Philippine Sea Plate (PSP); the PSP and Amur Plate (a small eastern part of the Eurasian Plate); and the PSP and Eurasian Plate (Fig. 2.1). Tectonic activities since 30 Ma including volcanic activity near the subduction zones have formed mountains on the land, islands, submarine ridges, troughs, basins, and trenches in the sea (Nakajima 2018). In Japanese waters, three trenches are located along the subduction zones on the Pacific Plate—the Kuril Trench (deepest point at 9550 m deep, 44°09′N, 150°30′E), Japan Trench (8058 m, 36°05′N, 142°46′E), and Izu-Ogasawara Trench (9780 m, 29°28′N, 142°42′E)—while the Ryukyu Trench (=Nansei-Shoto Trench, 7480 m, 24°52′N, 128°02′E) is located along the subduction zone on PSP (Taira 2001; National Astronomical Observatory of Japan 2020; Fig. 2.1). Also, three troughs run along the subduction zone of PSP from east to west [i.e., the Sagami Trough (from the "Triple junction" meeting point of the three tectonic plates to Sagami Bay), the Suruga Trough (from Suruga Bay to Enshu-nada sea), and the Nankai Trough (off the Kii Peninsula and Shikoku Island or including Suruga Trough in a broad sense)], while the Okinawa Trough in the East China Sea is an expanding back-arc basin of the Ryukyu Arc (Taira 2001; Mahony et al. 2011: Fig. 2.1). Further, the Kyushu-Palau Ridge, extending from north to south, is located on the center of the PSP off Shikoku and Kyushu and is regarded as a remnant of the proto-Izu-Ogasawara (Bonin) Arc (Mahony et al. 2011; Nishizawa et al. 2016).

Before 30 Ma, the Japanese region was part of the eastern margin of the Eurasian Continent. Subsequently, the opening of the Sea of Japan by the "back-arc expansion" began in ca. 30 Ma and finished in 15 Ma (Nakajima 2018; Tsutsumi 2021). At present, two models for explaining the opening of the Sea of Japan—the "double-door opening"and the "pull-apart basin"—are predominant (Tsutsumi 2021). Both are identical with respect to the formation of two island arcs [the Northeastern (NE) Japan Arc (=NE Honshu Arc) and Southwestern (SW) Japan Arc (=SW Honshu and Shikoku)], which migrated separately from the Eurasian Continent. During the period of 18–16 Ma, the NE and SW Japan arcs had rotated rapidly counterclockwise and clockwise, respectively (Nakajima 2018; Tsutsumi 2021). During 16–13 Ma, the volcanic front on the SW Japan Arc was active when the PSP began to subduct beneath the Eurasian Plate (Tsutsumi 2021).

After 3 Ma, the NE and SW Japan arcs rifted actively due to the east–west contraction related to the Pacific and PSP subducting underneath the Amur Plate (Takahashi 2017). The rifted arcs are bordered by the Fossa Magna area, marking a critical boundary of fauna and flora on land. For example, the Central Highlands formed by uplifting in this area is a significant and well-documented barrier for many primary freshwater fishes (Watanabe et al. 2017).

The Sea of Japan was wide open in 15 Ma, because most of the NE Japan Arc had not rifted above sea level (Tsutsumi 2021). This opening event formed three basins; the Japan Basin (maximum depth of ca. 3800 m) is the largest and located on the north side of the Yamato Basin, which is separated by the Yamato Bank from other areas of the Sea of Japan, and the Tsushima Basin located near the Tsushima Strait and surrounded by the Korean Peninsula and Honshu Island (Shinohara et al. 2011; Nakajima 2018). At present, the Sea of Japan is narrowly connected to the Pacific Ocean by four shallow straits, i.e., Mamiya (=Tatar, ~10 m maximum depth), Soya (=La Pérouse, 60 m), Tsugaru (140 m), and Tsushima (120 m), that act as barriers for most deep-sea fishes trying to enter the Sea of Japan (e.g., Nishimura 1992; Nakaya and Shirai 1992; Shinohara et al. 2011; Nakayama 2020). Also, the Tsugaru and Tsushima straits were probably not closed even at the lowest sea level (approximately −120 m) during the last glacial period in the Late-Quaternary (e.g., Ohshima 1990; Tsutsumi 2021). Furthermore, although a land bridge between Hokkaido and Sakhalin was formed over the present-day Soya Strait (Ono 1990; Watanabe et al. 2017), the Tsugaru and Tsushima straits were boundaries for freshwater fishes in Far East Asia. Hence, these geographical events have played an important role in the diversity and evolution of inshore marine and freshwater fishes of Japan during sea-level fluctuations of repeated glaciations in the Pleistocene (e.g., Watanabe et al. 2017; Kato et al. 2021; Hirase 2021).

Hokkaido, located on the Okhotsk Plate, facing the Pacific Ocean, Sea of Japan, and Okhotsk Sea, was formed by two old arc-trench systems (i.e., old Japan and Kuril trenches) and related to movements of the North American, Pacific, and Amur plates, and the Kuril Forearc Sliver (a microplate of the Okhotsk Plate along the Kuril Trench, the western end of the Hidaka Collision Zone) (Taira 2001; Tsutsumi 2021; Fig. 2.1). The western part of Hokkaido belonging to the NE Japan Arc originated from the Eurasian Continent's margin, while the eastern part of Hokkaido was an island belonging to the Kuril Arc 20 Ma (Tsutsumi 2021). From 15 to 10 Ma, the eastern part of Hokkaido collided with the western part via the westward movement of the Kuril Forearc Sliver, resulting in the formation of the Hidaka Mountains (Tsutsumi 2021: Fig. 2.1). Also, the Kuril Basin (=Chishima Basin, 3521 m maximum depth) in the Okhotsk Sea was formed by a back-arc spreading from ca. 24 to 15 Ma (the late-Oligocene to middle-Miocene) in the same period of time the Japan and Shikoku Basins were formed (Nakajima 2018).

On PSP, the separation of the Kyushu-Palau Ridge (KPR) from the proto-Izu-Bonin Arc was caused by the southwest-northeast expansion of the Shikoku Basin (and Parece Vera Basin, located south of the former) from ca. 26 to 15 Ma (e.g., Mahony et al. 2011; Nishizawa et al. 2016). This expansion, which was linked to the origin and extension of the Nankai Trough started at the Shikoku Basin Spreading Center on PSP between KPR and the Izu-Ogasawara Arc, and the boundary of the Pacific Plate also moved toward the northeast (oblique against the zone) during the formation of the Shikoku Basin from 15 to 5 Ma (Mahony et al. 2011). Subsequently, the direction of subduction underneath the Amur Plate changed toward the northwest (vertical against the zone) in 3 Ma (Mahony et al. 2011; Tsutsumi 2021). On the other hand, the western area of the northern KPR, subducting at the Ryukyu Trench, is older than the eastern area (60–40 Ma), where the Amami Plateau, the Daito Ridge, and the Oki-Daito Ridge (remnants of paleo-island arcs) are located from north to south (Nishizawa et al. 2014; Tsutsumi 2021). These complex seafloors characterize the area.

2.3 Currents

The Kuroshio and Oyashio currents are the major warm and cold western boundary currents in the western North Pacific Ocean, which strongly affect climate and the marine biota around Japan (e.g., Nishimura 1992; Fujikura et al. 2010; Qiu 2019: Fig. 2.2). The Kuroshio Current acts as a conveyer for supplying eggs and larvae of various tropical and subtropical fishes and invertebrates, and warm water reef-building corals to southern Japan (Nishimura 1992). Conversely, it acts as a barrier for the dispersal of many temperate shore fishes from southern Japan to the Ryukyu Islands (Matsuura and Senou 2012). Also, the Oyashio Current (=Kuril Current) brings cold oxygen- and nutrient-rich waters to the Pacific coasts of northern Japan (Qiu 2019).

"Kuroshio" is a Japanese name meaning "black stream" and is derived from its blackish-blue water coloration that indicates the deficiency of nutrients and sediments, and resulting in high transparency and low biological productivity (Qiu 2019). The Kuroshio is a western flow of the North Pacific Gyre known as a wind-driven clockwise circulation between the equator and 50° N latitude (Gallagher et al. 2015; Qiu 2019). It originates from the western end of the North Equatorial Current in the gyre, flowing north along with the eastern Philippine Islands, to the East Taiwan Channel, entering the East China Sea, flowing northwest along the Ryukyu Arc to the Tokara Strait, and inflowing the open Pacific Ocean off southern Japan between 136° E and 140° E (off Kyushu, Shikoku, and Honshu). The Kuroshio Current displays frequent meanders of various scales and finally leaves Japan at central Honshu, and then running eastward to the Hawaiian Islands as the Kuroshio Extension (Gallagher et al. 2015; Qiu 2019).The Tsushima Current is separated from the Kuroshio Current in the East China Sea and flows along the western coast of Kyushu, continuing northward along the coasts of Honshu and Hokkaido in the Sea of Japan, and reaching the Sea of Okhotsk through the Soya Strait before re-entering the Pacific Ocean through the Tsugaru Strait (Gallagher et al. 2015; Qiu 2019).

With respect to the diversity of marine shore fishes, Carpenter and Springer (2005) estimated that the area of the Philippine Islands shows the highest species richness in the Indo-Malay-Philippines Archipelago (IMPA), which has been known as the area of highest marine biodiversity (e.g., Briggs and Bowen 2013; Gaither and Rocha 2013). In addition, the Coral Triangle (an area extending from the Philippines to the Solomon Islands), overlapping the IMPA, indicates the highest species richness for hermatypic (zooxanthellate, reef-building) corals, reaching more than 500 species (Venon et al. 2009). Because the upstream location of the Kuroshio Current is adjacent to this biodiversity hotspot, its warm water mass has been supplying eggs and larvae of tropical shore fishes and invertebrates, including hermatypic corals, to the coasts of Japan. The distribution of major coral reefs in Japanese waters is restricted to the Ryukyu Islands and Ogasawara Islands, ranging from 24° N to 30° N (lowest sea surface temperature is 18 °C in winter) (Gallagher et al. 2015). Although the previous southern limit of coral reefs along the Kuroshio Current is known at the northeast of Tanegashima Island (31° N), isolated coral reefs were found in inner bays of Iki Island (33°48′N), Nagasaki Prefecture, south of Tsushima Island (Yamano et al. 2012).

In the Pliocene and middle Pleistocene, the Kuroshio Current is estimated to have flowed along the Ryukyu Islands fluctuating north to south, on the basis of various paleoceanographic proxies collected in the area (e.g., microfossils and geochemical data) (Gallagher et al. 2015; Ujiié et al. 2016). During the lowest sea level of the Last Glacial Maximum, the Kuroshio Current did not flow in the East China Sea because of the East Taiwan Channel restriction (Gallagher et al. 2015). Until 3 Ma, the Kuroshio Current reached its present latitude (35° N), and a weak Tsushima Current started flowing into the Sea of Japan when the southern Tsushima channel narrowly opened by transgression (the sea level was estimated 40 m higher than the present) in interglacial periods (Gallagher et al. 2015). After 2 Ma, crustal expansion in the northern Okinawa Trough deepened the Tsushima Strait, which enabled continuous inflowing of the Tsushima Current to the Sea of Japan. This expansion of the Okinawa Trough was caused by that change in the Philippine Sea Plate subduction (Gallagher et al. 2015). Until 1 Ma, the intensity and flow path of the Kuroshio Current became the same as the present by increased glacial and interglacial periods, and the coral reef front along the Ryukyu Arc advanced to 31° N; subsequently, the coral reef front of the islands fluctuated from 24 to 31° N (Gallagher et al. 2015).

According to Venon (1992), 400 hermatypic coral species were recorded from the Ryukyu Islands and the Pacific coasts of southern Japan from Tanegashima Island, Kagoshima to Tateyama (southernmost part of Boso Peninsula, Chiba Prefecture, Honshu). The distributional limits of hermatypic corals on rocky reefs in Japan were found in Sado Island, Niigata (Sea of Japan), and Katsuura located on the east coast of Boso Peninsula, Honshu (Pacific side) (e.g., Sugihara et al. 2009; Zayasu et al. 2017). On the other hand, occurrences of tropical and subtropical fishes in temperate rocky reefs of the Pacific coasts of southern Japan have been recently increasing (e.g., Hirata et al. 2011; Nakamura et al. 2013; Tose et al. 2017). These facts strongly indicate that global warming has been affecting marine organisms in the sea around Japan.

The Japanese name "Oyashio" means "child-raising parent" and refers to the high biological productivity of the oxygen- and nutrient-rich water in the current. In the northern North Pacific Ocean, the cold-water mass of the Oyashio Current originates from a subarctic westward flow of the Alaskan Stream, including rejoined waters from the Bering Sea and the Sea of Okhotsk, and the Alaska Gyre and Western Subarctic Gyre (Qiu 2019). The Alaskan Stream is located north of, and connects, the two gyres, flowing along the southern side of the Aleutian Islands, reaching the eastern side of the Kamchatka Peninsula (Qiu 2019). Also, this stream partly flows into the western Bering Sea, forming the Bering Sea Gyre, and turns southwestward as the East Kamchatka Current, passing along the eastern coast of the Kamchatka Peninsula to the southern side of the Kuril Islands. Water from this current partly intrudes the northern Sea of Okhotsk, circulates in a counterclockwise gyre inside the Kuril Basin, outflows through the Bussol Strait (46.5° N, 151.5° E), and rejoins the East Kamchatka Current (Qiu 2019). The downstream East Kamchatka Current south of the Bussol Strait is renamed as the Oyashio Current because of the different water properties compared with those upstream (Qiu 2019). Recent observations of the water in the southern part of the Oyashio Current off Hokkaido revealed a well-defined annual cycle: increase in winter and spring [20–30 Sverdrup (Sv), surface to bottom] and decrease in summer and fall (3–4 Sv, restricted upper of 2000 m depth) (Qiu 2019). Further, the Oyashio Current is divided into two paths off Hokkaido: the first turns off-shoreward and joins the east-northeastward flowing Subarctic Current; the second path flows along with Tohoku District, its front showing fluctuation from 38.5 to 41.5° N (Qiu 2019; Fig. 2.2).

The area off the Pacific coast of Tohoku District is known as the world's most significant fishing grounds with high biological productivity, where the Oyashio and Kuroshio currents supply nutrient-rich and warm waters, respectively. In addition, the Tsugaru Warm Current, an offshoot of the Tsushima Current outflowing through the Tsugaru Strait, intrudes southward along the coast of Tohoku. As a result, this food-rich area has various habitats for marine fishes from coasts to deep bottoms, down to the Japan Trench. Although the diversity of marine fishes in the area has been investigated mainly by bottom trawls, new species and additional records of deep-sea or deep demersal fishes were often reported (e.g., Shinohara et al. 2009; Misawa et al. 2020; Kai et al. 2021).

2.4 Species Diversity of Fishes of Japan

As stated above, the Japanese Archipelago is located on the western side of the Pacific Ocean and extends for 3000 km from the northern tip of the Soya Peninsula (45°31′N) in Hokkaido Island to Hateruma-jima Island (24°03′N) in the Ryukyu Islands. Although the terrestrial realm of Japan is included in the temperate zone, the marine environments are more diverse. The northeastern coast of Hokkaido Island, facing the Okhotsk Sea, is covered by ice in winter. However, in the Ryukyu Islands, there are well-developed coral reefs similar to the coral reefs in the tropical western Pacific (Allen and Erdmann 2012). Between these two extremes, there exists a wide variety of marine habitats such as sandy beaches, mud flats, mangroves, estuaries, rocky shores, kelp beds, and very deep trenches exceeding 8000 m in depth (e.g., Japan Trench on the Pacific side of Honshu Island). Contrary to the marine environments, the freshwater habitats in Japan are less diverse, being composed of short rivers and small- to medium-sized lakes (except for Lake Biwa). These aquatic environments have resulted in a great diversity of fishes. According to Motomura (2021), the number of valid fish species in Japan has reached 4476 representing 12.5% of the 35,898 valid species worldwide (Fricke et al. 2021). Motomura (2021) also included 141 species that are considered distinct by Japanese ichthyologists and have been given Japanese names, but are undescribed scientifically. This makes the total number of fish species in Japan 4617.

We examined the number of species in all families found in Japan to produce a list of the top 35 most speciose families in Japan (Table 2.1). This list shows that the members of 35 families represent 57.4% of the total valid species reported from Japan. Within the top 35 families (Table 2.1), many are represented by species occurring in shallow water (here defined as depths shallower than 200 m). In addition, most of the shallow water fishes live in warm waters, although some of them (e.g., Stichaeidae, Sebastidae and Pleuronectidae) also include species living in cold waters. The typical shallow water fishes found in warm waters are as follows: Gobiidae, Serranidae, Labridae, Pomacentridae, Apogonidae, Blenniidae, Scorpaenidae, Muraenidae, Syngnathidae, Carangidae, Lutjanidae, Tetraodontidae, Chaetodontidae,

Table 2.1 A list of top 35 most speciose families in Japan

Family	No. of species	% of total valid species in Japan	Habitat
Gobiidae	469	10.5	Shallow water
Serranidae	156	3.5	Shallow water
Labridae	153	3.4	Shallow water
Pomacentridae	111	2.5	Shallow water
Apogonidae	102	2.3	Shallow water
Cottidae	88	2.0	Shallow water/deep sea
Myctophidae	88	2.0	Deep sea
Blenniidae	81	1.8	Shallow water
Cyprinidae	78	1.7	Freshwater
Macrouridae	70	1.6	Deep sea
Liparidae	68	1.5	Deep sea/shallow water
Scorpaenidae	68	1.5	Shallow water
Muraenidae	64	1.4	Shallow water
Ophichthidae	64	1.4	Shallow water/deep sea
Syngnathidae	64	1.4	Shallow water
Carangidae	62	1.4	Shallow water
Zoarcidae	62	1.4	Deep sea
Lutjanidae	54	1.2	Shallow water
Tetraodontidae	54	1.2	Shallow water
Chaetodontidae	52	1.2	Shallow water
Ophidiidae	49	1.1	Shallow water
Stichaeidae	48	1.1	Shallow water
Acanthuridae	45	1.0	Shallow water
Bothidae	42	0.9	Shallow water
Holocentridae	41	0.9	Shallow water
Sebastidae	40	0.9	Shallow water/deep sea
Callionymidae	36	0.8	Shallow water
Melanostomiidae	36	0.8	Deep sea
Scaridae	36	0.8	Shallow water
Monacanthidae	33	0.7	Shallow water
Pleuronectidae	33	0.7	Shallow water
Pomacanthidae	32	0.7	Shallow water
Tripterygiidae	32	0.7	Shallow water
Lethrinidae	30	0.7	Shallow water
Pinguipedidae	30	0.7	Shallow water
Total	2571	57.4	

"Shallow water/deep sea" indicates that the family includes many shallow water species and a small number of deep-sea species. "Deep sea/shallow water" indicates that the family includes many deep-sea species and a small number of shallow water species

Acanthuridae, Bothidae, Holocentridae, Callionymidae, Scaridae, Monacanthidae, Pomacanthidae, Tripterygiidae, Lethrinidae, and Pinguipedidae. These 23 families are composed of 1847 species representing 72% of the total number of species in the top 35 most speciose families. This figure suggests that the shallow water fishes living in warm waters are the main components of Japan's fish diversity.

On the other hand, Table 2.1 clearly shows that among the top 35 most speciose families in Japan, primary freshwater fishes are represented only by Cyprinidae. In addition to Cyprinidae, there are 24 families that include primary freshwater fish species, although nine families are represented

Table 2.2 The number of primary freshwater fish species in 24 families in Japan

Family	Number of species	Remarks
Cyprinidae	68	
Cobitidae	19	
Poeciliidae	7	All species invasive
Nemacheilidae	6	
Salmonidae	6	Including only landlocked forms
Bagridae	5	
Cichlidae	4	All species invasive
Gasterosteidae	4	
Odontobutidae	4	
Siluridae	4	
Centrarchidae	3	All species invasive
Channidae	3	All species invasive
Gobiidae	3	
Lepisosteidae	3	All species invasive
Adrianichthyidae	2	
Osphronemidae	2	All species invasive
Sinipercidae	2	
Amblycipitidae	1	
Atherinidae	1	Invasive
Botiidae	1	
Clariidae	1	
Ictaluridae	1	Invasive
Loricariidae	1	Invasive
Synbranchidae	1	
Total	152	

only by invasive species. The total number of the primary freshwater fish species (here defined as fishes strictly confined to freshwater) is 152 (Table 2.2), occupying only 3.4% of the total valid species in Japan. If only the native primary freshwater fishes are counted, the total number of species decreases to 125. However, Hosoya (2015) showed that there are 498 species (including the species given only Japanese names without scientific names) of freshwater fishes in Japan, including not only the primary freshwater fishes but also diadromous fishes, brackish-water fishes, and those occasionally entering freshwater. When we follow Hosoya's (2015) definition of freshwater fishes, the percentage of freshwater fish species in the total number of Japanese fish species is 10.8%, significantly higher than the figure of 3.4% based on the primary freshwater fishes. These figures are low when compared to the number of freshwater fish species in the world, which is 18,132 and is half the total number of fish species (Fricke et al. 2021).

We examined the number of deep-sea fishes in Japan to recognize 1005 species belonging to 155 families; deep-sea fishes are defined here as those usually occurring in depths exceeding 200 m, and depth records are taken from the literature (Carpenter and Niem 1998–2001; Mundy 2005; Nakabo 2013). These species represent about 22.5% of the total valid species of Japan, clearly showing that deep-sea fishes have diversified broadly in Japan. This is not surprising due to the many deepwater habitats in seas around Japan (e.g., the Japan Trench off the Pacific coast of Honshu Island exceeding 8000 m, and the Sea of Japan at 3700 m). Our examination of Japanese fishes also listed the 26 most speciose families of deep-sea fishes (Table 2.3). The total number of deep-sea species in 26 families is 607, about one-third of the total number of shallow water

Table 2.3 A list of 26 most speciose deep-sea families among 155 deep-sea families found in Japan

Family	Number of deep-sea species found in Japan	Number of total species of family found in Japan	% of deep-sea species in total species of family found in Japan
Myctophidae	88	88	100
Macrouridae	70	70	100
Ophidiidae	48	49	98.0
Liparidae	36	68	52.9
Melanostomiidae	36	36	100
Zoarcidae	33	62	53.2
Alepocephalidae	26	26	100
Ogcocephalidae	21	21	100
Arhynchobatidae	19	19	100
Paralepididae	19	19	100
Astronesthidae	17	17	100
Sternoptychidae	17	17	100
Oneirodidae	15	15	100
Acropomatidae	14	17	82.4
Melamphaidae	14	14	100
Moridae	14	16	87.5
Peristediidae	14	20	70.0
Chiasmodontidae	13	13	100
Etmopteridae	13	13	100
Gempylidae	12	13	92.3
Gonostomatidae	12	12	100
Sebastidae	12	40	30.0
Bothidae	11	42	26.2
Psychrolutidae	11	11	100
Scopelarchidae	11	11	100
Synaphobranchidae	11	11	100
Total	607	740	82.0

species in the top 35 most speciose families as shown above.

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3

Origins and Present Distribution of Fishes in Japan

Yoshiaki Kai and Hiroyuki Motomura

Abstract

Studies of fishes distributed in the Japanese Archipelago and their evolution from biogeographic and phylogeographic perspectives are reviewed. The rich marine species diversity around Japan can be attributed to a combination of various historical and environmental factors. The Ryukyu Islands, located in the northern peripheral region of the Indo--Australian Archipelago hotspot, possess the most diversified fish fauna in Japan, with the Kuroshio Current playing an important role in the transportation of coral reef fishes from the Ryukyu Islands to the Japanese mainland, as well as forming a barrier to the southward migration of temperate species. In addition, recent molecular phylogenetic studies have suggested that the Kuroshio Current, in acting as a barrier to the latter, has contributed to the speciation or diversification of marine fishes. The marginal seas around Japan, such as the Seas of Japan and Okhotsk, reinforced the isolation of populations during the last glacial period, thereby driving the diversification of fishes distributed in the western North Pacific. Disjunct distributions of taxa across the tropics or between the western and eastern Pacific have also shaped the fish fauna of Japan. The distributions of genetic divergence suggest that movements across the northern and southern or western and eastern Pacific have occurred with past climatic changes.

Keywords

Japanese Archipelago · Biogeography · Phylogeography · Pacific Ocean · Sea of Japan · Disjunct distribution

3.1 Overview of the Fish Fauna of Japan

A total of 4617 fish species have been reported from Japanese waters (Motomura 2021), their distributional patterns along the Japanese Archipelago having long been of interest from the viewpoints of biogeography and biodiversity (Tanaka 1931; Aoyagi 1957). Such rich marine species diversity can be attributed to a combination of various historical and environmental factors (Fujikura et al. 2010). The Japanese Archipelago encompasses six climatic regimes from north to south (the subboreal, cool temperate, middle temperate, warm temperate, subtropical, and tropical zones), as well as four tectonic plates (the Eurasian, North American, Pacific, and

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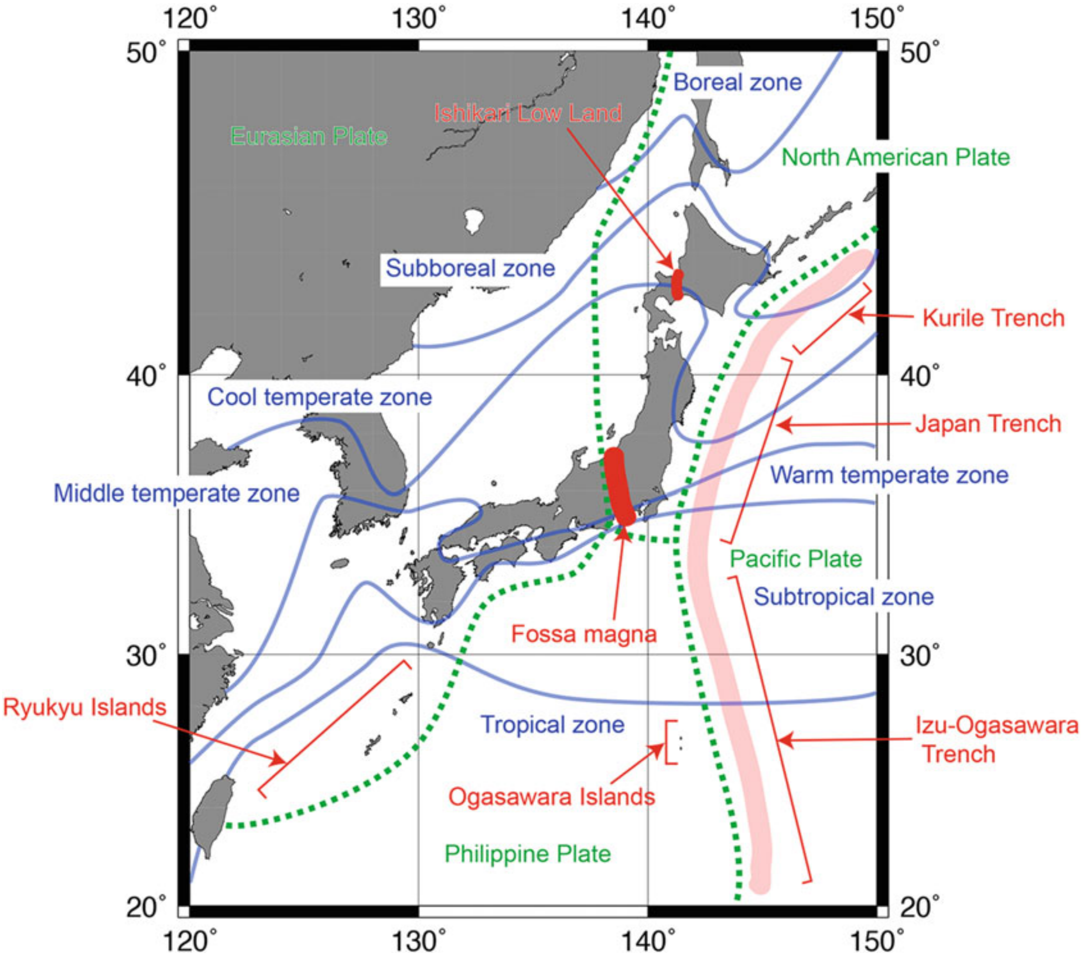

Fig. 3.1 Schematic diagram of marine climatic regimes (after Nishimura 1992: fig. 2) and bottom topology around Japan. *Blue* and *Green lines* indicate boundaries of climatic regimes and plates, respectively

Philippine plates) (Nishimura 1992; Fujikura et al. 2010) (Fig. 3.1). Both the climatic regimes and tectonic plates may impact on fish distributions (Springer 1982; Nishimura 1992). In addition, three major currents flowing along the Japanese Archipelago, the Kuroshio Current northward along the Pacific coast of southern Japan, Tsushima Current northward along the Sea of Japan coast, and Oyashio Current southward along southern Hokkaido and the Pacific coast of northern Honshu Is., have also strongly influenced fish faunal composition and distribution (Tanaka 1931; Nakabo 2002, 2013; Senou et al. 2006) (Fig. 3.2).

Marine biogeographical provinces along the Japanese Archipelago have been subject to frequent studies, being variously defined on the basis of breaks in species diversity gradients, surface temperature, routes of ocean currents, and endemism of local species (e.g., Kafanov et al. 2000; Parenti and Ebach 2009; Briggs and Bowen 2012). Nakabo (2002) defined the biogeographic areas of Japan and adjacent waters on the basis of the distributional patterns of fishes, viz. northern Japan, southern Japan, the boundary zone between northern and southern Japan, Pacific coast of southern Japan, and Ryukyu Islands, and suggested that the distributions of

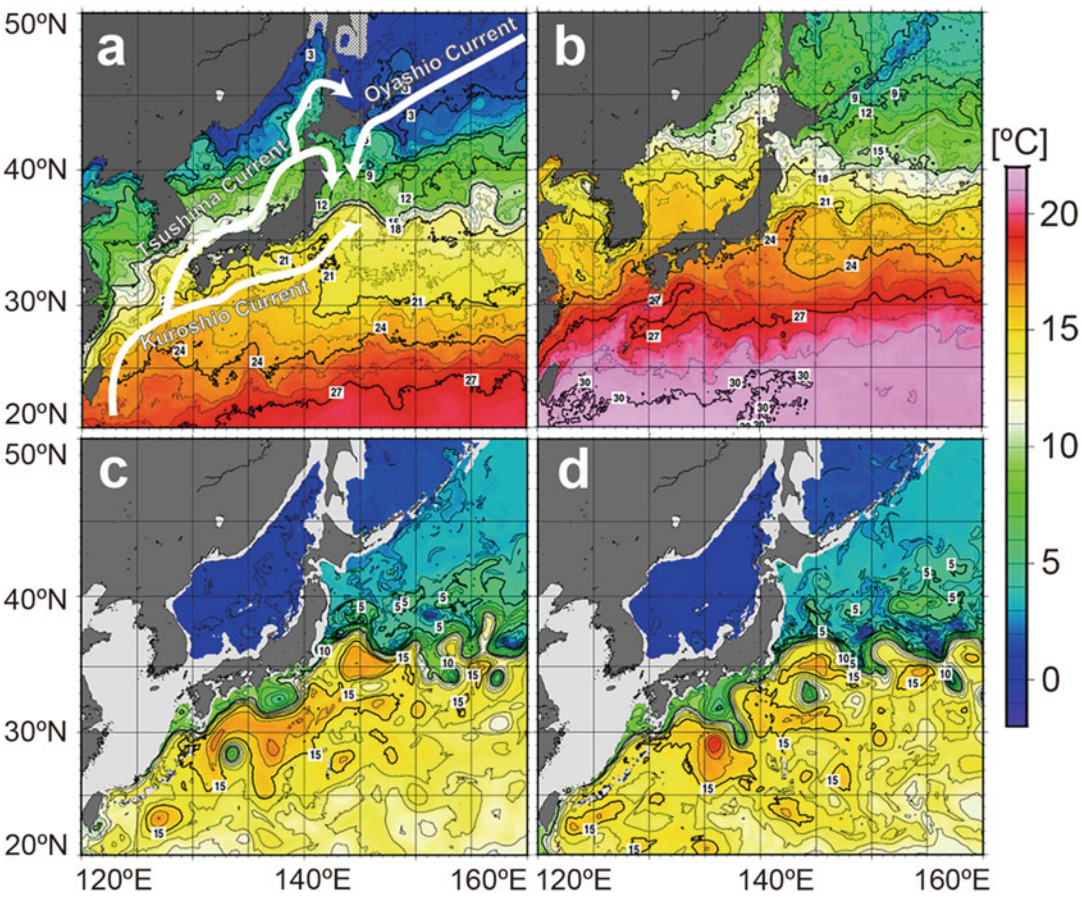

Fig. 3.2 Horizontal distribution of ocean temperatures. Data from Japan Meteorological Agency. (**a**) Surface temperatures in winter (30 Dec. 2020), (**b**) surface temperatures in summer (30 Jun. 2020), (**c**) temperatures at 400 m depth in winter (30 Dec. 2020), (**d**) temperatures at 400 m depth in summer (30 Jun. 2020). *White arrows* indicate major currents around Japan

fishes differed from each other according to habitat requirements and sea water temperatures, as well as current patterns. Senou et al. (2006) compared fish faunas of southern Japan influenced by the Kuroshio Current and showed that the latter played an important role in transporting coral reef fishes from south to north, as well as forming a barrier to temperate fishes migrating south toward the Ryukyu Islands. Nakabo (2013) also discussed in detail the distributional patterns of fishes in East Asia, including Japanese species, taking into account habitat preferences and depth segregation, as well as "biogeographic elements," and recognized ~90 patterns for marine and freshwater fishes.

More than 300 species are known from freshwater habitats in Japan (Watanabe et al. 2017), the origins, and present distribution of Japanese freshwater fishes having been reviewed by Watanabe (2012) and Watanabe et al. (2017) (see also Chap. 12). These studies demonstrated that the Japanese freshwater fish fauna comprised two groups, divided by the Ishikari Low Land area in Hokkaido: one in northeastern Hokkaido and the other in the remaining southwestern areas (Fig. 3.1). The latter was further divided into two subgroups by the Fossa Magna area, a great rift lowland traversing Honshu from the Sea of Japan to the Pacific, and partially occupied by mountains (Fig. 3.1). On the other hand, Itsukushima (2019) classified the freshwater fish fauna into 15 groups, suggesting associations of the latter with watershed characteristics, such as floodplain scale, river conflicts, or river formation processes. Traditional beliefs support the Japanese freshwater fish fauna having formed as a result of repeated connections and separations between continental and Japanese freshwater systems, caused by tectonic movements and repeated sea level regressions during the Plio-Pleistocene era (Lindberg 1972; Nishimura 1974). However, recent phylogenetic and phylogeographic analyses have estimated that divergence between continental and Japanese lineages occurred much earlier, in the Early Pliocene or Late Miocene (e.g., Tominaga et al. 2016; Watanabe et al. 2018).

Recent phylogeographic studies, based on molecular phylogeny and population genetics, have provided new insights into the historical processes shaping the distribution of fishes along a time scale, with the assumptions of time scales given in most earlier hypotheses having been revised. In this chapter, faunal studies and recent advances in phylogeographic studies of Japanese marine fishes are reviewed in order to outline the processes that shaped their distributional patterns.

3.2 Distributional Pattern in the Pacific Ocean

The faunal structure of the Pacific coast along the Japanese Archipelago is strikingly different between the Japanese mainland and the Ryukyu Islands, as indicated by many authors (e.g., Senou et al. 2006; Nakabo 2013). The Ryukyu Islands are biogeographically defined as the islands of Amami-oshima and southward, being included in the tropical zone vide Nishimura (1992) (Fig. 3.1). The Ryukyu Islands are located in the northern peripheral region of the Indo-Australian Archipelago (IAA) hotspot (Cowman et al. 2017), the fish fauna of the Ryukyu Islands being more diversified than that of the main islands of Japan (Nakae et al. 2018). Species richness of reef associated fishes forms an enigmatic “bullseye” pattern centered on IAA, known as the largest marine biodiversity hotspot, covering two-thirds of the global equatorial tropics (Cowman 2014; Cowman et al. 2017; Carpenter and Springer 2005). The marine biodiversity hotspots have moved from the West Tethyan region via the Arabian region to IAA with major tectonic events during the past 50 million years (Renema et al. 2008). Recent molecular phylogeographic studies have provided some insights into the nature and timing of IAA origins, most lineages of coral reef fishes in the IAA arising in the Late Miocene to Pliocene (Barber and Bellwood 2005; Read et al. 2006; Santaquiteria et al. 2021).

The fish fauna of the Ryukyu Islands has been variously investigated (Jordan and Starks 1907; Schmidt 1930; Yoshino et al. 1975), with characteristics found attributable to the route of the Kuroshio Current (Senou et al. 2006; Chap. 5) (Fig. 3.2). This current flows from east of the Philippines to the Pacific coast of southern Japan, via Taiwan and west of the Ryukyu Islands, then turning to the east and passing through the Tokara Islands, before finally turning northward toward the Pacific coasts of the islands of Kyushu, Shikoku, and Honshu (main islands of Japan). The Kuroshio Current is a major world current, transporting northward the larvae and juveniles of many tropical fishes. While most of the latter never become established in the areas to which they have been transported, such as off Honshu Island (Senou et al. 2006), those species having a wide distributional area in southern Japan may have been dispersed by the Kuroshio Current during larval stages. For example, Watanabe et al.’s (2006) examination of genetic diversity in the amphidromous goby *Sicyopterus japonicus*, based on specimens collected from the Ryukyus and the Pacific coast of the Japanese mainland, found no evidence of genetic subdivision within the species. Elsewhere, He et al.’s (2015) study of the genetic population structure of the amphibious mudskipper *Periophthalmus modestus*, based on sequence variations of mitochondrial DNA, indicated that the high level of genetic homogeneity could be partly attributed to contemporary larval transportation by the Kuroshio Current.

In contrast, the Ryukyu Islands, being the northern peripheral region of IAA, can be prone to edge effects that significantly alter the genetic characteristics relative to central counterparts of a species, known as the central-peripheral population model (CPPM; Mayr 1963). For example, Ackiss et al. (2018) investigated the genetic patterns of populations of *Caesio cuning*, known widely from the Indo-Pacific region, and found the Ryukyu Islands population had clearly diverged from other southerly populations along the Kuroshio Current. They considered the impacts of genetic drift and natural selection in increasing smaller peripheral populations appear to be probable influences on the lineage divergence found in the Ryukyu Islands.

The Kuroshio Current is also known to be a barrier to the dispersal of marine fishes (see Chap. 5). In fact, Senou et al. (2006) noted two sister species (e.g., *Acanthopagrus schlegelii* and *Acanthopagrus sivicolus*) that were distributed allopatrically in the Japanese mainland and the Ryukyu Islands. Intraspecific genetic divergence between populations off the Japanese mainland and the Ryukyu Islands is known in Grass Puffer *Takifugu alboplumbeus* (see Takagi et al. 2019). Such distributional patterns and population structures suggest that the Kuroshio Current plays an important role in the speciation or diversification of marine fishes.

Although Nishimura (1992) placed both the Ryukyu Islands and the Ogasawara Islands in the tropical zone (Fig. 3.1), the biogeographic study of Senou et al. (2006) showed that the fish fauna of the Ogasawara Islands was more similar to that of the Japanese mainland, rather than the Ryukyu Islands. Because the Ogasawara and Ryukyu islands are separated by wide and deep sea, Senou et al. (2006) considered that movement of coral reef fishes between the two regions was difficult. A population genetics study of the grouper *Epinephelus fasciatus* supported Senou et al. (2006), demonstrating clear genetic differentiation between the Ryukyu and Ogasawara Islands populations (Kuriiwa et al. 2014). Although the Ogasawara Islands are oceanic and not influenced strongly by the Kuroshio Current, the latter fluctuates greatly north and south between the Ogasawara Islands and the Honshu coast, sometimes transporting a number of species endemic to the Ogasawara Islands, such as *Chaetodon daedalma* and *Scarus obishime,* to the southern Izu Islands (Senou et al. 2006). The population genetic analysis of Kuriiwa et al. (2014) also suggested northward dispersal of *E. fasciatus* from the Ogasawara Islands, small volcanic islands between the latter and the Japanese mainland possibly acting as "stepping stones," thereby aiding in the dispersal of the species.

Along the Pacific coast of Honshu Island (Tohoku District), the cold southward directed Oyashio Current and north directed Kuroshio Current result in highly productive water masses (Kuroda et al. 2017) (Fig. 3.2). The confluence of the two currents has been called the Kuroshio–Oyashio transition region and is known to be the spawning and nursery grounds of many commercially important fishes, such as *Sardinops melanostictus*, *Engraulis japonicus*, *Cololabis sairai*, and *Scomber japonicus*. Because of these rich fishery resources, considerable research efforts (e.g., Shinohara et al. 2009; Misawa et al. 2020) have investigated the faunal structure of the region since Mead and Taylor (1953). According to Yabe (2018), 578 fish species in 165 families are known from the area, characterized particularly by high species diversity of Myctophidae, Cottidae, Gobiidae, and Sebastidae. Due to the deep Japan Trench off the Tohoku District, species of Stomiiformes, Aulopiformes, and Argentiniformes are also abundant (Yabe 2018) (Fig. 3.1).

Along the northern Japanese Archipelago, part of the Pacific Plate, moving from the eastern Pacific, subducts beneath the North American Plate, forming the Japan and Kurile trenches (Fig. 3.1). The Pacific Plate also subducts beneath the Philippine Plate to the south of the Japan Trench, forming the Izu-Ogasawara Trench, in which occurs the maximum depth within Japanese waters (9780 m). Although many fishes inhabiting the bathyal, abyssal, and hadal zones are still to be described (e.g., Kai et al. 2021), hadal snailfishes, *Pseudoliparis amblystomopsis* (6156–7579 m depth) and *Pseudoliparis belyaevi*

(7000–7579 m depth), and the abyssal macrourid *Coryphaenoides yaquinae* (6945 m depth) have been recorded from these trenches (Jamieson et al. 2009; Gerringer 2019).

Deep-sea fishes of Japan have been well studied in Suruga Bay, located in the central part of the Japanese Archipelago, and Tosa Bay, located off Shikoku Island (Shinohara and Matsuura 1997; Shinohara et al. 2001). Suruga Bay is unique in having steep slopes to a depth of 2500 m and several endemic species, including the snailfishes *Careproctus surugaensis*, *Paraliparis dipterus*, *Paraliparis hokuto*, *Paraliparis ruficometes*, and *Paraliparis variabilidens*. The high degree of endemism of deep water snailfishes in Suruga Bay may be attributable to their large hatching size, direct development, and putative limited dispersal ability (Stein and Mundy 2021). Recently, Yokozuna Slickhead, *Narcetes shonanmaruae*, reaching ~140 cm in total length and 25 kg in body weight, was newly described (Fujiwara et al. 2021), the specimens having been collected during bottom longline surveys, undertaken to reveal the diversity of deep-sea fast-swimming predators. Tosa Bay, an open-type bay with semicircular shelf-slope topography, has been one of the most studied bays in Japanese ichthyology since Kamohara (1958). Although separated from Suruga Bay by only ~500 km, the fish fauna of the former differs from the latter, comprising a greater number of gadiform species and fewer myctophiforms (Shinohara et al. 2001). The rich species diversity of Gadiformes in Japanese waters has been comprehensively reviewed in Nakayama (2020).

3.3 Distributional Patterns in the Seas of Japan and Okhotsk

The Japanese Archipelago separates the Sea of Japan from the western North Pacific Ocean. The Sea of Japan is a semi-enclosed marginal sea with an area of ~1,000,000 km^2 and an average depth of 1350 m (Kitamura et al. 2001). All straits connecting the Sea of Japan and neighboring waters are narrower than 160 km and shallower than 130 m. Paleomagnetic evidence indicates that the Sea of Japan was formed about 15 million years ago (MYA) by the separation of the ancient Japanese Islands from the eastern periphery of the Eurasian Continent into northeast and southwest arcs (Otofuji et al. 1991, 1994). The Tsushima Warm Current, a branch of the Kuroshio Current, enters the Sea of Japan through the Tsushima Strait, flowing near the surface northward to Tsugaru Strait, thereby supplying a large quantity of heat, as well as transporting marine organisms (Kitamura et al. 2001) (Fig. 3.2). In contrast, the deep region of the Sea of Japan is characterized by cold, high dissolved oxygen water, called “Japan Sea Proper Water” (Gamo and Horibe 1983) (Fig. 3.2), resulting in very different fish faunas characterizing the shallow and deep regions. Origins of the marine fauna in the Sea of Japan were discussed in a series of papers published in the 1960s (Nishimura 1965a, b, 1966, 1967, 1969), mainly on the bases of paleoclimates and distributional patterns of marine organisms. However, recent molecular phylogenetic studies with updated paleogeographic evidence have provided new insights for the origins of the marine fauna of the Sea of Japan (e.g., Akihito et al. 2008; Kai et al. 2011; Kokita and Nohara 2011; Hirase et al. 2012; Sakuma et al. 2014, 2015, 2020; Hirase 2021).

The shallow area of the Sea of Japan coast of Japan is dominated by the Tsushima Current, flowing from south to north, with warm water inhabitants being dominant in the area (Nakabo 2013; see Chap. 6). Nishimura (1969) implied that cold water inhabitants were dominant in the northern half of the Sea of Japan and in deep water, both characterized by low temperatures, whereas warm water inhabitants occurred in shallower water influenced by the Tsushima Current (Nishimura 1969). In addition, the Sea of Japan coasts of Russia and Korea are dominated by the Liman Current, a cold water current from the north. Accordingly, the fish faunas of western and eastern Sea of Japan regions are strikingly different, faunal breaks existing approximately at Akita Prefecture, northern Honshu Island and Pohang, South Korea (Kafanov et al. 2000). On the other hand, Briggs and Bowen (2012) suggested that a Sea of Japan faunal break existed off Hamada, Shimane Prefecture. Historically, several views on biogeographic breaks in the Sea of Japan have been advanced, inconsistencies in the breaks being attributable to the large overlap between warm and cold-water provinces (Nishimura 1965a). In fact, recent molecular phylogeographic studies have suggested various patterns of genetic breaks in the Sea of Japan (Han et al. 2018; Takada et al. 2018; see also Chap. 10).

The Sea of Japan has a unique deep-sea fauna, characterized by both low species diversity and relatively few endemic species (Okiyama 2004; Shinohara et al. 2014), due to that water body being the newest marginal sea around Japan and characterized as having undergone drastic environmental changes during the last 85,000 years (Oba et al. 1991). The deep-sea fish fauna of the Sea of Japan is characterized by species of Cottidae, Liparidae, and Zoarcidae, a faunistic character similar to that of the Sea of Okhotsk and the Bering Sea, rather than that off the Pacific coast of Japan (Nishimura 1967; Briggs and Bowen 2012; Watling et al. 2013). In addition, the representative families of the deep-sea Pacific Ocean, such as Stomiidae, Myctophidae, and Macrouridae, are almost completely absent from the Sea of Japan (Nishimura 1967; Shinohara et al. 2014). Due to the lack of deep-water connections to neighboring water bodies, the density stratification in the water column which developed in the Sea of Japan during the last glacial period with regression of the sea level, resulted in fatally anoxic sea-bottom conditions over a large area (Itaki et al. 2004). Furthermore, some deep-sea species in the Sea of Japan may have experienced a rapid increase in population size after the last glacial period, as demonstrated by Shirai et al. (2006), Sakuma et al. (2014), and Kai et al. (2014). In the post-glacial period, the circulation pattern has been invigorated by surface production of dense cold water resulting from winter surface cooling, which ventilated deeper waters and allowed their reinvasion. The low species diversity may reflect the short period of time for colonization (Nishimura 1967; Tyler 2002). Okiyama (1985) also considered that the colder water temperature in the Sea of Japan has lowered the survival rate of larvae transported from the southern neighboring seas.

Nishimura (1967) noted examples of closely related species that were distributed, respectively, in the Seas of Japan and Okhotsk, such as *Peteroschmidtia toyamensis* (Sea of Japan) and *Petroschmidtia albonotata* (Sea of Okhotsk), and considered that the deep-sea fishes in the Sea of Japan had originated from the Sea of Okhotsk. Recent molecular genetic studies have revealed cryptic speciation in deep-sea fishes between the Sea of Japan and neighboring seas, such as the *Careproctus rastrinus* species complex and *Bothrocara hollandi*, as a result of the isolation of the Sea of Japan during the last glacial period (Kodama et al. 2008; Kai et al. 2011). Such isolation of marginal seas during the last glacial period played an important role in faunal diversification in the western North Pacific (Liu et al. 2007; Briggs and Bowen 2012; see also Chap. 10).

A major part of the Sea of Okhotsk lies in the boreal zone of Nishimura (1992), the Sea of Okhotsk coast of Hokkaido being known as the southern limit of drifting sea-ice in winter. The fish fauna of the Sea of Okhotsk is characterized by cold-water inhabitants, including species of Zoarcidae, Liparidae, and Cottidae (Yabe 2018). However, the Soya Current, a branch of the Tsushima Current, enters through the Soya (La Perouse) Strait, warming the surface layers of the southern Sea of Okhotsk to 15–20 °C (Shuntov et al. 2019) (Fig. 3.2), and warm-water inhabitants are often recorded from the region (see Chap. 7). Because of the Kurile Trench, running along the Pacific side of the Kuril Islands, and separating the Sea of Okhotsk and Pacific Ocean, deep-water species (e.g., Myctophiformes, Stomiiformes, Ceratioidei) are also abundant (Yabe 2018).

3.4 Origins from Disjunct Distributions

A major part of the Japanese Archipelago is in the temperate zone, including cool temperate, middle temperate, and warm temperate zones vide

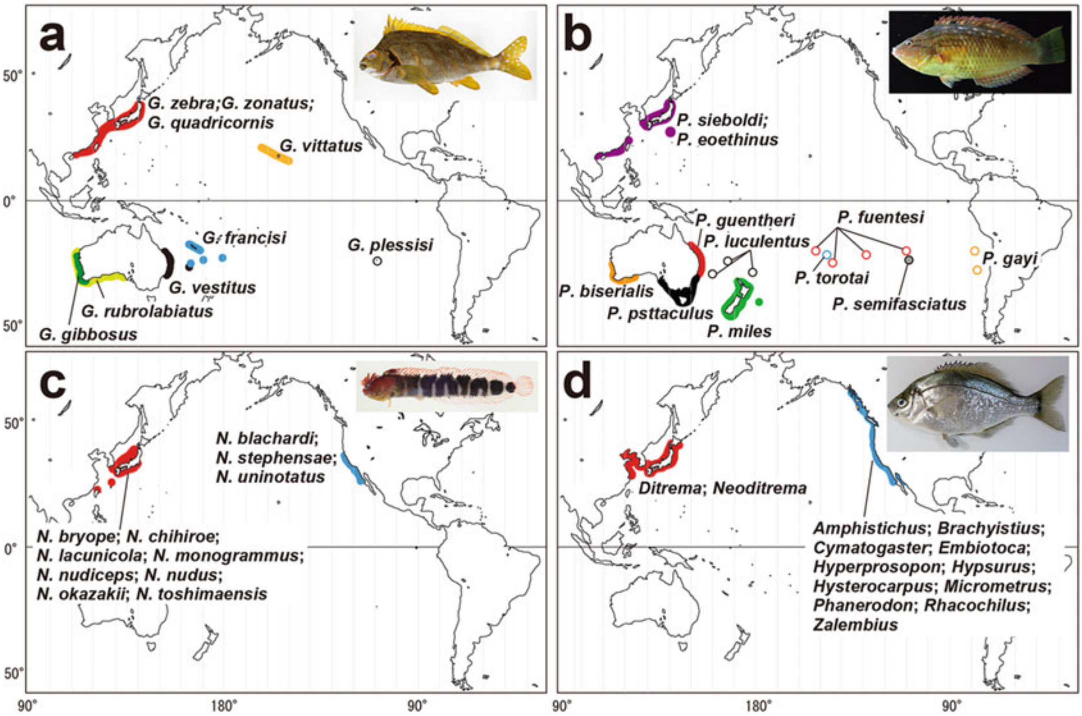

Fig. 3.3 Antiequatorial (**a**, **b**) and trans-Pacific (**c**, **d**) distributions of temperate species. (**a**) Species of *Goniistius*. (Modified from Burridge 2002). (**b**) Species of *Pseudolabrus*. (Modified from Mabuchi et al. 2004). (**c**) Species of *Neoclinus*. (Modified from Hongjamrassilp et al. 2020). (**d**) Genera of Embiotocidae

Nishimura (1992) (Fig. 3.1). Several species inhabiting temperate regions exhibit disjunct distributions, including Japan and other temperate areas, thereby presenting interesting biogeographic phenomena. Disjunct distributions of taxa across the tropics have been observed for a variety of organisms, such distributions being most commonly known as antitropical or antiequatorial (Fig. 3.3). Antitropical distribution refers to taxa that occur both north and south of the tropics, but not within tropical latitudes. Antiequatorial distribution has been further proposed for taxa that occur within tropical latitudes (south of the Tropic of Cancer or north of the Tropic of Capricorn) but do not penetrate lower latitudes (Randall 1981). Antiequatorial distributions are known across a variety of fish genera, including *Pseudolabrus* (Labridae), *Goniistius* (Latridae), *Assessor* (Plesiopidae), *Prionurus* (Acanthuridae), *Macrocanthus* (Macrocanthidae), and *Callanthias* (Callanthiidae) (Burridge 2002; Tea et al. 2019). Although the mechanisms behind antitropical and antiequatorial distributions are poorly understood, recent molecular genetic studies have revealed some biogeographical histories. For example, certain species of *Goniistius*, including *Goniistius francisi*, *Goniistius gibbosus*, *Goniistius plessisi*, *Goniistius rubrolabiatus*, and *Goniistius vestitus*, are found in temperate waters off eastern and western Australia and among south Pacific islands, including Easter Island, in the Southern Hemisphere (Ludt et al. 2019) (Fig. 3.3a). In the Northern Hemisphere, three species, *Goniistius quadricornis*, *Goniistius zebra*, and *Goniistius zonatus*, occur in Japan, Korea, China, and Taiwan, and *Goniistius vittatus* in Hawaii (Ludt et al. 2019) (Fig. 3.3a). According to the molecular phylogenetic studies of Burridge and White (2000), Burridge and Smolenski (2004), and Ludt et al. (2019), the three Asian species are not monophyletic, a minimum of three antiequatorial divergences being suggested. Burridge (2002) estimated that one antiequatorial divergence occurred 12.7–18.3 Mya, during the mid-Miocene, and the other two 4.8–6.9 Mya, during the late Miocene–early Pliocene. Similarly, Mabuchi et al. (2004) reconstructed a molecular phylogeny among 11 species of *Pseudolabrus*, two species occurring in East Asia and the remaining nine in the Southern Hemisphere, mainly in the temperate Pacific, and found the two Asian species to be monophyletic, thereby suggesting only a single antiequatorial divergence within the genus (Fig. 3.3b). They further estimated the antiequatorial divergence of *Pseudolabrus* as 3.8–4.1 Mya, corresponding to early to mid-Pliocene.

In a recent study, Tea et al. (2019) found *Microcanthus strigatus* to comprise at least two genetically distinct populations, with one additional population exhibiting strong genetic structuring but with intermittent, historical gene flow. They further suggested that the southwest Pacific was the center of origin for *Microcanthus*, subsequent colonization of Western Australia through the Bass Strait being followed by antiequatorial dispersals to the Northern Hemisphere during the Pleistocene. As demonstrated by Burridge (2002), Plio-Pleistocene antiequatorial divergence has been suggested for approximately half of the taxa studied, consistent with movement across the tropics during glacial periods. Besides the movement across the tropics at shallow depths during glacial periods, migration can take place via isothermic submergence, whereby species could maintain a suitable temperature by moving beneath the tropics at great depth (e.g., Hardy 1980).

On the other hand, a disjunct distribution between the eastern and western Pacific Ocean of temperate marine taxa has been recognized and referred to as trans-Pacific or amphi-Pacific distributions (Andriashev 1939; Briggs 1974). In the north Pacific, an east–west vicariance pattern may have become established from widely distributed ancestral species, distributed along the entire northern Pacific rim during warm interglacial periods, and subsequent extinction of northern populations during cold climates (Cox et al. 2014). Trans-Pacific distribution is well known for Japanese fishes, having been of particular interest in historical biogeography (e.g., Briggs 1974; Nishimura 1974).

Shelter-dwelling blennies of the genus *Neoclinus* exhibit trans-Pacific distribution, with three species in the eastern North Pacific and eight in the western North Pacific (Fig. 3.3c). Hongjamrassilp et al. (2020) undertook a molecular phylogenetic study of the genus and recovered the reciprocal monophyly of the eastern and western Pacific species. They suggested a single trans-Pacific divergence event from east to west, estimating the divergence time as 24 Mya, corresponding to the Oligocene. A similar divergence pattern is known for the surfperches (family Embiotocidae), represented by four species in the western and 20 in the eastern North Pacific and found in temperate coastal waters (absent from the boreal region) (Tarp 1952; Katafuchi and Nakabo 2007) (Fig. 3.3d). On the basis of genome-wide RAD (restriction-site associated DNA) markers, Longo and Bernardi (2015) showed that the western North Pacific species recovered a monophyletic group, which diverged approximately 7 Mya, and may have migrated across the northern Pacific during a warmer climatic period. Trans-Pacific distribution, including the Japanese Archipelago, is well known in other fishes, including rockfishes and gobies, for which similar species are found in the eastern and western North Pacific (Ingram and Kai 2014; Thacker 2015). As suggested in above studies, trans-Pacific divergence times vary widely, ranging from relatively recent dispersal events during Pleistocene warm interglacial periods to much older events during the late Eocene/early Oligocene.

3.5 Future Perspectives

Recently, a number of checklists of fishes in Japan, especially southern Japan, have been published, based on voucher specimens and underwater photographs (e.g., Motomura and Matsuura 2010, 2014; Motomura et al. 2013, 2018; Motomura and Harazaki 2017). Such checklists contribute to a more detailed understanding of distributional patterns and biogeography of fishes of Japan, as well as illustrating biogeographic provinces defined by taxonomy, endemism, and species composition. Molecular phylogenetic and phylogeographic studies have also identified clusters, concordant with biogeographic provinces (Bowen et al. 2016). In Japan, comparisons of phylogeographic patterns of multiple species have revealed previously unrecognized biogeographic patterns in freshwater fishes (Tabata et al. 2016; Watanabe et al. 2017; see also Chap. 12). At present, such studies are few for Japanese marine taxa, probably due to the absence of obvious geographic barriers and the high dispersal ability of marine fishes. However, as reviewed above, recent phylogeographic studies in Japanese waters have indicated that current distributions of genetic diversity are accompanied by evidence from geography, current systems, and habitats shifting in response to glaciation. Understanding how various historical and environmental factors in Japan shaped marine biodiversity requires an alignment of phylogeographic patterns across multiple taxa.

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Ichthyology and Collection Building in Japan

4

Masanori Nakae and Keiichi Matsuura

Abstract

Histories of ichthyology and fish collection building in Japan were reviewed in this chapter. Our historical research revealed that systematic studies of Japanese fishes began with European zoologists in the late 1700s, and many new species were reported from Japan by European and American ichthyologists in the 1800s and the early 1900s. After the Meiji restoration in 1867, Japanese zoologists started systematic studies of fishes and building fish collections under the influence of European and American zoologists. Most new Japanese fishes were reported by foreign ichthyologists (e.g., David Starr Jordan and his colleagues) by 1920; however, after 1921, the number of new species described by Japanese ichthyologists became more than that by foreign ichthyologists. Before World War II, three distinguished ichthyologists, Shigeho Tanaka, Kiyomatsu Matsubara, and Keitaro Uchida, appeared to make great contributions to ichthyology in Japan. They developed not only systematic studies but also fish collections at their research institutions. After World War II, Matsubara and Uchida educated many graduate students who made subsequent contributions to ichthyology and collection building at their universities. Beginning in the 1970s and continuing to the present, large fish books were published under coauthorship with many Japanese ichthyologists, which provided beautiful color photographs and/or identification keys with helpful illustrations, making it easier for ichthyologists to understand the fish diversity of Japan. When comparing ichthyological studies before and after World War II, it is clear that there were few phylogenetic studies before the War but afterward, Matsubara, his colleagues and students, published many phylogenetic monographs based on detailed comparative anatomical studies. This tradition has been maintained by young generations at several universities and institutions, but phylogenetic methodologies have recently been changing from morphological comparisons to molecular analysis. Thanks to the efforts of many Japanese ichthyologists, the number of recognized Japanese species has been greatly increased, now numbering 4617. Still, however, about 25 new species have been described from Japan every year for the past several decades. It will therefore be a long time before ichthyologists have a full understanding of the fish diversity of Japan.

Keywords

History · Systematics · Phylogeny · Larvae · Fauna · Japanese ichthyologists

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4.1 Introduction

Japan is an island country composed of two major island chains: four main islands, Hokkaido, Honshu, Shikoku, and Kyushu in the north, and the Ryukyu Islands in the south. The two island chains that make up the Japanese Archipelago extend for 3000 km from north to south, being almost equal in length to the east coast of Australia. The northeastern coast of the northernmost main island, Hokkaido, facing the Okhotsk Sea, is covered by ice in winter. However, even in winter, there are well-developed coral reefs in the Ryukyu Islands. Between these two extremes, there is a wide variety of aquatic habitats: sandy beaches, mud flats, estuaries, rocky shores, kelp beds, and very deep trenches exceeding 8000 m in depth; and in fresh waters, there are rivers, lakes, ponds, and marshes.

These diverse aquatic habitats have resulted in a great diversity of fishes, reaching around 4600 species (Motomura 2021), which includes about 12% of the total number of recognized fish species on the planet (Fricke et al. 2021). This great diversity has fascinated naturalists and ichthyologists since the eighteenth century and has contributed to the development of ichthyology in Japan. In this chapter, a history of ichthyology and collection building in Japan is presented with comments on Japanese ichthyologists.

4.2 History of Ichthyology in Japan

4.2.1 Dawn of Ichthyology in Japan

Because fishes have been important food resources in Japan from prehistoric times to the present, the Japanese people have been interested in fishes. Fishes had been reported in detail by Japanese naturalists before ichthyology was introduced to Japan from Europe, but the species had not been given Latinized scientific names by the Japanese, making it impossible to assign authorship to those who first reported these species (Abe 1986; Matsuura 1997). On the other hand, the rich fish fauna has attracted western naturalists since the eighteenth century (Matsuura 1997) including a Swedish naturalist, Carl Peter Thunberg (1743–1828), and a Dutch naturalist, Maarten Houttuyn (1720–1798). Based on fishes collected by Thunberg in Japan, Houttuyn (1782) reported 36 species, including 23 new species (e.g., *Scomber japonicus*, *Callionymus japonicus*, and *Uranoscopus japonicus*) of which 14 are currently valid (Boeseman 1995). This report was the earliest systematic study of fishes of Japan using binominal nomenclature (for pre-Linnean studies of Japanese fishes, see Boeseman 1947 and Abe 1986). Subsequently, Thunberg described 10 additional new species (e.g., *Diagramma pictum*, *Hyporthodus septemfasciatus*, and *Scorpaenopsis cirrosa*) based on specimens that he himself collected in Japan. A German naturalist, Georg Heinrich von Langsdorff (1774–1852), came to Japan as a member of a Russian expedition led by Adam Johann von Krusenstern (1877–1846). For about 6 months, between 1804 and 1805, while stationed at Nagasaki on the west coast of Kyushu (Paepke 2001), Langsdorff made large collections of fishes that were deposited at a museum in Berlin. The specimens were later studied by two famous French zoologists, Georges Cuvier (1769–1832) and Achille Valenciennes (1794–1865), who made great contributions to systematics and comparative anatomy of various groups of animals including fishes, and described hundreds of new species, including many commonly found in the waters of Japan such as *Lateolabrax japonicus*, *Sebastes inermis*, and *Chelidoperca hirundinacea*, in a series of great books titled *Histoire naturelle des poissons* (22 vols).

A German physician and naturalist, Phillipp Frantz von Siebold (1796–1866), visited Japan twice, from 1823 to 1829 and 1859 to 1862. Because the Tokugawa Shogunate closed the door of Japan to western countries except for the Dutch, Siebold came to Japan as a physician of the Dutch East Indian Company. During his first visit, Siebold obtained many fish specimens in collaboration with Japanese colleagues. He sent and brought back many specimens of not only fishes but also plants, amphibians, reptiles, birds, mammals, and various groups of aquatic invertebrates. Based on Siebold's collections, a series of monographs titled *Fauna Japonica* were published from 1842 to 1850. On the basis of Siebold's collection, two Dutch zoologists, Coenraad Jacob Temminck (1778–1858) and Hermann Schlegel (1804–1884), reported 358 species, including 234 new species (Temminck and Schlegel 1850), of which 167 are currently valid (Table 4.1), thus not only making a great contribution to understanding fish diversity of Japan but also providing precious materials for succeeding ichthyologists.

After the Tokugawa Shogunate had been defeated by the allied royalists led by the people of Satsuma and Choshu, a new government was established in 1868 and declared the new era called the Meiji. The Meiji government began to catch up with the more advanced western countries that were searching for opportunities to colonize Japan. The leaders of the Meiji government directed their emphasis and resources toward two major policies: to develop industry and to organize a strong army (Matsuura 1997).

The Meiji government also tried to introduce new scientific developments from western countries. They hired foreign personnel from various western countries as scientific advisers and professors and stationed them at Japanese educational institutions. A German zoologist, Frantz Martin Hilgendorf (1839–1904), and a German biologist, Ludwig Heinrich Philipp Döderlein (1855–1936), came to Japan as hired personnel in the 1870s. Hilgendorf arrived in Japan in 1873 and stayed for 3 years as a teacher at the Tokyo Medical School, which merged with the Imperial University of Tokyo in 1877 (Paepke 2001). During his stay, Hilgendorf made frequent visits to the Tokyo fish market where he obtained various species of fishes. He also traveled to many regions in central and northern Honshu where he collected fishes and aquatic invertebrates. His efforts resulted in finding 36 new species of fishes. Shinnosuke Matsubara, one of Hilgendorf's students, helped him in various ways during his stay in Japan and became a professor at the Tokyo Agricultural School in 1878. Their friendship and collaboration resulted in great success at the International Fisheries Exhibition held in Berlin in 1880 where Matsubara provided many exhibits about Japanese fisheries and fishes. In terms of ichthyology, important materials were displayed among the exhibits. Matsubara published a catalog of Japanese fishes using scientific names for the first time, which included about 250 species (Matsubara 1880).

The Tokio (i.e., Tokyo) Museum (1881) published a list of animal collections including more than 230 Japanese fishes. A couple of years later, Kanzo Uchimura, then well known in Japan as a Christian evangelist (Tokida and Kobayashi 1967), compiled a list of Japanese fishes in 1883 and 1884, while he worked as a staff member of the Ministry of Agriculture and Commerce. His manuscript, titled *Catalogue of Japanese Fishes*, included 640 species, but it was never published (Tokida and Kobayashi 1967). Although Uchimura did not collect or examine fish specimens, he wrote the catalog on the basis of publications such as Cuvier and Valenciennes (1829), Richardson (1846), Temminck and Schlegel (1850), Bleeker (1853, 1854), Brevoort (1856), Gill (1859), Günther (1877, 1880), Matsubara (1880), and Steindachner and Döderlein (1883). Following the work of Matsubara and Uchimura, several other Japanese zoologists reported various fishes from Japan. Shishido (1889) recorded 42 species of Chondrichthyes (1 species of *Chimaera* and 41 species of Elasmobranchii) found in Japan. Okada (1891) reported about 600 species of fishes as a part of list of vertebrates of Japan.

As the development of systematic ichthyology progressed, Japanese zoologists obtained adequate and appropriate scientific knowledge to describe new species of fishes. Kakich Mitsukuri, a zoologist and the first director of the Misaki Marine Biological Station of the Imperial University of Tokyo, was not only a pioneer in Japan in terms of systematics and embryology of animals, but he was also known as the first Japanese zoologist to describe a new fish species, *Rhinochimaera pacifica* (Mitsukuri 1895). In the same year, Chiyomastsu Ishikawa, a zoologist and professor at the Imperial University of

Table 4.1 Number of valid species described from Japan by 30 prolific authors in the period from 1758 to 2020

Rank	Author	No. of species
1	Jordan DS	202
2	Schlegel H	168
3	Temminck CJ	167
4	Snyder JO	107
5	Bleeker P	70
6	Tanaka S	66
7	Günther A	60
8	Suzuki T	51
9	Matsubara K	48
10	Starks EC	48
11	Senou H	45
12	Kamohara T	39
12	Motomura H	39
12	Yoshino T	39
15	Fowler HW	38
15	Valenciennes A	38
17	Randall JE	37
18	Shibukawa K	35
19	Cuvier G	34
19	Gilbert CH	34
21	Döderlein L	25
21	Hilgendorf FM	25
23	Steindachner F	23
24	Endo H	21
25	Richardson J	20
26	Katayama M	19
27	Nakabo T	18
28	Abe T	16
28	Bloch ME	16
30	Amaoka K	15

Tokyo, described a new freshwater fish, *Biwia zezera* (Ishikawa 1895), a cyprinid endemic to Japan.

4.2.2 Ichthyology Before World War II

In the 1900s and 1920s, David Starr Jordan (1851–1931) and his students and colleagues published a series of papers on Japanese fishes (e.g., Jordan and Snyder 1900, 1901a, b, c, d, e, f, g, 1902a, b, c, d, e, 1903, 1904a, b, 1906; Jordan 1902; Jordan and Fowler 1902a, b, c, d, e, 1903a, b, c, d; Jordan and Starks 1902, 1903, 1904, 1906a, b, 1907; Jordan and Seale 1906; Jordan and Herre 1907; Jordan and Richardson 1908; Jordan and Thompson 1911a, b, 1912; Jordan et al. 1913; Jordan and Tanaka 1927a, b), including descriptions of many new fishes (of which 281 species are now considered valid; Motomura 2021). These publications were great contributions to understanding the fish diversity of Japan. Under the influence of Jordan and his students, Shigeho Tanaka (1878–1974) became known as the “Father of Ichthyology” in Japan (Matsuura 1997). He described two new species of chimaerids in 1905, and from then on, he continued to describe new fishes for a career total of about 170, but 60% were later recognized as synonyms by other ichthyologists (Tominaga 1988, Eschmeyer et al. 2010; Table 4.1). He also worked to disseminate knowledge of ichthyology to the general public. In 1913, he began publishing *Gyogaku-zasshi* (*Ichthyological Journal*), but it was short-lived, lasting only through seven issues and discontinued in the same year due to inadequate financial support.

In 1913, Tanaka published a monumental work titled *A Catalogue of Fishes of Japan*, with coauthors Jordan and Snyder, in which 1230 species of fishes were described in detail, with beautiful illustrations (Jordan et al. 1913). Although Tanaka was the second author of this catalog, he wrote most of the manuscript (Tominaga 1988; Matsuura 1997). In 1911, Tanaka started publishing a long series of articles entitled *Figures and Descriptions of the Fishes of Japan*, with detailed descriptions and excellent illustrations. By 1930, this series totaled 48 volumes, containing descriptions of 267 species, 41 of which were new (Tanaka 1911–1930).

In 1931, Tanaka published another important paper, on the distribution of fishes in Japanese waters, the culmination of faunal studies initiated in 1921 that focused on fishes found in the four major islands of Japan, Hokkaido, Honshu, Shikoku, and Kyushu. His project was greatly supported by a large grant provided by two newspaper companies, making it possible for him to collect fishes from all four regions, from 1921 to 1924. His great efforts resulted in a large collection, including 961 species of marine fishes and 44 species of freshwater fishes. His detailed studies revealed two zoogeographic boundaries for marine fishes: on the Pacific side, warm-water fishes distributed south of Inubo-zaki Cape on the Boso Peninsula, central Honshu, and cold-water fishes found north of this point; and on the Sea of Japan side, warm-water fishes distributed south of Hamada, Shimane Prefecture, western Honshu, and cold-water fishes found north of that point. He also showed that three species, *Coilia mystus*, *Acanthogobius hasta*, and *Boleophthalmus pectinirostris*, are found only in the Ariake and Yatsushiro sounds on the west coast of Kyushu. Turning to the freshwater fish fauna, Tanaka divided the main four islands into the three areas: southern Japan defined as the area south of the Tama-gawa River, central Honshu; northern Honshu, north of the Tama-gawa River; and Hokkaido. He showed that the number of species in southern Japan is much greater than those of northern Honshu and Hokkaido. In addition, he stated that two species are endemic to Lake Biwa, and six species are abundant in the lake but rarely found in other areas in Japan. Many of his findings about fish distribution patterns have been confirmed by succeeding Japanese ichthyologists. Just before Tanaka's (1931) great zoogeographic paper came out, one of his students, Toshiji Kamohara (1901–1972), who had obtained a professorship at Kochi University, began publishing his serial articles on the fishes of Tosa Bay (e.g., Kamohara 1929, 1930, 1934a, b, c), one of the best examples of long-term observations of a fish fauna in a targeted area. There was another long-term study, of the fish fauna of Suruga Bay, central Honshu, published by Nagamichi Kuroda (e.g., Kuroda 1931, 1935a, b, 1938). Tanaka's (1931) great work and the subsequent long-term studies of Kamohara, Kuroda, and others have continuously provided better views of the Japanese ichthyofauna.

Before World War II, there were few phylogenetic studies of Japanese fishes. Kishinouye (1923), in pioneering work, studied in detail the musculature and circulatory systems of the Scombridae. Based on these studies, he considered that the cutaneous vascular system of scombrids was unique among bony fishes and thus he classified them in a new taxon, the Plecostei. Takahashi (1926), however, clarified that the cutaneous vascular system of scombrids was found in other fishes such as *Coryphaena hippurus*, *Xenocephalus elongatus*, and *Xiphias gladius*. Takahashi concluded that Kishinouye's Plecostei was therefore invalid. Tomiyama (1931, 1934) studied the cranial osteology of several species of the Sparidae and found that *Acanthopagrus latus*, *Acanthopagrus schlegelii*, *Evynnis tumifrons*, *Pagrus major*, and *Rhabdosargus sarba* differed significantly in their frontal and nasal bones, although some of them had been classified by previous authors in a catch-all genus, *Sparus*. Masuda (1942) found that the many species of *Epinephelus* represented 28 morphs belonging to four groups on the basis of osteological characters of the cranium, the shape of the preopercle, scales, the shape of the gill rakers and teeth, and color pattern. He did not clearly assign taxonomic status to his 28 morphs, but Matsubara (1955) concluded that it was reasonable to recognize the 28 morphs as species. Matsubara (1943a, b) published a two-part monograph on the taxonomy and phylogeny of scorpaenoid fishes titled *Studies on the Scorpaenoid Fishes of Japan* based on osteological and myological characters. In terms of taxonomic coverage and use of well-defined anatomical characters, his study stood out among all Japanese works on fish systematics published before World War II.

As shown above, ichthyology in Japan was developed on the basis of studies of adult fishes; however, there were several Japanese ichthyologists who focused on early life histories. Studies on larval fishes in Japan began with a report on the larvae of *Salangichthys microdon* in Lake Kasumiga-ura (Kitahara 1895). From the 1910s to 1930s, there were serial studies on larval fishes of various taxonomic groups found around the Boso Peninsula of central Honshu by Kamiya (e.g., 1916, 1925, larval fishes of Tateyama Bay) and Nakamura (e.g., 1932, 1936, larval fishes found in tidepools at Kominato). Keitaro Uchida (1896–1982) studied systematics based on adult fishes, but he was also well known in Japan for his studies of larval fishes. He published 30 papers on larval fishes between 1924 and 1938 covering various groups such as the Elopidae, Congridae, Monocentridae, Atherinidae, Hemrhamphidae, Scorpidae, Oplegnathidae, Terapontidae, Embiotocidae, Gobiidae, Trichiuridae, Antigonidae, Pleuronectidae, and Monacanthidae (e.g., Uchida 1926a, b, c, 1935, 1936a, b). However, all these papers were published only in Japanese, making it almost impossible for western ichthyologists to appreciate his contributions. He was a pioneer among ichthyologists in Japan, recognizing that early developmental series are necessary to understand fully the characteristics of species (Matsuura 1997). When Uchida was given an opportunity to study the fishes of Korea in the 1930s, at the Fisheries Experimental Station in Busan, he planned to publish a monographic series to treat all 650 species then known from the seas and freshwaters of Korea (Matsuura 1997). The first issue of his series was titled *The fishes of Tyōsen (Korea). Part I. Nematognathi and Eventognathi* in which he provided for each species a detailed description of larvae, juveniles, and adults, along with a summary of geographic distributions and notes on ecology (Uchida 1939). Although Uchida had plans to produce another ten parts to the series, the work was interrupted by World War II and never reappeared (Matsuura 1997). In 1941 Uchida was offered a professorship at the Imperial University of Kyushu. Although he knew that the research facilities of the Fisheries Experimental Station at Busan were much better than that of the university, he understood that his ichthyological knowledge and expertise were required to produce the next generation of students of early life histories of fishes. This made him return to Japan to devote himself to the education of graduate students. There is no doubt that Uchida, Tanaka, and Matsubara were the most important ichthyologists to the development of ichthyology before World War II. Each built a major center of ichthyology at their universities after the War and educated students who became the successors of ichthyology.

As stated above, many Japanese ichthyologists worked to advance the study of fishes in Japan, and their efforts resulted especially in the development of taxonomic studies. This is clearly seen in the numbers of new species described by Japanese and foreign ichthyologists (Fig. 4.1). Prior to 1920, most Japanese fishes were described by foreign ichthyologists, but after that time, the majority were described by Japanese ichthyologists.

4.2.3 Ichthyology After World War II

Ten years after the end of World War II, Kiyomatsu Matsubara (1906–1968) published a monumental book, *Fish Morphology and Hierarchy*, which contained identification keys to all families, genera, and species (2714 species then known) found in Japan and adjacent waters

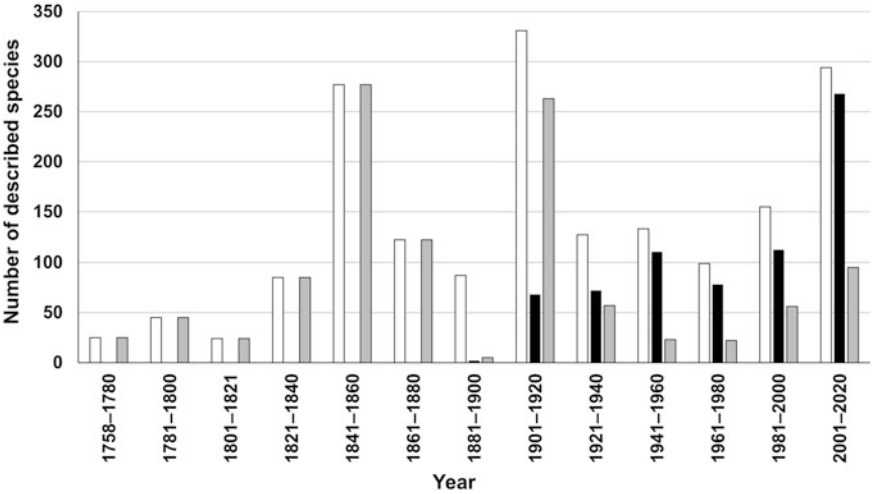

Fig. 4.1 Numbers of species described from Japan, including name-bearing type specimens. Even when paratypes were collected from Japan but name-bearing type specimens were collected outside Japan, those species were not included in the figure. *Open bar* total number of species; black *solid bar* number of species described by Japanese ichthyologists; *gray solid bar* number of species described by foreign ichthyologists. Species described under coauthorship with foreign ichthyologists are included both in black and gray solid bars

(Matsubara 1955). When compared to the earlier book of Okada and Matsubara (1938), which included identification keys to all 1946 Japanese species then known, it is clear how greatly Matsubara (1955) contributed to the understanding of Japanese fish diversity. This great book also provided anatomical characters and proposed phylogenetic relationships of many families and higher taxa. Matsubara (1963) published another great book, *Systematic Zoology, Pisces*, which focused on phylogenetic relationships of higher taxa of fishes of the world based on comparative morphology. Okada (1959, 1960a, b) published detailed accounts of 147 freshwater fishes (including invasive species) of Japan, which was the first publication in Japan devoted solely to freshwater fishes.

In 1975, Hajime Masuda (1921–2005), Chuichi Araga (1932–2020), and Tetsuo Yoshino published a beautiful book titled *Coastal Fishes of Southern Japan*, consisting of short descriptions and excellent color photographs of 1252 species (Masuda et al. 1975). In this book, Yoshino and Araga (1975) described a new genus and species, *Pseudotrichonotus altivelis* from Sagami Bay, central Honshu. They also erected a new family, Pseudotrichonotidae, based on their new genus. Its phylogenetic position was studied by Johnson et al. (1996) to confirm its familial status. Masuda et al. (1984) reported more than 3200 species in another book, titled *The Fishes of the Japanese Archipelago*, in which 43 ichthyologists, including young graduate students, provided accounts. This book stands out when compared to previous publications in terms of species coverage (Fig. 4.2) and the number of authors. In 1985, the Second Indo-Pacific Fish Conference (IPFC2) was held at the Tokyo National Museum in which 251 ichthyologists from 26 countries participated (about half of the participants were Japanese). This international conference stimulated greatly the ichthyological community in Japan. During the conference, young Japanese students were given opportunities to communicate and get acquainted with foreign colleagues, which resulted in many subsequent collaborative studies. Following the IPFC2, Uyeno et al. published *Indo-Pacific Fish Biology: Proceedings of the Second International Conference on Indo-Pacific Fishes*, which included 94 papers submitted by ichthyologists

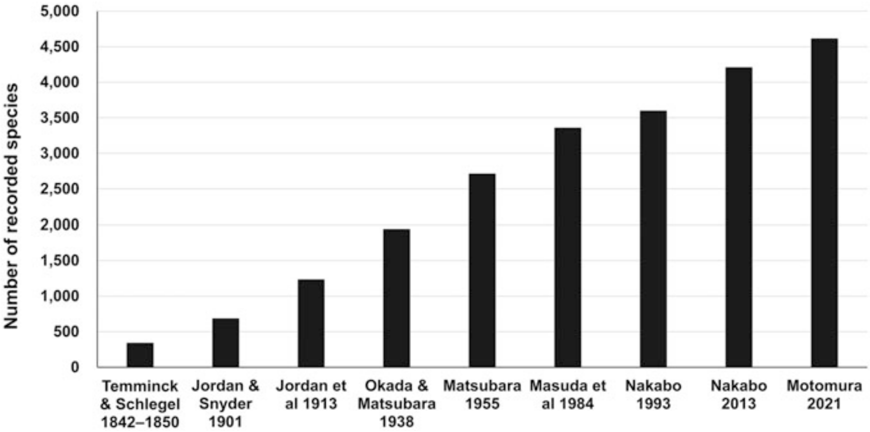

Fig. 4.2 Numbers of species recorded from Japan and adjacent waters in nine major publications

throughout the Indo-Pacific region and beyond (Uyeno et al. 1986).

In 1988, the second edition of *The Fishes of the Japanese Archipelago* was published, increasing the Japanese ichthyofauna to more than 3360 species (Masuda et al. 1988). Tetsuji Nakabo and his colleagues provided illustrated keys to the identification of the 3608 species then known from Japan (Nakabo 1993). They expanded the coverage from 3608 to 3863 species in two subsequent editions, one in Japanese and the other in English (Nakabo 2000, 2002; Fig. 4.2), and 4210 species in a third edition (Nakabo 2013).

With the development of ichthyology in Japan, the number of ichthyologists has increased (Figs. 4.3, 4.4, 4.5 and 4.6), and about 25 new species of fishes are now being described every year (Matsuura and Kimura 2013). In 2006, Keiichi Matsuura and Seishi Kimura obtained financial support from the National Museum of Nature and Science to publish a series of papers devoted to describing new fishes from Japanese waters (Matsuura and Kimura 2013). This series, titled *New Fishes of Japan*, resulted in many papers published by Japanese as well as several foreign authors in five issues of supplements to the Bulletin of the museum (Series A, Zoology). In the final issue, Matsuura and Kimura (2013) stated that four new genera and 77 new species belonging to 25 families of fishes had been described from 2007 to 2013. In that period, 156 new fishes were described from Japan, half of which were described in *New Fishes of Japan*. Consequently, the number of new Japanese species jumped from 112 (from 1981 to 2000) to 268 (from 2001 to 2020) (Fig. 4.1). Recently, Motomura (2021) compiled a list of all Japanese fishes: as of April 7, 2021, 4617 species are included in the list. Because more than 200 fishes (including invasive species) have been reported as either of new species or newly recorded species from Japan in the past 5 years (2016–2020), it is easily expected that the number of Japanese fishes will reach beyond 5000 by 2030.

As described above, few phylogenetic studies of Japanese fishes were published before World War II. There were only two ichthyologists, Kamakichi Kishinouye (1867–1929) and Kiyomatsu Matsubara, who made significant contributions to the relationships of higher taxa of fishes (Kishinouye 1923; Matsubara 1943a, b). After World War II Matsubara's laboratory in Kyoto University became a center of systematic studies of fishes, attracting a large number of students who published a series of monographs: Hoplichthyidae by Matsubara and Ochiai (1950a, b, c), Spariformes by Akazaki (1962), Congridae by Asano (1962), Pleuronectiformes by Amaoka (1969), and Macrouridae by Okamura (1970). In addition to these phylogenetic studies, Matsubara and his students published many taxonomic studies of various groups of fishes (e.g., Matsubara and Ochiai 1955; Akazaki 1961; Ochiai and

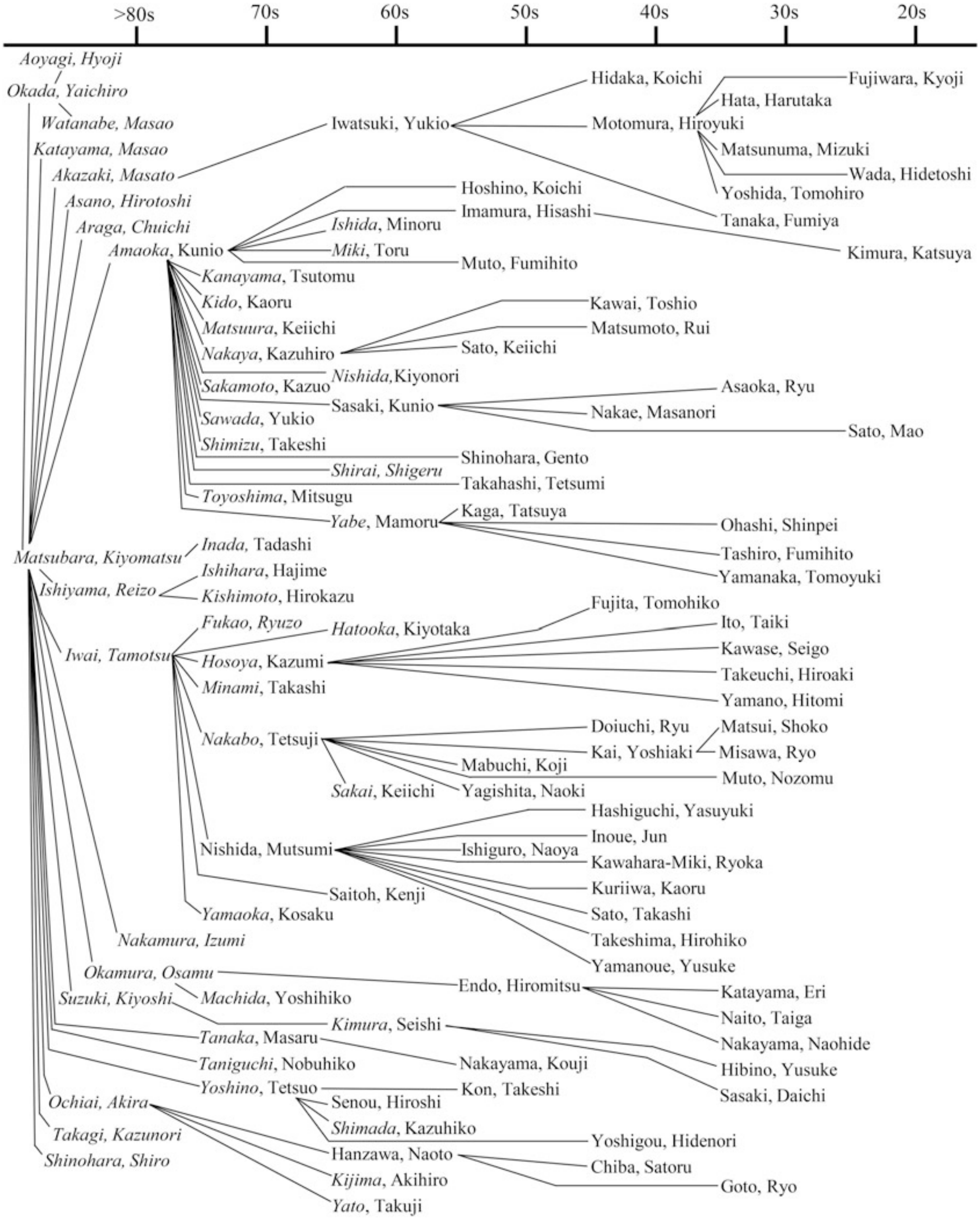

Fig. 4.3 Japanese ichthyologists associated with Kiyomatsu Matsubara. Surnames of retired workers in italics; names of deceased workers in full italics. Workers studying mainly on systematics (taxonomy and phylogeny) of fishes are included in Figs. 4.3, 4.4, 4.5, and 4.6, but those studying mainly on other subjects of fishes (e.g., ecology and physiology) are excluded. Workers before the retirement and not publishing systematic papers in the past 10 years are excluded. Ages of the ichthyologists are as of the end of 2021

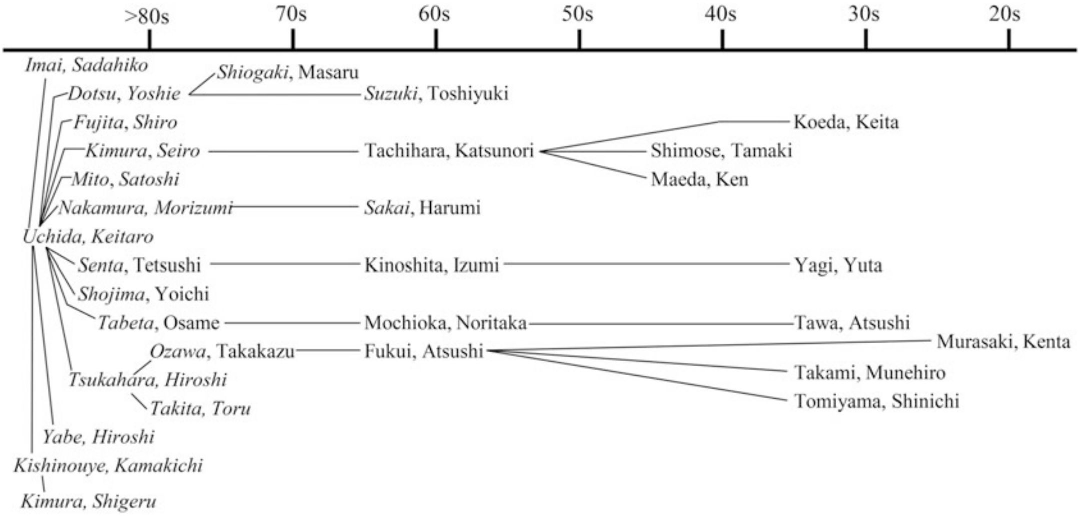

Fig. 4.4 Japanese ichthyologists associated with Shigeho Tanaka. Surnames of retired workers in italics; names of deceased workers in full italics

Amaoka 1962; Ochiai 1963; Okamura 1963; Ochiai and Mori 1965; Matsubara et al. 1964). Unfortunately, Matsubara passed away in 1968 while he was actively studying fishes. After his untimely passing, fish systematics at Kyoto University fell off sharply. However, Matsubara's students who obtained positions in universities in other regions of Japan followed him in studying fish systematics and building research facilities and fish collections. Examples include Masato Akazaki (1926–1999) at Miyazaki University, Hirotoshi Asano (1930–2017) at Kinki University, Osamu Okamura (1933–2008) at Kochi University, and Kunio Amaoka at Hokkaido University. Among these new centers of ichthyology, Amaoka and his students took the lead from 1975 to 2018 to publish a series of phylogenetic studies of many groups of fishes (Table 4.2). Since 2001, Mutsumi Nishida, Masaki Miya, and their students have published a series of phylogenetic studies of higher taxa of fishes based on molecular analysis (Table 4.2, Miya and Nishida 2015).

Also as shown above, studies on larval fishes were relatively less developed than those on adult fishes prior to World War II. Thanks to Keitaro Uchida, the situation was greatly changed. His many students (Fig. 4.5) studied various groups of larval fishes: e.g., gobioids by Yoshie Dotsu (1923–2016), tetraodontiforms by Shiro Fujita (1925–2011), salmonids by Seiro Kimura (1932–2009), various groups of coastal and pelagic fishes by Satoshi Mito (1927–2009), various groups of coastal fishes by Tetsushi Senta, elopiforms by Osame Tabeta, clupeids, sciaenids, and gobiids by Toru Takita (1937–2014), and various coastal and pelagic fishes by Hiroshi Yabe (1901–2001). In addition to these

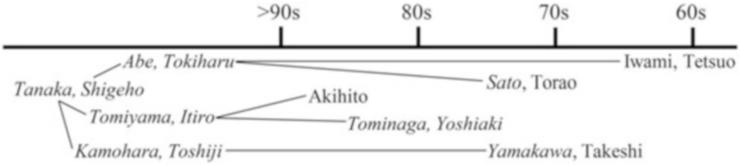

Fig. 4.5 Japanese ichthyologists associated with Keitaro Uchida. Surnames of retired workers in italics; names of deceased workers in full italics

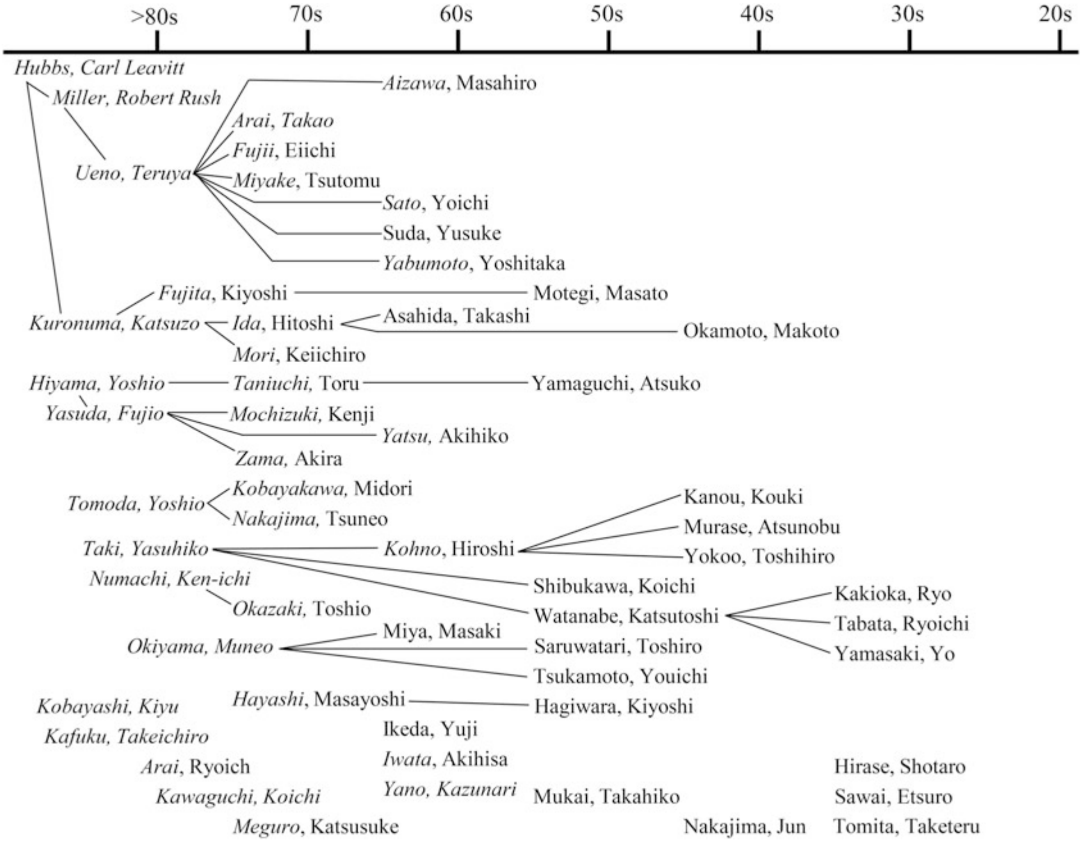

Fig. 4.6 Japanese ichthyologists not included in Figs. 4.5 and 4.6. Although Hubbs and Miller are Americans, they are included here to show their association with their Japanese "descendants." Surnames of retired workers in italics; names of deceased workers in full italics

ichthyologists, "grandsons" of Uchida initiated studies on larval fishes collected from the waters of Japan and seas in the tropical western Pacific. Muneo Okiyama (1937–2013), another distinguished ichthyologist, made significant contributions to larval fishes of Japan (as well as deep-sea fishes), publishing numerous articles. He organized many colleagues to publish a great book titled *An Atlas of Early Stage Fishes in Japan* (Okiyama 1988), which provided detailed descriptions and excellent illustrations of 1100 species. Of this book, Leis and Trnski (1989: 4) wrote: "Most recently, a very impressive volume on the fish larvae of Japan under the editorship of Dr Muneo Okiyama (1988) has appeared. This volume covers 220 families, . . . Okiyama's book is invaluable but, unfortunately, much of its contents are unavailable to the western reader because its text is in Japanese." Unfortunately, Okiyama passed away, on September 7, 2013, 1 year before publication of the second edition of *An Atlas of Early Stage Fishes in Japan*, which expanded coverage to 1550 species (Okiyama 2014).

4.2.4 History of the Ichthyological Society of Japan

In 1946, just after World War II ended, Japanese ichthyologists established a society called "Uo-no-kai" (Japanese Society of Ichthyologists) and began publishing a journal *Uo* (Fish) that emphasized the dissemination of ichthyological

Table 4.2 Phylogenetic studies of fishes by Japanese ichthyologists from the 1940s to 2010s

Author(s) and year	Method	Taxa
Akazaki (1962)	Comparative morphology/ conventional	Lethrinidae, Nemipteridae, and Sparidae (Spariformes)
Amaoka (1969)	Comparative morphology/ conventional	(Bothidae, Citharidae, Paralichthyidae, and Psettodidae (Pleuronectiformes)
Asano (1962)	Comparative morphology/ conventional	Congridae (Anguilliformes)
Endo (2002)	Comparative morphology/ cladistics	Gadiformes
Goto (2001)	Comparative morphology/ cladistics	Orectolobiformes
Honma et al. (2013)	Comparative morphology/ cladistics	Perryenidae (Scorpaeniformes)
Hosoya (1986)	Comparative morphology/ cladistics	Gobioninae (Cypriniformes)
Imamura (1996)	Comparative morphology/ cladistics	Platycephalidae (Scorpaeniformes)
Imamura (2000)	Comparative morphology/ cladistics	Dactylopteridae (Perciformes)
Imamura (2004)	Comparative morphology/ cladistics	Scorpaenoidea (Perciformes)
Imamura et al. (2005)	Comparative morphology/ cladistics	Trichodontidae (Perciformes)
Imamura and Matsuura (2003)	Comparative morphology/ cladistics	Pinguipedidae (Perciformes)
Imamura and Yabe (2002)	Comparative morphology/ cladistics	Scorpaenoidei (Perciformes)
Inoue et al. (2001)	Molecular analysis	Osteoglossomorpha, Elopomorpha, Clupeomorpha, Ostariophysi, and Protacanthopterygii
Inoue et al. (2003a)	Molecular analysis	Eurypharyngidae and Saccopharyngidae (Anguilliformes)
Inoue et al. (2003b)	Molecular analysis	Acipenseriformes, Amiiformes, Polypteriformes, and Lepisosteiformes
Inoue et al. (2004)	Molecular analysis	Elopomorpha
Inoue et al. (2010)	Molecular analysis	Chimaeriformes
Imoto et al. (2013)	Molecular analysis	Leuciscinae (Cypriniformes)
Ishida (1994)	Comparative morphology/ cladistics	Scorpaenoidei (Scorpaeniformes)
Ishiguro et al. (2003)	Molecular analysis	Protacanthopterygii
Ishiguro et al. (2005)	Molecular analysis	Sundasalangidae (Clupeiformes)
Ishii and Imamura (2008)	Comparative morphology/ cladistics	Congiopodidae (Perciformes)
Iwami (1985)	Comparative morphology/ cladistics	Channichthyidae (Perciformes)
Kaga (2013)	Comparative morphology/ cladistics	Sillaginidae (Perciformes)
Kanayama (1991)	Comparative morphology/ cladistics	Agonidae (Scorpaeniformes)
Kanehira et al. 2012	Comparative morphology/ cladistics	Notacanthoidei (Albuliformes)
Kang et al. (2017)	Comparative morphology/ cladistics	Polynemidae (Perciformes)
Kawahara et al. (2008)	Molecular analysis	Gasterosteiformes

(continued)

Table 4.2 (continued)

Author(s) and year	Method	Taxa
Kawai (2008)	Comparative morphology/ cladistics	Peristediidae (Scorpaeniformes)
Kido (1988)	Comparative morphology/ cladistics	Liparidae (Scorpaeniformes)
Kim (2002)	Comparative morphology/ cladistics	Mullidae (Perciformes)
Kimura et al. (2018a)	Comparative morphology/ cladistics	Cheilodactylidae and Latridae (Perciformes)
Kishinouye (1923)	Comparative morphology/ conventional	Scombridae (Scombriformes)
Matsubara (1943a, b)	Comparative morphology/ conventional	Scorpaenoidei (Scorpaeniformes)
Matsubara and Ochiai (1950a, b, c)	Comparative morphology/ conventional	Hoplichthyidae (Scorpaeniformes)
Matsubara and Ochiai (1955)	Comparative morphology/ conventional	Platycephalidae (Scorpaeniformes)
Matsuura (1979)	Comparative morphology/ cladistics	Balistoidea (Tetraodontiformes)
Miya et al. (2013)	Molecular analysis	Scombridae (Perciformes)
Miya et al. (2007)	Molecular analysis	Stylephoridae (Stylephoriformes)
Miya et al. (2010)	Molecular analysis	Lophiiformes
Miya et al. (2005)	Molecular analysis	Batrachoidiformes
Miya et al. (2003)	Molecular analysis	Neoteleostei
Nakabo (1983)	Comparative morphology/ conventional	Callionymidae (Perciformes)
Nakae and Sasaki (2004)	Comparative morphology/ cladistics	Tetraodontiformes
Nakae and Sasaki (2010)	Comparative morphology/ cladistics	Tetraodontiformes
Nakamura (1983)	Comparative morphology/ conventional	Xiphiidae and Istiophoridae (Istiophoriformes)
Nakatani et al. 2011	Molecular analysis	Otophysi
Nakaya (1975)	Comparative morphology/ conventional	Scyliorhinidae (Carcharhiniformes)
Nishida (1990)	Comparative morphology/ cladistics	Myliobatoidei (Myliobatiformes)
Ochiai (1966)	Comparative morphology/ conventional	Cynoglossidae (Pleuronectiformes)
Odani and Imamura (2011)	Comparative morphology/ cladistics	Leptoscopidae (Perciformes)
Okamura (1970)	Comparative morphology/ conventional	Macrouroidei (Gadiformes)
Oku et al. (2017)	Comparative morphology/ cladistics	Cyclopteridae (Perciformes)
Orr et al. (2019)	Molecular analysis	Cyclopteridae (Perciformes)
Saitoh et al. (2003)	Molecular analysis	Ostariophysi
Saitoh et al. (2006)	Molecular analysis	Cypriniformes
Sakamoto (1984)	Comparative morphology/ phenetics	Pleuronectidae (Pleuronectiformes)
Sasaki (1989)	Comparative morphology/ cladistics	Sciaenidae (Perciformes)

(continued)

Table 4.2 (continued)

Author(s) and year	Method	Taxa
Sato and Nakabo (2002)	Comparative morphology/ cladistics	Paraulopidae (Aulopiformes)
Satoh et al. (2006)	Molecular analysis	Macrouridae (Gadiformes)
Sawada (1982)	Comparative morphology/ cladistics	Cobitoidea (Cypriniformes)
Setiamarga et al. (2008)	Molecular analysis	Atherinomorpha
Shinohara (1994)	Comparative morphology/ cladistics	Hexagrammloidei (Scorpaeniformes)
Shinohara and Imamura (2005)	Comparative morphology/ cladistics	Scorpaenidae (Perciformes)
Shirai (1992)	Comparative morphology/ cladistics	Squalomorphi
Shirai (1996)	Comparative morphology/ cladistics	Galeomorphi
Takagi (1988)	Comparative morphology/ conventional	Gobioidei
Takahashi (2002)	Comparative morphology/ cladistics	Trematocarini (Cichlidae, Perciformes)
Tominaga (1968)	Comparative morphology/ conventional	Pempheridae (Perciformes)
Tominaga et al. (1996)	Comparative morphology/ conventional	Percoidei (Perciformes)
Toyama et al. (2020)	Comparative morphology/ cladistics	Belonidae (Beloniformes)
Vilasri (2013)	Comparative morphology/ cladistics	Uranoscopidae (Perciformes)
Yabe (1981)	Comparative morphology/ cladistics	Icelidae (Scorpaeniformes)
Yabe (1985)	Comparative morphology/ cladistics	Cottoidei (Scorpaeniformes)
Yamanaka et al. (2010)	Comparative morphology/ cladistics	Teleostei
Yamanoue et al. (2004)	Molecular analysis	Molidae (Tetraodontiformes)
Yamanoue et al. (2007, 2008)	Molecular analysis	Tetraodontiformes

Works by foreign students whose studies were done at Japanese universities are included

knowledge to the general public. However, a scientific journal to publish professional papers on fishes was needed. In 1950, the Japanese Society of Ichthyologists published the first issue of the *Japanese Journal of Ichthyology* (JJI). In the first issue, Yaichiro Okada (1892–1976) stated that the Society planned to publish issues bimonthly, each issue with about 64 pages, and in that first year, the Society succeeded in publishing six issues and 44 articles in volume 1. Then, in volume 2, they published five issues and 38 articles, in volume 3, five issues, and 44 articles. However, in volume 3, only four issues appeared, and in volume 4 only two issues. By 1967, only a couple of issues appeared in each volume (Fig. 4.7), apparently due to a failure to organize the members of the Society and to collect adequate numbers of manuscripts.

This made several leading members of the Society realize that it required reorganization. In 1968, a revived Ichthyological Society of Japan (ISJ) was independently established by a group of ichthyologists led by Reizo Ishiyama (1912–2008). Their first meeting, held on April 3, 1968, at Nihon University in Tokyo, was attended by about 30 ichthyologists who declared

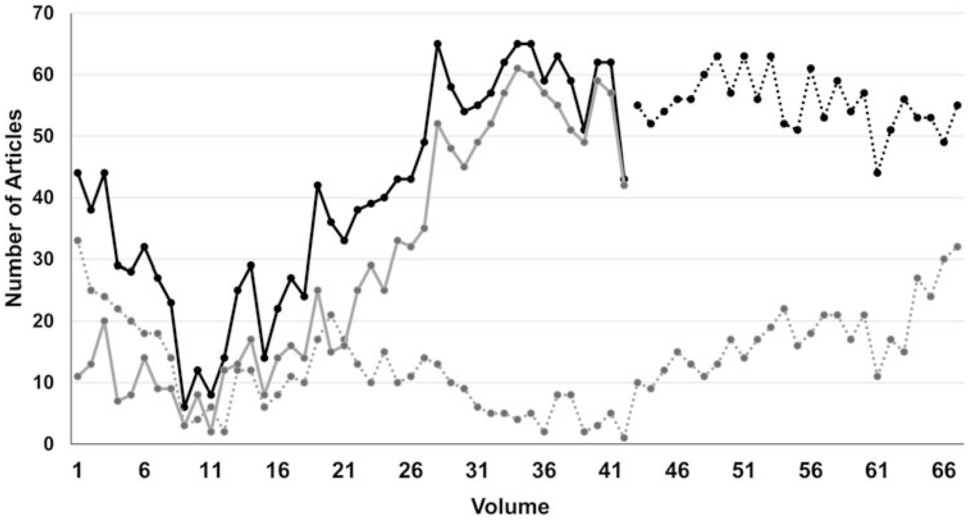

Fig. 4.7 Number of articles in two journals of Ichthyological Society of Japan. *Black solid line* number of articles in Japanese Journal of Ichthyology (JJI); *gray solid line* number of English articles in JJI; *gray dotted line* number of Japanese articles in JJI; *black dotted line* number of articles in Ichthyological Research in which all articles published in English

the establishment of the new society. They adopted a constitution and elected Yaichiro Okada as the first president and Kiyomatsu Matsubara, president elect. They also decided to publish an official journal, titled the *Japanese Journal of Ichthyology* (JJI), the same title of the preceding society's journal. Capable ichthyologists were chosen to serve on the Editorial Board, and plans were made to publish four issues per year, a rate of publication that has continued without exception since 1968.

Subscriptions to the journal increased gradually, the number of members reaching 1200 in 1996, a level of membership that has been maintained as of 2020. Papers were published in both Japanese and English, but as articles in English increased at the expense of those in Japanese (Fig. 4.7), the Society decided in 1996 to produce two official journals, one in Japanese (JJI) for articles that focused on domestic subjects and the other for articles in English, called *Ichthyological Research* (IR), for a worldwide audience. This policy resulted in a marked increase in the numbers of submitted manuscripts to both of ISJ and IR, making it possible for the Society to publish a greater number of articles.

Two international fish conferences were held in Japan under the auspices of ISJ: the IPFC2 in Tokyo in 1985 and, 28 years later, the IPFC9 at Ginowan in Okinawa in 2013. The IPFC2 was held by the organizing committee chaired by Teruya Uyeno (1930–2021) and the IPFC9 by another organizing committee chaired by Keiichi Matsuura. Both the conferences were extremely successful, the first attracting 251 participants from 26 countries, and the second, 532 participants from 36 countries.

4.3 Major Fish Collections in Japan

It is not easy for foreign ichthyologists to know the details of fish collections in Japan because material is widely scattered throughout the country (Table 4.3). We provide information about noteworthy fish collections in Table 4.3, and comments on five major fish collections below.

4.3.1 National Museum of Nature and Science

The fish collection of this museum stands out among fish collections in Japan, housing 1.5 million cataloged specimens, including 2670 type specimens of 648 species. There are also many uncataloged specimens reaching about one million. The collection includes 7800 species collected not only from Japan but also from throughout the Pacific, Indian, and Atlantic oceans. It is a national fish collection including 3200 species of fishes collected from 10,742 sites in various regions throughout the Japanese Archipelago, from Hokkaido in the north to the Ryukyu Islands in the south. It covers 70% of the valid species reported from Japan. Approximately 65% of the cataloged specimens have been registered in a computerized database, available through a website of the museum.

The National Museum of Nature and Science was founded at Ueno Park in the central part of Tokyo in October 1877. It was called the Museum of Education at that time and focused primarily on education to the general public rather than scientific research, although it did contain a small number of specimens, only about 502, used mainly for exhibits. At 11:58 a.m. on September 1, 1923, a huge earthquake rocked Tokyo and neighboring areas, causing serious damage, including the death of 100,000 people. A big fire followed in Tokyo decimating the entire central part of the city including the area where the museum had once stood.

Two years after the earthquake, the fish collection of the Natural History Division of the Imperial Museum was transferred to the National Museum of Nature and Science (then called the Tokyo Museum). According to the ledger of the Imperial Museum about 3000 specimens were sent but, before the transfer, many specimens had been lost in the earthquake or had already been transferred to other institution, so that the real number was only about 2000. Before World War II the fish collection had not developed well because of the lack of research departments but afterward the Ministry of Education changed its policy and research departments, including a Department of Zoology, were finally established, although there were no fish curators in the Department until 1963.

Ryoichi Arai, the first curator of fishes, came to the museum (then called the National Science Museum) in September 1963 and began studying fish systematics by using chromosomes. Two years later, in July 1965, Yoshio Tomoda (1922–2017) joined Arai in the Fish Section and began studying the systematics and ecology of catfishes and other freshwater taxa. Both of them worked to expand the fish collection, Arai mainly in marine fishes and Tomoda in freshwater fishes; by 1969, the fish collection through their joint efforts reached around 20,000 specimens. In June 1969, Morizumi Nakamura (1914–1998) was transferred to the museum from the Research Institute for Natural Resources (Sigenkagaku Kenkyusho), along with 1.16 million fish specimens (about 28,600 lots; mainly freshwater fishes). In the 1970s, research activities of the Fish Section flourished but the curation of the collection remained relatively poor; specimens were not arranged systematically, existing more like private collections of the curators.

This situation was finally changed when Nakamura retired and was replaced by Keiichi Matsuura. When he arrived at the museum in April 1979, Matsuura immediately began to make improvements in curation, rearranging the collection following Nelson's (1976) classification system and adding a large number of specimens through many collecting trips to the tropical Indo-West Pacific, from Thailand to the Solomon Islands. He also encouraged colleagues throughout Japan to send their private collections to the museum. Whenever he learned that fish collections of research institutions and/or universities were about to be discarded, he approached authorities to ask for transfer of collections to the museum. His continuous efforts resulted in many donations from private collectors and institutions, including the invaluable larval fish collection of the National Research Institute of Far Seas Fisheries (FSFL) collected from the tropical Indo-Pacific; the coral

Table 4.3 Fish collections in Japan. Institutions housing more than 10,000 specimens are included

Institution code	Institution	Number of cataloged specimens	Curator(s)	Remarks
NSMT	National Museum of Nature and Science, Tsukuba	1,500,000	Shinohara G, Nakae M	Started in 1877; largest fish collection in Japan; specimens collected worldwide; 1500 types of specimens
FAKU	Maizuru Fisheries Research Station and Kyoto University Museum, Kyoto	400,000	Kai Y	Started in 1947; specimens mainly collected around Japan; 1300 types of specimens
HUMZ	Hokkaido University Museum, Hakodate	250,000	Tashiro F	Started in 1958; specimens collected from northern Japan and western North Pacific; 1300 types of specimens
KAUM	Kagoshima University Museum, Kagoshima	250,000	Motomura H	Started in 2005; specimens collected from Kagoshima prefecture and Southeast Asia; 800 types of specimens
OMNH	Osaka Museum of Natural History, Osaka	230,000	Matsui S	Started in 1953; specimens mainly collected from Osaka Prefecture and set Inland Sea; 80 types of specimens
CBM CMNH	Natural History Museum and Institute, Chiba	163,500	Miya M, Kawase H	Started in 1987; 148,500 specimens housed at the main campus of the museum (CBM) and 15,000 specimens at a branch (CMNH); specimens of shallow water fishes collected around Boso Peninsula and mesopelagic fishes from seas outside Japan
BSKU	Faculty of Science and Technology, Kochi University, Kochi	150,000	Endo H	Started in 1927; specimens mainly collected from seas around Shikoku; 1400 types of specimens
YCM	Yokosuka City Museum, Yokosuka	150,000	Hagiwara K	Started in 1973; specimens mainly collected from Sagami Bay and Ryukyu Islands; 110 types of specimens
TKPM	Tokushima Prefectural Museum, Tokushima	138,000	Ito T	Started in 1990; most specimens collected from Tokushima Prefecture, Shikoku and adjacent area
KPM	Kanagawa Prefectural Museum of Natural History, Odawara	108,000	Senou H	Started in 1994; specimens mainly collected from Kanagawa Prefecture and Ryukyu Islands; fish collection of the Izu Oceanic Park (IOP) transferred to the KPM in 2005; 288 types of specimens
MUFS	Faculty of Fisheries Sciences, Miyazaki University, Miyazaki	104,000	Iwatsuki Y	Started in 1970; specimens mainly collected from southern Kyushu; 200 types of specimens
OCF	Okinawa Churashima Foundation Research Center, Motobu	93,000	Miyamoto K	Started in 1979; specimens mainly collected from the Ryukyu Islands; fish collection of the University of the Ryukyus (URM) transferred to the OCF in 2011; 200 types of specimens

(continued)

Table 4.3 (continued)

Institution code	Institution	Number of cataloged specimens	Curator(s)	Remarks
ZUMT	University Museum, University of Tokyo, Tokyo	81,500	Koeda K	Started in 1904; core of the collection built by Shigeho Tanaka; 300 types of specimens
FRLM	Graduate School of Bioresources, Mie University, Tsu	60,000	Yodo T	Started in 1978; specimens collected from Japan and Southeast Asia; 200 types of specimens
KUN	Faculty of Agriculture, Kindai University, Nara	60,000	Matsunuma M	Started in 1964; core of collection composed of freshwater fishes of Japan
LBM	Lake Biwa Museum, Kusatsu	60,000	Tabata R	Started in 1996; freshwater fishes collected from Lake Biwa and adjacent areas
SNFR	Fisheries Technology Institute, Japan Fisheries Research and Education Agency, Nagasaki	38,000	Hoshino K	Started in the early 1980s; mainly collected from the East China Sea, Yellow Sea, and the Sea of Japan
FUMT	Department of Fisheries, University Museum, University of Tokyo, Tokyo	32,600	Kuroki M	Started in 1967; specimens mainly collected from seas around Japan; 100 types of specimens
MTUF	Museum of Marine Science, Tokyo University of Marine Science and Technology, Tokyo	30,000	Motegi M	Started in 1968; mainly collected from southern Japan and Boso Peninsula; many larval fish specimens; 140 types of specimens
SPMN	Museum of Natural and Environmental History, Shizuoka	20,000	Shibukawa K	Started in 2003; most specimens collected from Shizuoka Prefecture
MNHAH	Museum of Nature and Human Activities, Santa	13,700	Takahashi T	Started in 1992; most specimens collected from Hyogo Prefecture

reef fishes of the Institute of Oceanic Research and Development, Tokai University (IORD) from the southernmost part of the Ryukyu Islands; the cold-water fishes of the Saito-Ho-on Kai Museum of Natural History (SMNH); the coral reef fishes of the Kochi Senior High School (KSHS); and the tropical freshwater fishes collected in Southeast Asia by Yasuhiko Taki. These combined efforts resulted in rapid growth of the fish collection, which now numbers about 1.5 million cataloged and one million uncataloged specimens. In April 1995, Arai was transferred to the University of Tokyo and replaced by Gento Shinohara.

When the museum celebrated its 130th anniversary in 2007, its name was changed from the National Science Museum to the National Museum of Nature and Science. While research activities and collections of the museum were increasing rapidly, a lack of space became crucial. Because the research part of the museum was located in central Tokyo, there was no space to expand into new buildings. This situation was resolved when the museum began in July 2011 moving everything of the research part from central Tokyo to Tsukuba City (55 km northeast of central Tokyo); it took 8 months to finish this nightmare project. Matsuura retired from the museum in March 2013 and was replaced by Masanori Nakae.

4.3.2 Hokkaido University Museum

The Hokkaido University Museum houses about 250,000 specimens, including 1300 type specimens, representing some 6000 species, collected mainly from the northern part of Japan (e.g., Hokkaido and the Tohoku District of Honshu) and the western North Pacific (e.g., the Okhotsk and Bering seas). Since the early 1980s, the collection has been computerized, and most documentation is now available through a database.

The fish collection was relatively small when it was established in 1958, composed of about 23,000 specimens collected by Kiyu Kobayashi and his students. The collection was housed at the Fisheries Museum located at the Hakodate campus of Hokkaido University. Kobayashi was an active ichthyologist, author of many articles on cold-water fishes (e.g., Kobayashi 1958, 1962), but unfortunately he passed away in December 1969. Two years after his passing, Kunio Amaoka, one of Matsubara's students, arrived at the university and immediately began to develop systematic ichthyology. Together with colleagues and students, Amaoka organized many collecting trips to various regions of Japan. In addition, he obtained large numbers of fishes collected in foreign countries by Japanese research vessels, including expeditions to the Russian Far East Russia, the Kuril Islands, and other areas in the western North Pacific. The size and diversity of the collection increased rapidly, now reaching beyond 250,000 specimens. In 2007, the Fisheries Museum was amalgamated with the Hokkaido University Museum, providing better facilities and increased financial support.

4.3.3 Kyoto University: Maizuru Fisheries Research Station and Kyoto University Museum

More than 400,000 specimens, including 1300 type specimens, representing 4200 species, are housed at the Maizuru Fisheries Research Station, Field Science Education and Research Center (FSERC), and Kyoto University Museum. In 1947, Kiyomatsu Matsubara moved from the Tokyo University of Fisheries to the Faculty of Agriculture of Kyoto University located at Maizuru. He took his fish collection with him and began expanding it. His students went on collecting trips to many regions of Japan to help expand the collection. However, following Matsubara's untimely death in 1968 at the age of 61, the Faculty of Agriculture moved in 1972 to the main campus of Kyoto University in Kyoto, while the fish collection remained at Maizuru. This change of venue created difficulties—because Kyoto is located 60 km south of Maizuru, it was not easy for students and ichthyologists to access the fish collection to conduct daily activities. This led the ichthyological staff and their students to build another fish collection at the main campus. In 2001, the Kyoto University Museum was established for natural history and cultural history. The fish collection at the main campus was transferred to the new Museum where it was provided with better facilities. Therefore, since 2001, there existed two major fish collections at Kyoto University, a larger collection at Maizuru (FSERC) under the care of Izumi Nakamura (1938–2021) and a smaller collection at the Kyoto University Museum under the care of Tetsuji Nakabo (Kai 2015). Since the retirement of Nakabo in 2015, the fish collection of the Kyoto University Museum has been curated by temporal assistants, including Naohide Nakayama (2016–2018), Takashi P. Satoh (2018–2021), and Mao Sato (2021–). On the other hand, at Maizuru, Nakamura retired in 2002 and was replaced in 2004 by Yoshiaki Kai. Since the Kyoto University Museum was established in 2002, the Fish Section of the Museum has been receiving fish collections housed in other institutions of the University: 100,000 specimens collected from southern Japan and housed at the Seto Marine Biological Station, Shirahama (SMBL); 3000 specimens of freshwater fishes collected from Japan, Korea, and Taiwan and housed at the Otsu Hydrobiological Station, Otsu (OHS); and 5000 specimens collected from the Amami Islands and housed at the Misaki Marine Biological Institute, Osaka (MIKU) (Kai 2015).

4.3.4 Kagoshima University Museum

Before Hiroyuki Motomura arrived at Kagoshima in 2005, a fish collection composed of about 10,000 specimens existed in the Faculty of Fisheries of Kagoshima University, which was transferred to the Kagoshima University Museum. Immediately after his arrival, Motomura took charge of ichthyology and collection building at the museum where many students have since been studying fish systematics. Motomura and his colleagues, including ichthyologists of Southeast Asian countries, surveyed shallow-water fishes of Indonesia, Malaysia, Philippines, Thailand, and Vietnam, which resulted in a series of field guides to fishes of Southeast Asia (e.g., Matsunuma et al. 2011; Yoshida et al. 2013; Motomura et al. 2017; Kimura et al. 2018b). Motomura also took a leadership role in organizing field surveys to many islands located in the northern part of the Ryukyu Archipelago where the fish fauna had been poorly studied. Motomura and his collaborators produced a series of identification guides to fishes in this region (e.g., Motomura and Matsuura 2010, 2014; Motomura et al. 2013, 2019; Mochida and Motomura 2018; Nakae et al. 2018; Fujiwara and Motomura 2020; Motomura and Uehara 2020). These activities resulted in a rapid growth of the collection, eventually reaching beyond 250,000 specimens, including 800 type specimens, representing 5525 species.

4.3.5 Kanagawa Prefectural Museum of Natural History

When Hiroshi Senou was made fish curator of the Kanagawa Prefectural Museum of Natural History, the small fish collection that was there at the time was greatly expanded. Under his leadership, numerous collecting trips were made in Sagami Bay and the Ryukyu Islands, with the collaboration of citizen scientists. Their continuous efforts resulted in rapid growth of the collection, which by 2020 reached beyond 108,000 specimens, including 308 type specimens, representing 4453 species. Senou also built a large database of more than 200,000 images of fishes which currently grows at a rate of about 5000 pictures every year, provided by SCUBA divers and members of the general public. About 150,000 images have now been digitized and made available in a computerized database called FishPix (http://fishpix.kahaku.go.jp/fishimage-e/index.html), built under the cooperation of the Kanagawa Prefectural Museum of Natural History and the National Museum of Nature and Science. FishPix has proven to be very helpful to zoogeographical studies of fishes, in particular shallow-water species. By analyzing the huge geographical database of shallow-water fishes provided by FishPix, Senou et al. (2006) and Matsuura (2012) were able to show that the strong warm Kuroshio Current creates an invisible barrier for shallow-water fishes at the Tokara Strait in southern Japan.

4.3.6 Department of Zoology, University Museum, University of Tokyo

In 1904, Shigeho Tanaka, “Father of Ichthyology” in Japan, started building a fish collection at the Faculty of Sciences of the Imperial University of Tokyo (now the University of Tokyo). He and his students searched continuously for opportunities to obtain fishes from various regions in Japan, Korea, and Taiwan. Tanaka’s enthusiasm for collecting resulted in an excellent fish collection, transferred in 1966 from the Faculty of Sciences to the University Museum and now reaching 80,000 specimens, including 300 type specimens. Unfortunately, in the 1980s, the collection languished due to a lack of staff members. In May 2021, however, Keita Koeda, a young ichthyologist, was appointed to take care of the collection.

4.3.7 Faculty of Science and Technology, Kochi University

The fish collection of Kochi University was built by Toshiji Kamohara from 1927 to 1965. Although he studied numerous groups of fishes, his favorites were those from the deep-sea and coral reefs. The location of Kochi University, at Kochi City facing Tosa Bay, with deep water providing habitat for deep-sea fishes, made it easy for Kamohara to make frequent visits Mimase, a fish landing place where bottom trawlers often brought in unusual and new fishes. Kamohara and his students also made numerous collecting trips to the Amami Islands, characterized by richly developed coral reefs, enabling him to build a good collection of reef fishes. However, on July 4, 1945, about a month before World War II ended, Kochi City was seriously damage by an air raid and subsequent fire, which engulfed many areas of the city including Kochi University, destroying Kamohara's research facility and fish collection. However, just after the War, Kamohara persevered to rebuild the fish collection and resume his systematic studies (Kamohara 1964).

In 1965, Kamohara retired from Kochi University and was replaced by Osamu Okamura who participated in many cruises aboard research vessels. These activities provided numerous opportunities to obtain interesting deep-sea fishes from the seas around Southeast Asian countries. Okamura also conducted studies of the fishes of the Okinawa Trough (Okamura and Kitajima 1984; Okamura 1985) and the Kyushu-Palau Ridge. Before Okamura retired in 1996 and was replaced by Hiromitsu Endo, two ichthyologists, Yoshihiko Machida and Kunio Sasaki, joined Okamura's laboratory in 1978 and 1989, respectively. Kamohara's tradition of collecting and studying fishes has been kept by all his successors. Their continuous efforts have resulted in 150,000 specimens, including 1400 type specimens, representing 4000 species.

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Part II

Habitat Distribution and Species Diversity

Fish Diversity Along the Kuroshio Current

5

Hiroyuki Motomura and Mizuki Matsunuma

Abstract

The present-day fish diversity and ichthyofauna of southern Japan, including the Izu, Ogasawara, and Nansei islands, have become established mainly due to the physical characteristics of the Kuroshio Current and associated currents. The Kuroshio Current plays dispersal and vicariance roles in the distribution of fishes in southern Japan, and the close interplay between the current and various life history and biological features of each species has created a complex ichthyofauna. Recent comprehensive ichthyofaunal surveys have revealed that the ichthyofauna of southern Japan is divided into two major groups, the boundary between them being between Yakushima Island and "Tanegashima, Iwo-jima, and Take-shima islands" in the Osumi Islands (called the Osumi Line), although such a boundary was previously thought to be located in the Tokara Islands. In this chapter, the relationship between the Kuroshio Current and ichthyofauna is reviewed, and the division of such fauna by the Osumi Line outlined. In addition, the unique ichthyofauna of Yakushima Island is introduced.

Keywords

Ichthyofauna · Dispersal · Vicariance · Southern Japan · Ogasawara Islands · Ryukyu Islands · Osumi Islands · Yaku-shima Island

5.1 Physical Characteristics

The Kuroshio Current, a strong warm water current of ~100 km width and flow rate >1 m/s, originates from the North Equatorial Current and continues from east of the Philippines to the Pacific coast of southern Japan, via Taiwan and west of the Ryukyu Islands (Fig. 5.1). The northward flowing current west of the Ryukyu Islands then turns eastward to flow past the Tokara Islands, located between the Osumi and Amami islands (e.g., Lee et al. 2001; Figs. 5.1 and 5.2), before resuming its northward path toward the Pacific coasts of the islands of Kyushu, Shikoku, and Honshu (the main island of Japan) (e.g., Kamachi et al. 2004; Fig. 5.1). Part of the Kuroshio Current, a warm water mass west of Kyushu becomes the Tsushima Current, which flows into the Sea of Japan through the Tsushima Strait, located between the southern Korean Peninsula and northern Kyushu (e.g., Qiu 2001; Fig. 5.1).

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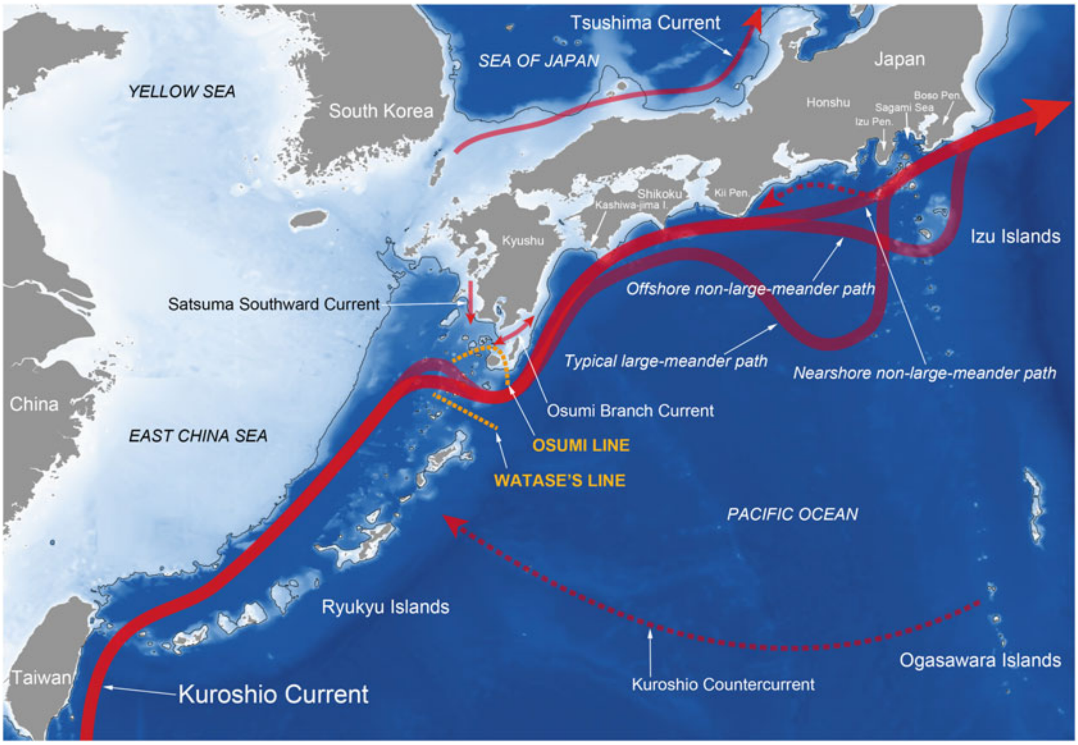

Fig. 5.1 Map of southern Japan, showing the Kuroshio Current with associated currents and biogeographical boundaries. *Dotted red* and *orange lines* indicate countercurrents and biogeographical boundaries, respectively

The water mass, speed, and flow path of the Kuroshio Current frequently change, on a daily, monthly, or yearly basis. Two main flow paths of the current exist through the Tokara Islands (12 small islands extending in a row ~160 km north to south in the Ryukyu Islands); the more southerly route takes the current across the island chain from west to east around Nakano-shima Island; and the other, more northerly route flows along the southern coast of Yaku-shima Island (Fig. 5.1). The current alternates between the two flow paths on a 30- to 50-day cycle (Chaen and Ichikawa 2001). Changes in the flow path influence other minor water currents in the area, especially the Osumi Branch Current flowing between Yaku-shima Island and the southern tip of Osumi Peninsula (Fig. 5.1). During the period when the Kuroshio Current flows around Yaku-shima Island, the Osumi Branch Current flows northeastward from Yaku-shima Island to the Osumi Peninsula, but when the Kuroshio Current takes its more southerly route, the direction of the Osumi Branch Current is irregularly reversed to the southwest (Chaen and Ichikawa 2001; Fig. 5.1). The minor water currents associated with the Kuroshio Current are complex, their flow rates and directions changing with season, water temperature, and wind characteristics (Nakamura 2017). These factors have produced a unique ichthyofauna off each island, especially the Osumi Islands north of the northern extremity of the Ryukyu Islands (Motomura and Matsuura 2010; Fig. 5.2).

The lower reach of the Kuroshio Current in the vicinity of the Pacific coast of Honshu follows three major irregularly changing flow paths (Fig. 5.1). The current usually flows northeastward along the Pacific coast of Shikoku and central Honshu, following the nearshore non-large-meander path (Yoshida et al. 2006;

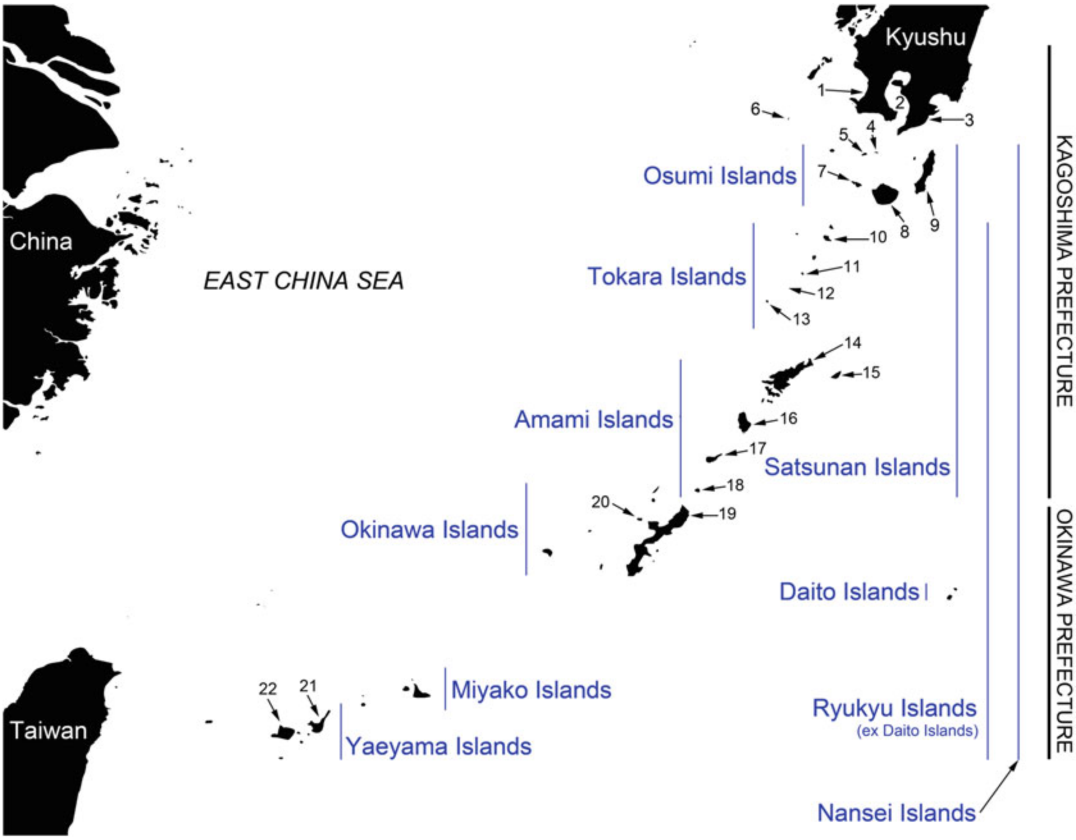

Fig. 5.2 Map of southern Kyushu and the Nansei Islands, showing names of islands and places appearing in the text. The Ryukyu Islands sometimes includes the Osumi Islands, but this is not followed in this chapter. The Daito Islands are included in the Nansei Islands, but excluded from the Ryukyu Islands. 1, Satsuma Peninsula; 2, Kagoshima Bay; 3, Osumi Peninsula; 4, Take-shima Island; 5, Iwo-jima Island; 6, Uji Islands; 7, Kuchinoerabu-jima Island; 8, Yaku-shima Island; 9, Tanegashima Island; 10, Nakano-shima Island; 11, Akuseki-jima Island; 12, Tokara Strait; 13, Takara-jima Island; 14, Amami-oshima Island; 15, Kikai-jima Island; 16, Tokunoshima Island; 17, Okinoerabu-jima Island; 18, Yoron-jima Island; 19, Okinawa-jima Island; 20, Ie-jima Island; 21, Ishigaki-jima Island; 22, Iriomote-jima Island

Fig. 5.1). However, it sometimes turns southward ~200 km south of the Kii Peninsula (southern current margin extending south to the latitude of the southern tip of Kyushu; Fujimoto and Tomosada 1980) before returning to a northward heading, flowing through the northern Izu Islands (the typical large-meander path; Fig. 5.1). The third path, the offshore non-large-meander path, generally follows a similar path to the nearshore non-large-meander path, but south of the Izu Islands (Fig. 5.1). The typical large-meander path sometimes continues for several years at a time.

In the past, the Kuroshio Current has been considered as biologically unproductive because of its oligotrophic conditions and low plankton standing stocks (Kobari et al. 2020), despite an abundance of migratory fishes. This apparent paradox has recently been partly resolved by Kobari et al. (2020), who showed that phytoplankton growth and consumption by microzooplankton are stimulated by a turbulent nitrate flux amplified by the Kuroshio Current, with significant rapid grazing on phytoplankton by microzooplankton. The latter are probably also rapidly consumed by larger zooplankton and fishes, the overall result being a balance between production and consumption. Thus, the Kuroshio Current should not be considered an ocean "desert" (oligotrophic with low plankton content) (Kobari et al. 2020).

5.2 Fish Dispersal by the Kuroshio Current

Many fishes at various life stages, including egg, larval, juvenile, young, and adult, are transported by the Kuroshio Current from the northern Philippines and eastern Taiwan to Japanese waters. Schools of tropical migratory fishes with high swimming ability have often arrived in southern Kyushu and along the Pacific coast of Honshu, usually in autumn from Taiwan and/or the Philippines, to be fished by set (fixed) nets established along the Kuroshio Current path. Such fishes include several carangids, such as *Atule mate* (reported by Ito et al. 2007; Fig. 5.3a), *Carangoides gymnostethus* (by Okamoto et al. 2019), *Caranx heberi* (by Motomura et al. 2007c), *Caranx tille* (by Kita 2007), and *Ulua mentalis* (by Motomura et al. 2007c). In some cases observed off southern Kyushu, adults of small-sized species (e.g., *A. mate* and *Sardinella aurita*; Fig. 5.3a,b) and young of large-sized species (e.g., *C. heberi* and *U. mentalis*) are usually transported as schools, although others, such as the clupeids *Amblygaster sirm* (Fig. 5.3c) and *Sardinella melanura* (Fig. 5.3d), have usually been observed singly in large set net hauls (or in schools primarily comprising a different species) (Hata et al. 2013, 2017b), although the former form single species schools in tropical waters. It is likely that such individuals become separated from their original schools early on in the Kuroshio Current and join other schools indiscriminately during transportation. Large individuals of large-sized tropical species have always been caught singly off the Japanese mainland: e.g., *Scomberoides commersonnianus* (four specimens recorded to date from the Japanese mainland, collected in December 1996, June 1997, December 2017, and March 2019; Motomura et al. 1998; Wada et al. 2019a; Matsunuma et al. 2019; Fig. 5.4a), *Trachinotus anak* (one specimen each in November 2018 and December 2019; Wada et al. 2019b; Ito 2020; Fig. 5.4b), *Eleutheronema rhadinum* (one specimen each in August 1999 and October 2006; Motomura et al. 2001, 2007b; Fig. 5.4c), and *Bolbometopon muricatum*

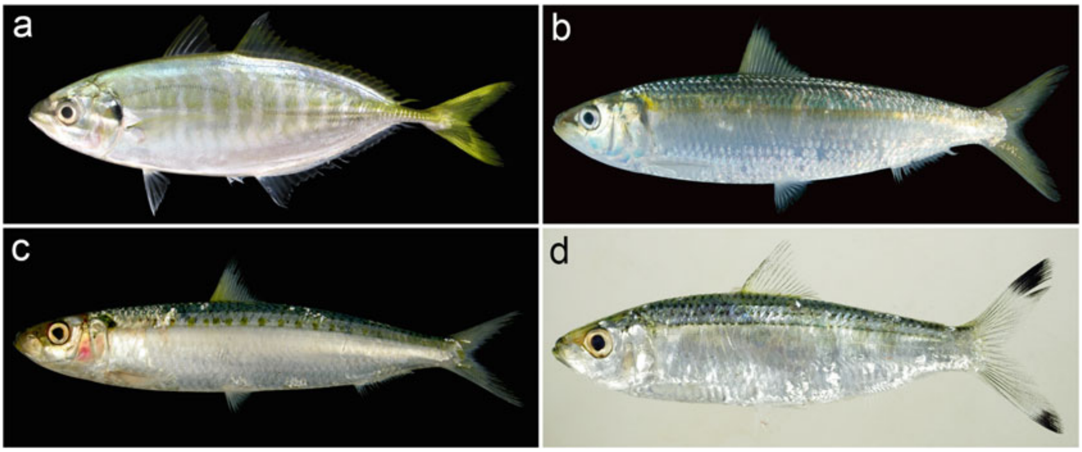

Fig. 5.3 Small-sized adult fishes (generally forming schools in tropical areas) occurring off southern Kyushu in a single-species school (**a**, **b**) and sole representatives in a different species school (**c**, **d**). (**a**) *Atule mate* (Kagoshima University Museum—Ichthyology, KAUM–I. 973, 156 mm standard length, SL); (**b**) *Sardinella aurita* (KAUM–I. 12684, 160 mm SL); (**c**) *Amblygaster sirm* (KAUM–I. 46904, 160 mm SL); (**d**) *Sardinella melanura* (KAUM–I. 123862, 75 mm SL)

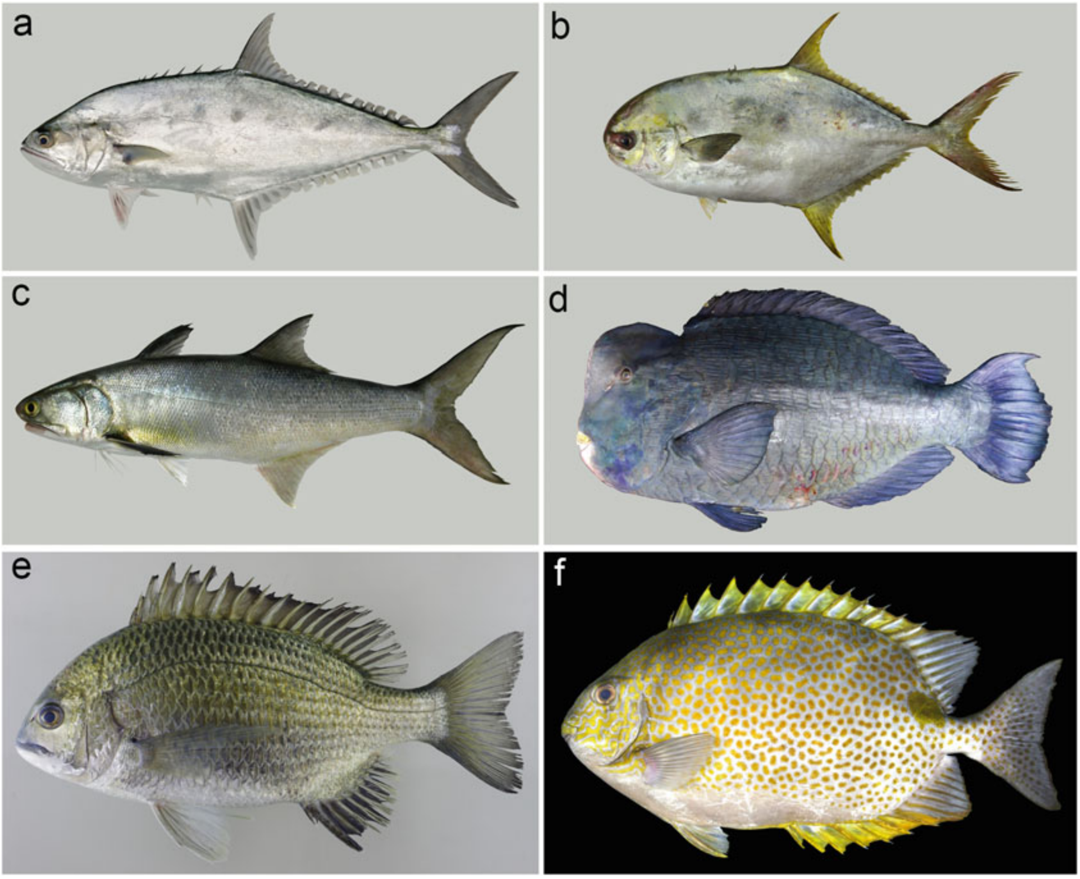

Fig. 5.4 Large- and medium-sized fishes occurring off southern Kyushu (adult stage transported by the Kuroshio Current). (**a**) *Scomberoides commersonnianus* (KAUM–I. 128805, 534 mm standard length, SL); (**b**) *Trachinotus anak* (KAUM–I. 123272, 748 mm SL); (**c**) *Eleutheronema rhadinum* (KAUM–I. 956, 420 mm SL); (**d**) *Bolbometopon muricatum* (KAUM–I. 25448, 953 mm SL); (**e**) *Acanthopagrus taiwanensis* (KAUM–I. 96697, 254 mm SL); (**f**) *Siganus guttatus* (KAUM–I. 34038, 336 mm SL)

(a single specimen in December 2009; Ogihara et al. 2010; Fig. 5.4d). Other medium-sized tropical species caught singly off the Japanese mainland include the nemipterid *Nemipterus japonicus* (January 2020; Nakamura and Motomura 2021), sparid *Acanthopagrus taiwanensis* (in December 2016; Fujiwara et al. 2017; Fig. 5.4e), drepaneid *Drepane punctata* (November 2011; Uejo et al. 2015), siganid *Siganus guttatus* (collected in November 2010; Itou et al. 2011; Fig. 5.4f), and acanthurid *Naso mcdadei* (in November 2009, November 2011; Senou et al. 2013). Most of the above individuals were caught during the autumn and early winter seasons due to the flow rate of the Kuroshio Current greatly increasing in summer in the East China Sea and off eastern Taiwan (Ichikawa and Beardsley 1993; Gilson and Roemmich 2002; Hsin et al. 2013); fishes are therefore most likely to arrive off the Japanese mainland in autumn, together with the current water mass that departed Taiwan the previous summer. This argument is supported by the above-mentioned species (except *B. muricatum* and *S. guttatus*) having been at no time recorded from the Ryukyu Islands well east of the Kuroshio Current, despite being abundant in Taiwanese waters. The single specimens of *B. muricatum* and *S. guttatus* collected off the

Japanese mainland are also considered to have been transported by the Kuroshio Current (Ogihara et al. 2010; Itou et al. 2011), there being no coral reefs (essential for *B. muricatum*) or mangrove areas (essential for juvenile *S. guttatus*) at the collection sites (Motomura 2019).

Juveniles of tropical and coral reef associated fishes, especially members of the families Chaetodontidae and Pomacentridae, can be observed along the Pacific coastal area of central Honshu in the autumn, only in years when the Kuroshio Current flows along the nearshore path. Some juveniles occur along the Pacific coast of Honshu between Shizuoka and Mie prefectures due to a counter current flowing east–west when the Kuroshio Current follows the offshore meander path (Fig. 5.1). Such fishes disappear during the winter season since sea water temperatures off Honshu become too low for tropical fishes to survive. Although some species, e.g., *Chaetodon auripes* (Chaetodontidae) and *Priacanthus hamrur* (Priacanthidae) (Fig. 5.5a), are known to survive over winter and subsequently develop, and are abundant off the Pacific coast of Honshu, sexually mature individuals have never been collected (or observed spawning) in that area. In their review of Japanese distributional records of *Epinephelus amblycephalus* (Epinephelidae) (Fig. 5.5b), Motomura et al. (2007a) concluded that individuals of the species found off the Japanese mainland had been transported from Taiwan or China by the Kuroshio Current when at the egg or larval stages, and could over-winter and attain adult size in Japan, but were unlikely to reproduce there. The above-mentioned species transported by the Kuroshio Current to waters off the Japanese mainland can all be said to represent "unsuccessful dispersal," due to their unlikelihood of reproducing.

On the other hand, *Pentapodus aureofasciatus* (Nemipteridae) and *Pomadasys quadrilineatusare* (Haemulidae) (Fig. 5.6a–e) are abundant in the Osumi Islands (just north of the Ryukyu Islands; Fig. 5.2) where both species have established their largest colonies in Japanese waters (Motomura and Harazaki 2007; Matsunuma et al. 2009; Motomura 2012, 2015). The forerunners of these populations probably originated in Taiwanese waters, rather than the Ryukyu Islands, and were transported by the Kuroshio Current. *Pentapodus aureofasciatus* at the Osumi Islands (Fig. 5.6a–c) is morphologically closer to a population off Taiwan than Ryukyu Islands specimens (Motomura 2012), and *P. quadrilineatusare* (Fig. 5.6d, e) is common in Taiwan, but has never been recorded from the Ryukyu Islands (Matsunuma et al. 2009; Motomura 2012, 2015). *Paramonacanthus pusillus* (Monacanthidae) (Fig. 5.6f) is common off Taiwan and in Kagoshima Bay (southern Kyushu), with a few sporadic records from the Pacific coast of Honshu, but has never been recorded from the Ryukyu Islands. In Kagoshima Bay, spawning behavior of the species has been observed by local divers, and several specimens with mature ovaries have been collected (Motomura 2012). The Kagoshima Bay

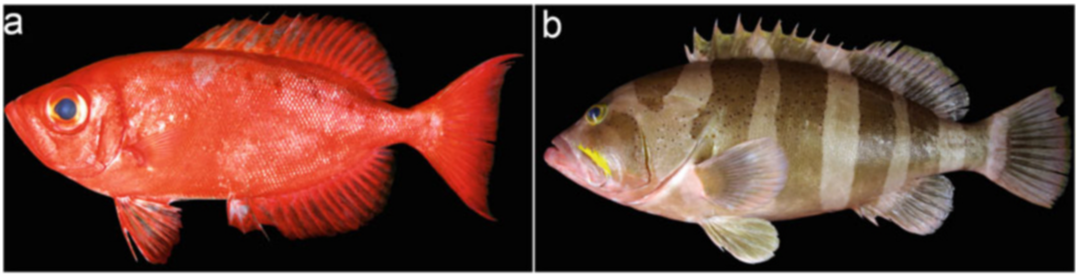

Fig. 5.5 Fishes transported (possibly at egg or juvenile stages) by the Kuroshio Current to the Japanese mainland, thereafter resident off the Pacific coast of Japan. (**a**) *Priacanthus hamrur* (KAUM–I. 21946, 261 mm standard length, SL); (**b**) *Epinephelus amblycephalus* (KAUM–I. 52298, 538 mm SL)

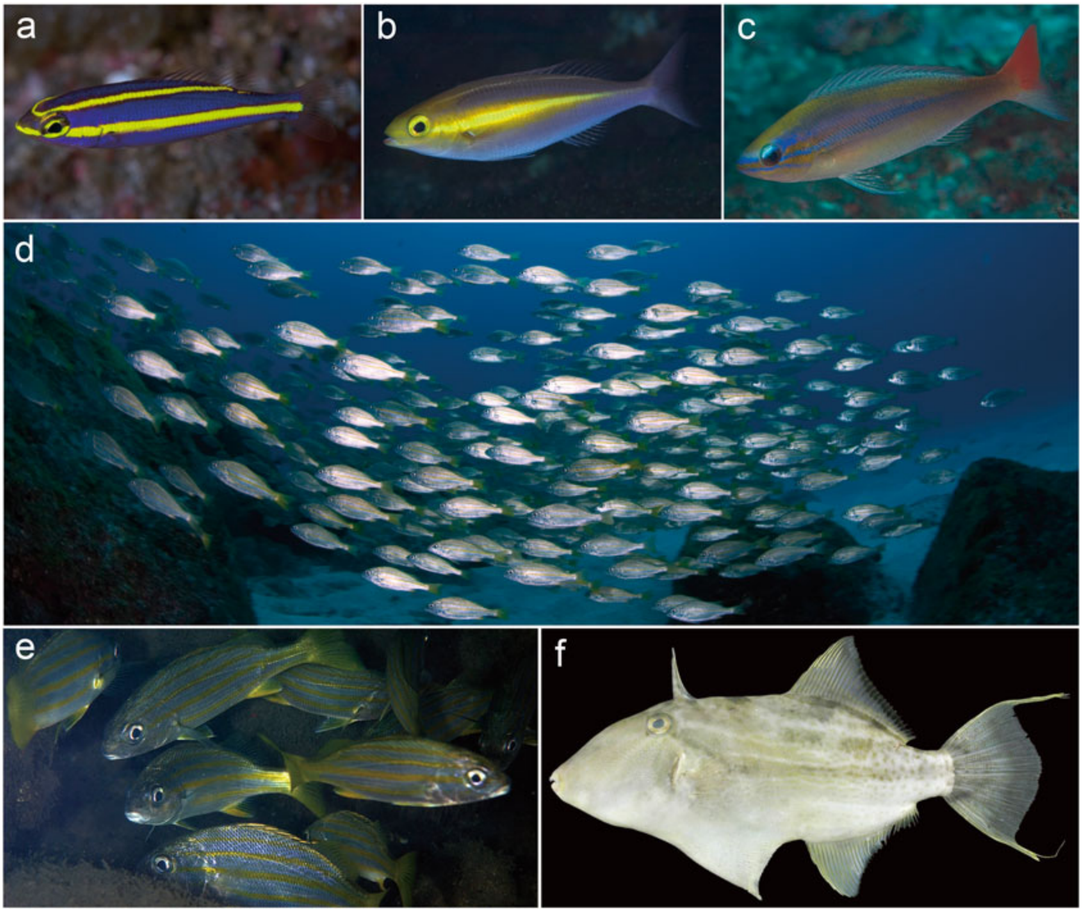

Fig. 5.6 Fishes (originally from Taiwan) transported by the Kuroshio Current and now in established populations in Japan. (**a**–**c**) *Pentapodus aureofasciatus* off Yaku-shima Island, photos by S. Harazaki (**a** juvenile, **b** female, **c** nuptial colored male); (**d**–**e**) *Pomadasys quadrilineatusare* off Yaku-shima Island, photos by S. Harazaki; (**f**) *Paramonacanthus pusillus* (KAUM–I. 1081, 154 mm standard length, Kagoshima Bay)

population is also considered to have originated in Taiwan, and the few records from the Pacific coast of Honshu (Kanagawa, Shizuoka, Mie and Kochi prefectures) have followed dispersal via the Kuroshio Current from Kagoshima Bay or directly from Taiwan (Motomura 2012). Similarly, *Navigobius dewa* (Ptereleotridae) has been reported as occurring in large schools of several hundred individuals each in Kagoshima Bay. Eggs and/or larvae of that species are also likely to have been transported to the Pacific coast of southern Japan by the Kuroshio Current (some records also from Izu Peninsula) (Dewa et al. 2010).

A single individual of the amphidromous goby *Stiphodon surrufus*, distributed from the Philippines to Australia, was collected from a hot spring river on southern Yaku-shima Island in the Osumi Islands (Yonezawa and Iwata 2001). Although there have been no investigations of the biology of this species, the closely related species *Sicyopterus japonicus* is known to spawn in rivers, migrate to the sea during the larval stage, and then return to rivers (Watanabe et al. 2006). This suggests that the Yaku-shima *S. surrufus* individual was transported from the Philippines by the Kuroshio Current during the larval stage, subsequently entering the Yaku-shima Island river where it matured and was eventually collected. Such a fortuitous event suggests that numerous fish larvae may be transported by the Kuroshio Current from the northern Philippines (more than previously thought).

The above examples have emphasized the role of the Kuroshio Current in transporting fishes to the Japanese mainland, most likely from Taiwan (and/or coastal mainland China) and the northern Philippines, bypassing the Ryukyu Islands, which lie well to the east of the main stream of the current. Such transported fishes generally do not occur at the Ryukyu Islands.

5.3 Vicariance Due to the Kuroshio Current

Not only does the Kuroshio Current contribute to the dispersal of fishes from Taiwan and/or the northern Philippines to the Japanese mainland, but also it works as a barrier to the movement of fishes from the Japanese mainland to the Ryukyu Islands. The latter are bordered by the broad and fast flowing Kuroshio Current on three sides (north, west, and south; Fig. 5.1), which largely inhibits the movement of fishes from the Japanese mainland, mainland China, and Taiwan toward the Ryukyu Islands. This has resulted in the ichthyofauna of southern Japan being divided into two major faunal groups (Senou et al. 2006; Motomura et al. 2010; Motomura 2015; Motomura and Suzuki 2019), such that many fishes are distributed only off the Japanese mainland or at the Ryukyu Islands. Pairs of sibling species in southern Japan may be similarly restricted, one species [e.g., *Ostracion immaculatum* (Ostraciidae)] occurring mainly off mainland Japan, the other (*Ostracion cubicum*) at the Ryukyu Islands (Fig. 5.7). Many such pairs, including *Acanthopagrus schlegelii* (mainland) and *Acanthopagrus sivicolus* (Ryukyu Islands) (Sparidae), *Gerres equulus* (mainland) and *Gerres oyena* (Ryukyu Islands) (Gerreidae), and *Tridentiger obscurus* (mainland) and *Tridentiger kuroiwae* (Ryukyu Islands) (Gobiidae) are known to occur allopatrically off the Japanese mainland and the Ryukyu Islands (Fig. 5.7). In addition to the examples stated above, Kuriiwa et al. (2014) showed a similar example by their mtDNA analyses of population structure of Blacktip Grouper, *Epinephelus*

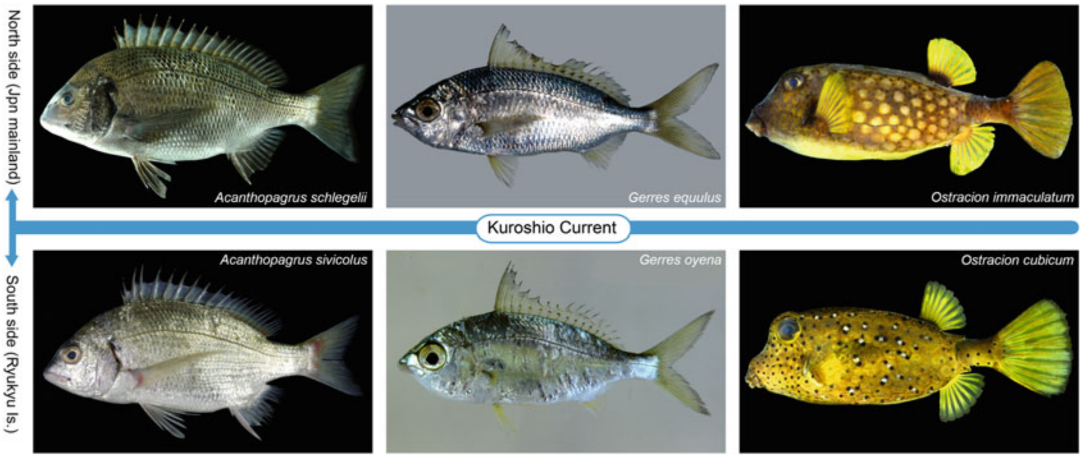

Fig. 5.7 Pairs of sister species occurring allopatrically to the north (*upper photos*: Japanese mainland) and south (*lower photos*: Ryukyu Islands) of the Kuroshio Current. *Left row*: *Acanthopagrus schlegelii* (KAUM–I. 86396, 290 mm standard length, SL) and *Acanthopagrus sivicolus* (KAUM–I. 55323, 181 mm SL); *middle row*: *Gerres equulus* (KAUM–I. 5508, 144 mm SL) and *Gerres oyena* (KAUM–I. 12208, 103 mm SL); *right row*: *Ostracion immaculatum* (KAUM–I. 29735, 143 mm SL) and *Ostracion cubicum* (KAUM–I. 39775, 73 mm SL)

fasciatus: the population of mainland Japan was clearly differentiated from that of the Ryukyu Islands.

Whereas larvae and juveniles of Ryukyu Islands species (one of a sibling pair) have often been recorded from the Japanese mainland, likely having been fortuitously transported by the Kuroshio Current, those of the Japanese mainland sibling species have been rarely found in the Ryukyu Islands. A single and two individuals of the mainland species *O. immaculatum* were recorded from the Amami Islands (Amami-oshima in 2016 and Okinoerabu-jima islands in 2018, respectively; Nakae et al. 2018; Motomura and Uehara 2020). *Parablennius yatabei* (Blenniidae) and *Scarus ovifrons* (Scaridae), distributed primarily off the Japanese mainland and Taiwan, have also been recorded from Amami-oshima Island (Motomura et al. 2019; Motomura and Suzuki 2019). The individuals found at the Amami Islands were likely to have been accidentally transported by branch currents derived from the Kuroshio Current, as no evidence exists to support their being part of a reproducing population at the islands.

The southernmost and northernmost limits, respectively, of the amphidromous fishes *Plecoglossus altivelis altivelis* and *Plecoglossus altivelis ryukyuensis* are Yaku-shima and Amami-oshima islands, the two subspecies being separated by the Kuroshio Current (see Fig. 5.1). Larvae and juveniles of *P. a. ryukyuensis*, usually inhabiting estuaries and inshore waters, may be sometimes transported northwards by the Kuroshio Current and associated streams, but their highest survival rates occur in water temperatures and salinity of 15–18 °C and 5–15 psu, respectively (Kishino et al. 2008). Thus, they are unlikely to survive in Kuroshio Current water temperatures (21–28 °C) and salinity (about 35 psu). On the other hand, *P. a. altivelis* cannot disperse to the south due to the Kuroshio barrier, all these factors preserving the current disjunct distribution of the two subspecies.

Although *Chaetodon daedalma* and *Hemitaurichthys thompsoni* (both Chaetodontidae) (Fig. 5.8) are distributed primarily at the Ogasawara Islands, they have been recorded on rare instances from the Amami and Daito islands (Nakae et al. 2018; Fujiwara and Motomura 2020), having been transported from the Ogasawara Islands by several irregular weak water currents (sometimes called the Kuroshio Countercurrent) (Fig. 5.1). However, other species endemic to the Ogasawara Islands, such as *Alticus orientalis* (Blenniidae) and *Scarus obishime* (Scaridae), have at no time been recorded from the Ryukyu or Daito islands (e.g., Fujiwara et al. 2021). Due to the weak water

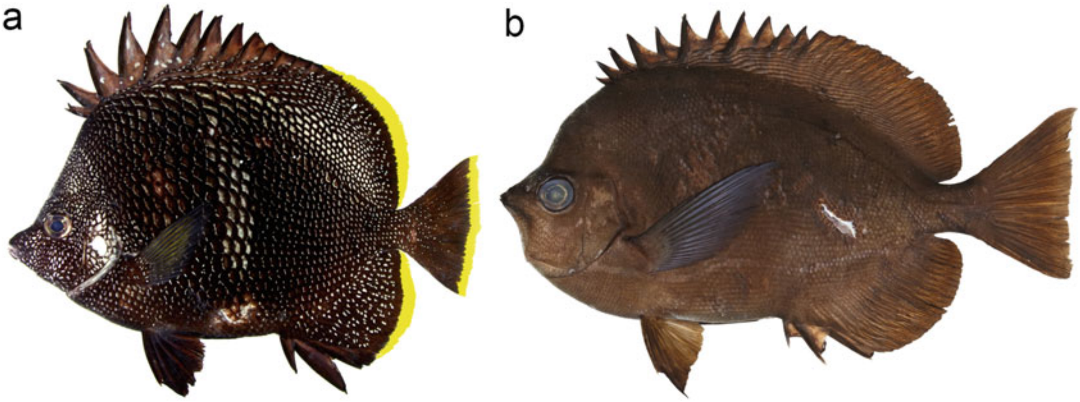

Fig. 5.8 Fishes endemic to the Ogasawara Islands but rarely recorded from the Ryukyu and Daito islands. (**a**) *Chaetodon daedalma* (KAUM–I. 62761, 121 mm standard length, SL); (**b**) *Hemitaurichthys thompsoni* (KAUM–I. 63486, 165 mm SL)

currents and lack of intermediate islands between the Ogasawara and Daito islands, it is likely that only fishes with a relatively long pelagic egg and larval stage can be transported to the Daito and Ryukyu islands from the Ogasawara Islands.

5.4 Southern Japan Ichthyofaunal Boundary

A major biogeographical boundary (Watase's Line) in southern Japan (Fig. 5.1), located in the Tokara Strait between Akuseki-jima and Takara-jima islands in the Tokara Islands, northern Ryukyu Islands (Fig. 5.1), constitutes a faunal boundary for terrestrial vertebrates (mammals, reptiles, and amphibians), the northern and southern sides of the line being categorized as the Palaearctic and Oriental regions, respectively. Approximately 1000 m in depth, the Tokara Strait has been unconnected by land since ca. 1.5 Mya BP, whereas most of the Ryukyu Islands were connected to the Chinese mainland during the last ice age.

The marine fish fauna of southern Japan has also long been considered to be separated by Watase's Line, since the Tokara Strait is the major pathway of the Kuroshio Current (Senou et al. 2006). Senou et al. (2006) compared the fish faunas at 12 sites [the Ogasawara Islands, Sagami Sea (Sagami Bay plus Izu-oshima Island), Osezaki (west coast of Izu Peninsula, Suruga Bay), Hachijo-jima Island (Izu Islands), Kushimoto (Kii Peninsula), Kashiwa-jima Island (Kochi), Yaku-shima Island (Osumi Islands), Okinawa-jima and Ie-jima islands (Okinawa Islands), the Miyako Islands, and Ishigaki-jima and Iriomote-jima islands (Yaeyama Islands)] (see Figs. 5.1 and 5.2), their cluster analyses (Senou et al. 2006: fig. 11) indicating two distinct biogeographical regions in Japanese waters, separated by the Tokara Strait: seven Japanese mainland and associated island sites, including the Sagami Sea, the Izu and Ogasawara islands, and Yaku-shima Island; and five Ryukyu Islands sites (the Okinawa, Miyako, and Yaeyama islands). The former region was subdivided into the Ogasawara Islands and the remaining six sites.

However, recent comprehensive ichthyofaunal surveys off southern Kyushu and each island of the Satsunan Islands, primarily led by the Kagoshima University Museum research team (i.e., northwestern Kagoshima mainland: Motomura et al. 2020; southern Satsuma Peninsula: Iwatsubo et al. 2016; Kagoshima Bay: Iwatsubo and Motomura 2017; eastern Osumi Peninsula: Koeda et al. 2018, 2020; Iwo-jima and Take-shima islands: Motomura et al. 2013; Kuchinoerabu-jima Island: Kimura et al. 2017; Yaku-shima Island: Motomura and Matsuura 2010; Motomura and Aizawa 2011; Motomura 2017; Motomura and Harazaki 2017, 2019; Tanegashima Island: Kaburagi 2016; Uji Islands: Motomura et al. 2016; Tokara Islands: Motomura 2020; Amami-oshima Island: Nakae et al. 2018; Akaike et al. 2021; Kikai-jima Island: Fujiwara and Motomura 2020; Tokunoshima Island: Mochida and Motomura 2018; Wada et al. 2021; Okinoerabu-jima Island: Motomura and Uehara 2020; Fujiwara et al. 2020; Yoron-jima Island: Motomura and Matsuura 2014; Motomura 2016; Amami Islands: Motomura et al. 2018, 2019), and resulting in more than 700 faunal reports since 2006, indicated that a major biogeographical boundary for marine fishes in southern Japan was, in fact, located in the Osumi Islands (not Tokara Islands) between Yaku-shima and Tanegashima islands (Motomura et al. 2010; Motomura 2015, 2017; Motomura and Harazaki 2017; Motomura and Suzuki 2019) (see names of places in Fig. 5.2). This boundary has been termed the Osumi Line sensu Motomura and Harazaki (2017: 182, fig. 1).

Because Senou et al.'s (2006) analysis incorporated only 567 species from Yaku-shima Island (1291 species currently recorded; Motomura and Harazaki 2019), their cluster analysis was misleading with regard to the position of Yaku-shima Island, and similarities between the fish faunas of Yaku-shima Island and the Ryukyu Islands were probably underestimated. Subsequently, Motomura et al. (2010) and Motomura (2012) suggested that the fish fauna of Yaku-shima Island was more similar to that of the

Ryukyu Islands, rather than off the Pacific coast of Japan, based on an analysis of the top eight most speciose families of fishes in the Sagami Sea, Yaku-shima Island, Ie-jima Island, and the Miyako Islands. In fact, the top eight families occurring at Yaku-shima and Ie-jima islands had identical ranking (first to last: Gobiidae, Labridae, Pomacentridae, Apogonidae, Serranidae, Blenniidae, Chaetodontidae, and Acanthuridae), and the percentages of the total fish fauna that those families represented were similar (48.5% at Yaku-shima Island vs. 53.6% at Ie-jima Island) (Motomura et al. 2010). An updated cluster analysis of fishes from the 12 sites considered by Senou et al. (2006) also placed Yaku-shima Island in the Ryukyu Islands clade (Matsuura and Senou 2012: fig. 1.5). The number of species in the top 10 most speciose families occurring in depths of less than 50 m at the 12 sites and Yoron-jima Island was summarized by Motomura (2016: tables 1, 2).

A recent fine scale analysis (Motomura, unpub. data), based on comprehensive ichthyofaunal surveys in the Ryukyu and Osumi islands, revealed a major biogeographical boundary for southern Japanese marine fishes (Osumi Line) located between Yaku-shima and "Tanegashima, Iwo-jima and Take-shima islands" (Figs. 5.1 and 5.9), although the distance separating Yaku-shima and Tanegashima islands is only about 20 km. The similarity between the fish faunas of Yaku-shima Island and the Ryukyu Islands is most likely due to the transportation of tropical fishes from Taiwan, China, and/or the Philippines to Yaku-shima Island by the Kuroshio Current (Motomura et al. 2010; Motomura 2012). Such transported fishes (including egg stages) are easily projected northward toward Yaku-shima Island by the redirection of the Kuroshio Current from northward to eastward (Senou and Motomura unpub. data; Motomura 2015; Fig. 5.1). In contrast, fewer opportunities exist

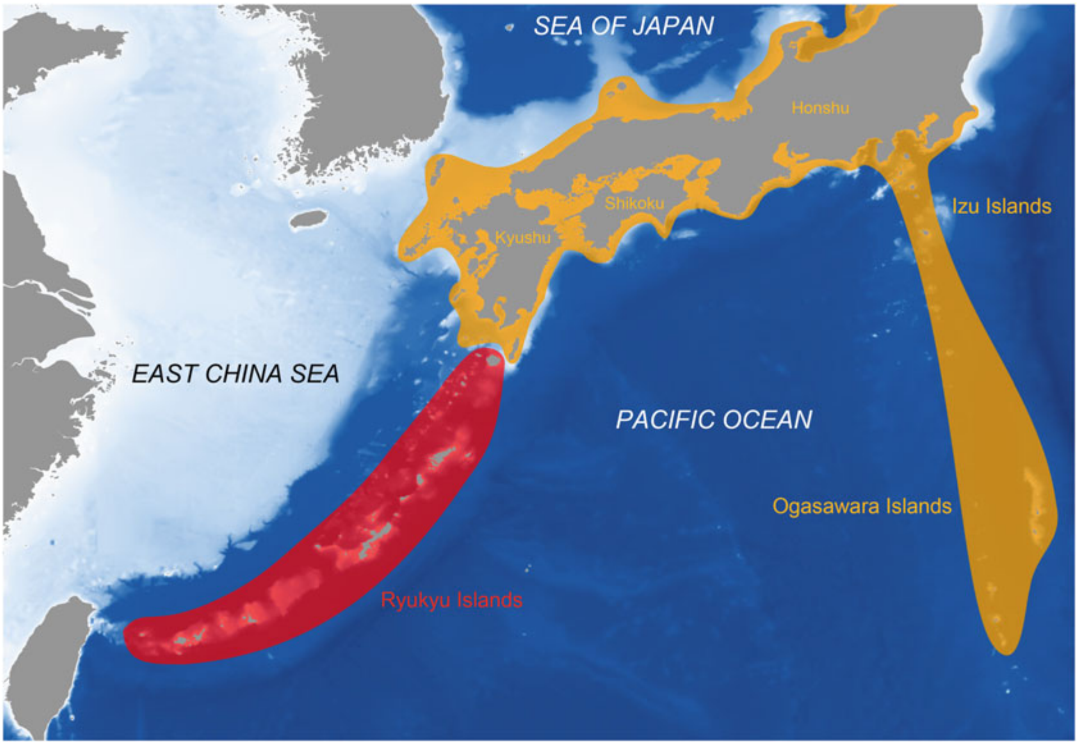

Fig. 5.9 Map of southern Japan, showing two major fish faunas. Boundary located in the Osumi Islands between Yaku-shima Island and "Tanegashima, Take-shima and Iwo-jima islands" (also see Figs. 5.1 and 5.2)

for transported fishes to arrive off Tanegashima Island since the latter is located inside the bend where the Kuroshio Current turns from eastward to northward, such fishes being more likely to be projected eastward into the Pacific Ocean (Fig. 5.1).

Tanegashima Island is the southernmost distribution limit for many temperate marine fishes, such as *Hemitrygon akajei* (Dasyatidae), *Scorpaenopsis cirrosa* (Scorpaenidae), *Pagrus major* (Sparidae), *Halichoeres tenuispinis* (Labridae), *Acanthogobius flavimanus* (Gobiidae), and *Paralichthys olivaceus* (Paralichthyidae) (Motomura 2015; Fig. 5.10), which also supports the existence of a distinct biogeographical boundary between Yaku-shima and Tanegashima islands. The fish fauna of Tanegashima Island is very similar to that of southern Kyushu, as revealed by the ongoing ichthyofaunal surveys. In fact, fishes of southern Kyushu may be transported to Tanegashima Island by the Osumi Branch Current, which occurs irregularly between Osumi Peninsula and the Osumi Islands. A further consideration, since Osumi Peninsula and Tanegashima Island were connected by land until ca. 130,000 years BP (Ôki 2000), is that some temperate fishes found at Tanegashima Island

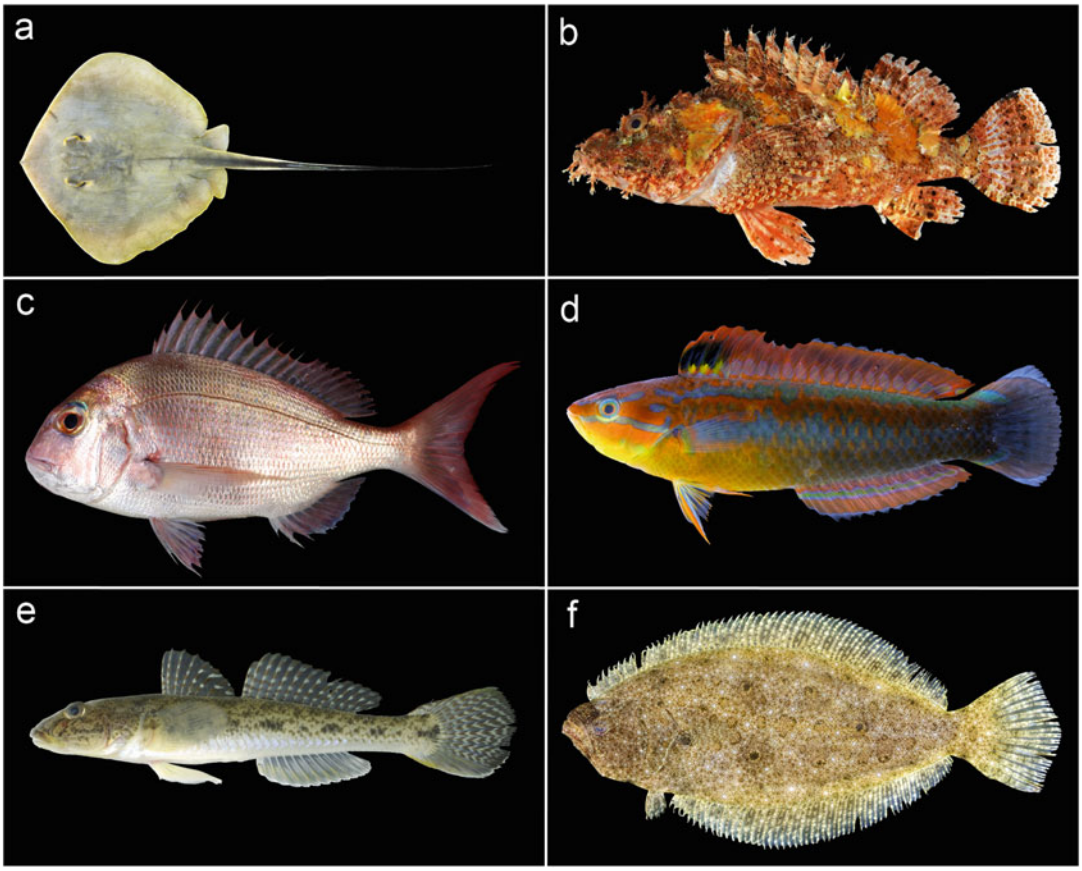

Fig. 5.10 Fishes commonly distributed off the Japanese mainland and Tanegashima Island but not occurring at Yaku-shima Island. (**a**) *Hemitrygon akajei* (KAUM–I. 95640, 299 mm total length); (**b**) *Scorpaenopsis cirrosa* (KAUM–I. 70133, 208 mm standard length, SL); (**c**) *Pagrus major* (KAUM–I. 124446, 242 mm SL); (**d**) *Halichoeres tenuispinis* (KAUM–I. 10759, 76 mm SL); (**e**) *Acanthogobius flavimanus* (KAUM–I. 75486, 89 mm SL); (**f**) *Paralichthys olivaceus* (KAUM–I. 131617, 128 mm SL)

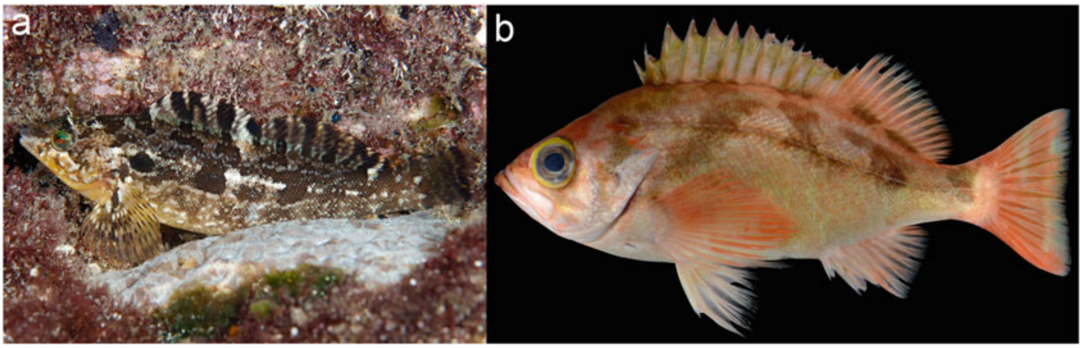

Fig. 5.11 Temperate fishes of Yaku-shima Island, possibly transported from the west coast of Kyushu by an unrecorded branch of the Satsuma Southward Current. (**a**) *Hexagrammos agrammus* (taken off northern Yaku-shima Island, ~5 m depth, 16 Apr. 2012, photo by I. Takaku); (**b**) *Sebastes thompsoni* (KAUM–I. 71407, 223 mm standard length)

may represent relictual populations (Motomura 2012).

5.5 Unique Ichthyofauna of Yaku-shima Island

The fish fauna of Yaku-shima Island has been found to cluster statistically with that of the Ryukyu Islands (see above). However, although pairs of sibling species are generally allopatrically distributed, off the Japanese mainland and associated islands (and Taiwan), and the Ryukyu Islands, respectively (see Sect. 5.3; Fig. 5.10), Motomura et al. (2010) found that both species of some sibling species pairs, such as *Ostracion immaculatum* and *O. cubicum*, *Acanthopagrus schlegelii* and *A. sivicolus*, *Gerres equulus* and *G. oyena*, and *Girella punctata* and *G. leonina*, co-occurred off Yaku-shima Island (Motomura 2012, 2015). This phenomenon (of mixed ichthyofauna) is known only from Yaku-shima Island (but also possibly from Kuchinoerabu-jima Island neighboring Yaku-shima Island; see Fig. 5.2). Characteristics of the Yaku-shima Island ichthyofauna were discussed in detail by Motomura et al. (2010) and Motomura (2012, 2015).

Motomura et al. (2010) also found that some temperate species, such as *Parupeneus spilurus* (Mullidae) and *Parapercis kamoharai* (Pinguipedidae), that occur off the Japanese mainland (and often off Taiwan), but not (or rarely) in the Ryukyu Islands, were well established at Yaku-shima Island. Subsequently, Motomura (2015) and Iwatsubo et al. (2015) reported two temperate species, *Hexagrammos agrammus* (Hexagrammidae) and *Sebastes thompsoni* (Sebastidae) [both usually distributed in northern Japan, but also common in northwestern Kyushu (Iwatsubo et al. 2015)] from Yaku-shima Island, a huge southward distributional range extension (Fig. 5.11). Neither species has been recorded from Tanegashima Island, suggesting the existence of an unknown southward water current (extension of Satsuma Southward Current; see Fig. 5.1) from western Kyushu to Yaku-shima Island, enabling infrequent movement of some temperate fishes to Yaku-shima Island (Motomura 2015; Iwatsubo et al. 2015; Hata et al. 2017a).

It is expected that the questions remaining about inshore fish diversity and ichthyofaunal characteristics of southern Japan, especially those of the Tokara Islands, will be clarified by future ichthyofaunal surveys.

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6 What Is Known of Fish Diversity in the Sea of Japan? Flatfishes: A Case Study

Fumihito Tashiro

Abstract

The pleuronectiform fauna in the Sea of Japan is considered as a case study exemplifying the diversity of fishes in the region. A total of 72 species plus one species complex in eight families is listed, with detailed distributional information based on voucher specimens and photographic records. A further 17 species listed in published literature are excluded from the Sea of Japan faunal list at this time, due to a lack of evidence of their occurrence. The species composition of pleuronectiform fishes changes drastically from warm-water to cold-water species along the coast of northern Japan and the east coast of the Korean Peninsula. A comparison of regional community structures in western Wakasa Bay, surveyed in the early 1970s and over 40 years later, indicated that the makeup of resident species and their abundance had changed significantly during the intervening time.

Keywords

Fish fauna · Pleuronectiformes · Tsushima Warm Current · Japanese Archipelago · Korea · Russia · Vouchers · Zoogeography

6.1 Sea of Japan

The Sea of Japan (also called the Japan Sea) is surrounded by the eastern margin of the Eurasian Continent and the Japanese Archipelago and is connected to the adjacent water bodies (East China–Yellow seas, Pacific Ocean, and Sea of Okhotsk) through shallow narrow straits (Fig. 6.1). The water mass structure of the Sea of Japan is characterized by surface water influenced by the Tsushima Warm Current and the Liman Cold Current, and a deep layer (Japan Sea Proper Water) occurring in depths of approximately 200–300 m and deeper. The Tsushima Warm Current, a combination of a branch of the Kuroshio Current and the Taiwan Current, enters the sea through the Tsushima Strait (situated to the southwest) and flows northward along the Japanese Archipelago and the east coast of the Korean Peninsula. On the other hand, the much weaker Liman Cold Current, fed by the Amur River, flows southward along the Eurasian Continent through the Tatar (Mamiya) Strait. The Japan Sea Proper Water is generated by the subsidence of surface water in winter, spreading evenly through the deep water layers without mixing with adjacent water bodies, due to the shallowness of the connecting straits (Kawamura 1998; Gamo et al. 2014).

Because the Sea of Japan is a semi-enclosed water body, the physical environment has been influenced by a number of environmental changes (mostly associated with changing climatic

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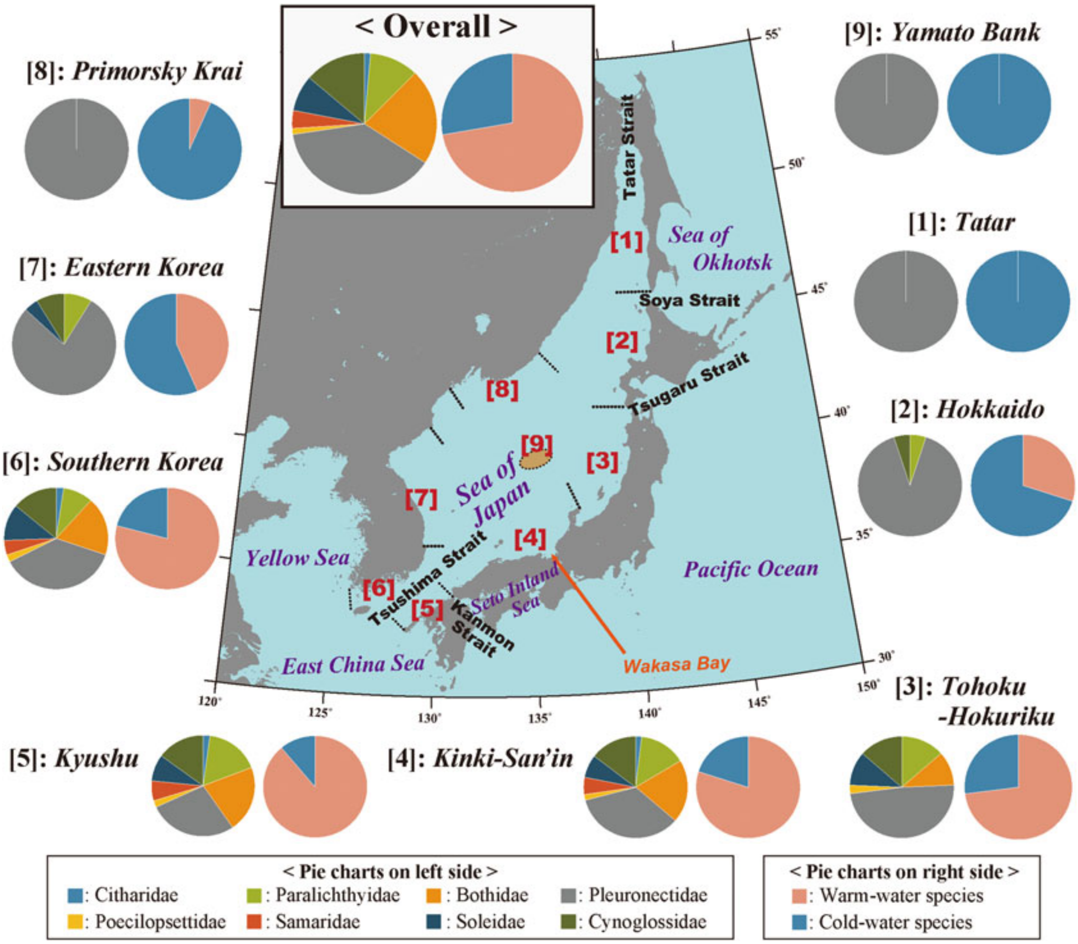

Fig. 6.1 Map of the Sea of Japan with flatfish species composition by family in the entire sea and each of nine areas (see text)

conditions) that have occurred in the past. These have corresponded with changing biocoenosis, with repeated mass mortality and recovery of certain marine fauna over the last 85,000 years. Many marine (especially deep-sea) species became extinct 27,000–20,000 years BP due to closure and isolation of the sea due to declining seawater levels, and the stratification of water layers, including strongly anoxic conditions caused by fresh water inflow from the land. Subsequently, a full-scale recovery of the Sea of Japan marine communities leading to their present condition, began 20,000–10,000 years BP with the inflow of the Oyashio Current from the Pacific Ocean through the Tsugaru Strait. From ca. 10,000–8000 years BP, intermittent inflows of the Tsushima Warm Current began from the southwest, becoming continuous some 8000 years ago, resulting in the present day oceanophysical environment. Details on the physical features and geological history of the Sea of Japan are shown in such as Oba et al. (1991), Tada (1994), and Koizumi (2006).

In general, the species diversity of marine organisms inhabiting the Sea of Japan is considered to be much poorer than that in the adjacent seas (Naganuma 2000; Tyler 2002), due primarily to the short geological history (only 8000 years since formation) and physical structure of the former (e.g., small tidal range and lack of coral reefs). Saburo Nishimura (1930–2001), an eminent Japanese biologist, published many works on the marine biology and zoogeography of the Sea of Japan, the series of publications comprising his doctoral thesis (Nishimura 1965a, b, 1966, 1968, 1969) revealing distributional aspects of marine animals in the Sea of Japan, based on a prodigious amount of data and literature information. Subsequently, zoogeography of the Sea of Japan, particularly with regard to marine fishes, was further explored from an evolutionary perspective (Nishimura 1974). Many of his findings are still considered basic to and important for the zoogeography of the Sea of Japan marine fauna.

6.2 Fishes of the Sea of Japan

Marine fishes are important food resources for the countries bordering the Sea of Japan, leading to many studies on fish species diversity. The first comprehensive survey of fish species diversity in the Sea of Japan originated from the USS Albatross cruise in 1906 (Nishimura 1974; Dunn 1996), a species checklist published by Snyder (1912) also including the distribution of each species in Japanese waters. A few years earlier, Schmidt (1904) had published a species list for the Russian Far East, based on Russian museum specimens. In subsequent years, researchers in Japan, Korea, and the Russian Far East have played central roles in clarifying the fish fauna of the Sea of Japan (e.g., Tanaka 1931; Kim et al. 2005; Parin et al. 2014; Kawano et al. 2014). However, because most of those studies emphasized the fish fauna of specific areas, species lists covering the entire Sea of Japan have been limited to a series of studies by the Russian Ichthyologist G. U. Lindberg and his colleagues, “Fishes of the Sea of Japan and the Adjacent Areas of the Sea of Okhotsk and the Yellow Sea, Parts 1–7” (Lindberg and Legeza 1959, 1965; Lindberg and Krasyukova 1969, 1975, 1987; Lindberg and Fedorov 1993; Lindberg et al. 1997). Although species commonly found in the sea were listed, it became obvious that the lists were inadequate due to limited materials (old specimens in the Zoological Institute, Russian Academy of Sciences, St. Petersburg, plus literature records).

Fish species lists for Japanese waters overall in the Sea of Japan were compiled by Kato (1956), Yoshida and Ito (1957), Tsuda (1990), Nakabo (2013), and Kawano et al. (2014). Additionally, many other species lists compiled over the same period focused on specific regions, habitats or taxa: e.g., Maeda and Tsutsui (2003) (Hokkaido); Shiogaki et al. (2004) (Aomori); Honma (2013) (Niigata); Nambu (2013) (Toyama); Sakai et al. (1991) and Yamamoto et al. (1995) (Ishikawa); Takegawa and Morino (1970), Minami et al. (1977), and Uchino et al. (1982) (Kyoto); Watanabe and Ito (1958) and Suzuki et al. (2000) (Hyogo); Moriwaki et al. (2007) (Shimane); Kawano et al. (2011), Fujiwara et al. (2018), and Sonoyama et al. (2020) (Yamaguchi); Yogo et al. (1986) and Nishida et al. (2004, 2005) (Fukuoka); Takeuchi et al. (2015) (Tsushima Island); Shinohara et al. (2011, 2014) (deep-water species in the entire sea); Tashiro et al. (2015) [*Pseudorhombus* (Paralichthyidae) of the coast of Japan]; Matsui et al. (2014) (gobioid species in Wakasa Bay); Matsunuma et al. (2019) (carangid species in Wakasa Bay and adjacent waters). Many more local lists were included in Kawano et al. (2014). In Korean waters, for example, Jordan and Metz (1913), Mori (1952), Chyung (1977), Kim et al. (2005), Kim and Ryu (2016), and Kim et al. (2020) compiled comprehensive species lists, with several additional lists compiled for Jeju Island, off the southern Korean Peninsula (e.g., Kim et al. 2009; Kim and Nakaya 2013; Kwun et al. 2017). Additionally, Ik-Soo Kim and his colleagues reviewed the taxonomy of several groups in Korean waters: e.g., Tetraodontoidei by Kim and Lee (1990); Blennioidei and Zoarcoidei by Kim and Kang (1991); Cottidae by Kim and Youn (1992); Cynoglossidae by Kim and Choi (1994); Pleuronectiformes by Kim and Youn (1994); and Percoidei by Kim et al. (2001). A considerable amount of additional information on Korean marine fishes was included in Kim et al. (2005) and Kim (2009). For Russian waters, an almost complete species list supported by a huge amount of literature information was published by Parin et al. (2014).

Clearly, despite a comprehensive list of fish species overall in the Sea of Japan having been limited to the studies of G. U. Lindberg and his colleagues, information on regional species diversity is vast. However, the compilation of a complete species list (with distributional ranges for each species) based on representative regional lists [Kawano et al. 2014 (Japanese), Kim et al. 2005 and Kim et al. 2020 (Korean), and Parin et al. 2014 (Russia)] is hampered by the existence of many unreliable records. Even now, some species identifications and distribution in the Sea of Japan are unclear.

6.3 Review of the Flatfish Fauna in the Sea of Japan

Flatfishes of the order Pleuronectiformes include many commercially important species for fishery activities in Japan, including several targeted for recreational angling. Significantly, these fishes comprise a principal catch component on the Japanese coast of the Sea of Japan (MAFF 2021). Accordingly, Japanese fisheries research institutions located along the Sea of Japan coast have actively engaged in various ecological (e.g., growth, population dynamics, and biomass) and aquacultural studies.

To date, a total of 88 valid flatfish species plus one species complex, representing eight families, have been recorded from the Sea of Japan (Table 6.1; Kawano et al. 2014; Parin et al. 2014; Kim et al. 2020; Sonoyama et al. 2020). However, records for many of these are not supported by vouchers, such as museum specimens. It is anticipated that flatfishes will be an important group for studying the evolution (including biogeography) of fishes inhabiting the Sea of Japan, since the former is one of the few groups distributed throughout the entire sea. Therefore, a clear understanding of flatfish species diversity may provide significant insight for our understanding of overall fish species diversity in the sea. Notwithstanding, our knowledge of flatfish species diversity—the most fundamental biological information—remains poor, with even the distribution of each species being poorly understood [see Nakabo 2013].

In this chapter, the flatfish fauna of the entire Sea of Japan is reviewed as a first step toward accurately understanding the process and drivers of species diversity of fishes in the Sea of Japan.

6.3.1 Species Checklist: What Species and Where?

A reconstructed species list based on museum specimens and photographic records is shown in Table 6.1 and Appendix. A total of 72 species plus one species-complex, all after metamorphosis, are recognized from the Sea of Japan, as follows: 27 species plus one species-complex in Pleuronectidae (37.5%), 16 species in Bothidae (22.2%), 10 species in Cynoglossidae (13.9%), eight species in Paralichthyidae (11.1%), six species in Soleidae (8.3%), three species in Samaridae (4.2%), and one species each in Citharidae and Poecilopsettidae (each 1.4%). At this time, no evidence has been found to support the occurrence of the following 17 species: *Lepidoblepharon ophthalmolepis* (Citharidae); *Pseudorhombus dupliciocellatus* (Paralichthyidae); *Arnoglossus japonicus*, *Bothus myriaster*, *Bothus pantherinus*, *Engyprosopon macroptera*, and *Parabothus coarctatus* (all Bothidae); *Pleuronectes bilineatus*, *Limanda proboscidea*, and *Reinhardtius hippoglossoides* (all Pleuronectidae); *Samariscus latus* (Samaridae); *Aesopia cornuta*, *Liachirus melanospilus*, and *Soleichthys heterorhinos* (all Soleidae); and *Cynoglossus arel*, *Cynoglossus bilineatus*, and *Cynoglossus nigropinnatus* (all Cynoglossidae) (Table 6.1). The Sea of Japan is divided into nine areas, together with the characteristics of each.

The "*Tatar*" area, located in the northernmost part of the sea, is connected to the Sea of Okhotsk, to the north via the Tatar Strait, and to the south via the Soya (La Pérouse) Strait (Fig. 6.1). A total of only 16 flatfish species are recognized (Table 6.1; Appendix), all being pleuronectids. On the other hand, no reliable

Table 6.1 Species list of flatfishes in the Sea of Japan

Family	Species	W/ C^{a}	Overall		Tatar	Hokkaido	Tohoku-Hokuriku	Kinki-San'in	Kyushu	Southern Korea	Eastern Korea	Primorsky Krai	Yamato Bank
			Previous^{b}	Revised									
Citharidae	*Lepidoblepharon ophthalmolepis*	W	Present										
	Citharoides macrolepidotus	W	Present	+				+	+	+			
Paralichthyidae	*Paralichthys olivaceus*	W	Present	+		+	+	+	+	+	+		
	Pseudorhombus arsius	W	Present	+				+	+				
	Pseudorhombus cinnamoneus	W	Present	+			+	+	+	+			
	Pseudorhombus dupliciocellatus	W	Present										
	Pseudorhombus oculocirris	W	Present	+			+	+	(+)				
	Pseudorhombus oligodon	W	Present	+				+	+				
	Pseudorhombus pentophthalmus	W	Present	+			+	+	+	+	+		
	Tarphops elegans	W	Present	+				+	(+)				
	Tarphops oligolepis	W	Present	+			+	+	+	+			
Bothidae	*Arnoglossus japonicus*	W	Present										
	Arnoglossus polyspilus	W	Present	+				+		+			
	Arnoglossus tenuis	W	Present	+				+					
	Arnoglossus yamanakai	W	Present	+				+	+				
	Asterorhombus intermedius	W	Present	+			+	+	(+)	+			
	Bothus myriaster	W	Present										
	Bothus pantherinus	W	Present										
	Crossorhombus kanekonis	W	Present	+					+				
	Crossorhombus kobensis	W	Present	+					+				
	Engyprosopon grandisquama	W	Present	+				+	+	+			

(continued)

Table 6.1 (continued)

Family	Species	W/ C[a]	Overall		Tatar	Hokkaido	Tohoku-Hokuriku	Kinki-San'in	Kyushu	Southern Korea	Eastern Korea	Primorsky Krai	Yamato Bank
			Previous[b]	Revised									
	Engyprosopon longipelvis	W	Present	+				+					
	Engyprosopon macroptera	W	Present										
	Engyprosopon multisquama	W	Present	+			+	+	(+)				
	Japonolaeops dentatus	W	Present	+				+		+			
	Kamoharaia megastoma	W	Present	+						+			
	Laeops kitaharae	W	Present	+			+	+	(+)	+			
	Parabothus kiensis	W	Present	+						+			
	Parabothus coarctatus	W	Present										
	Psettina iijimae	W	Present	+			+	+	(+)				
	Psettina tosana	W	Present	+				+	+	+			
	Tosarhombus octoculatus	W		+					+				
Pleuronectidae	*Acanthopsetta nadeshnyi*	C	Present	+	+	+	+	+			+	+	+
	Atheresthes evermanni	C	Present	+				+					
	Cleisthenes pinetorum	C	Present	+	+	+	+	+	+	+	+	+	
	Clidoderma asperrimum	C	Present	+	+	+	+	+	(+)	+	+	+	
	Dexistes rikuzenius	W	Present	+			+	+	(+)	+	+		
	Eopsetta grigorjewi	W	Present	+		+	+	+	+	+	+		
	Glyptocephalus kitaharae	W	Present	+			+	+	(+)	+			
	Glyptocephalus stelleri	C	Present	+	+	+	+	+	+	+	+	+	+
	Hippoglossoides dubius	C	Present	+	+	+	+	+			+	+	+
	Hippoglossoides elassodon/ Hippoglossoides robustus	C	Present	+	+	+							

	Hippoglossus stenolepis	C	Present	+		+							
	Pleuronectes bilineatus	C	Present										
	Lepidopsetta mochigarei	C	Present	+	+	+	+	+			+	+	
	Limanda aspera	C	Present	+	+					+	+	+	
	Limanda proboscidea	C	Present										
	Limanda sakhalinensis	C	Present	+	+								
	Liopsetta pinnifasciata	C	Present	+	+							+	
	Microstomus achne	C	Present	+		+	+	+	(+)	+	+		
	Myzopsetta punctatissima	C	Present	+	+	+	+	+		+	(+)	+	
	Platichthys bicoloratus	W	Present	+		+	+	+	(+)	+	+		
	Platichthys stellatus	C	Present	+	+	+	+	+			+	+	
	Pleuronectes quadrituberculatus	C	Present	+	+					+			
	Pleuronichthys cornutus	W	Present	+		+	+	+	(+)				
	Pleuronichthys lighti	W	Present	+			+	+	+	+			
	Pseudopleuronectes herzensteini	C	Present	+	+	+	+	+	(+)	+	+	+	
	Pseudopleuronectes obscurus	C	Present	+	+						+	+	
	Pseudopleuronectes schrenki	C	Present	+	+	+				+	+	+	
	Pseudopleuronectes yokohamae	W	Present	+		+	+	+	+	+	+		
	Reinhardtius hippoglossoides	C	Present										
	Verasper moseri	C	Present	+								+	
	Verasper variegatus	W	Present	+			+	+	(+)	+	(+)	+	
Poecilopsettidae	*Poecilopsetta plinthus*	W	Present	+			+	+	(+)	+			
Samaridae	*Plagiopsetta glossa*	W	Present	+				+	+	+			
	Samariscus latus	W	Present										
	Samariscus japonicus	W	Present	+				+	(+)	+			
	Samariscus xenicus	W	Present	+				+	(+)				

(continued)

Table 6.1 (continued)

Family	Species	W/ C[a]	Overall		Tatar	Hokkaido	Tohoku-Hokuriku	Kinki-San'in	Kyushu	Southern Korea	Eastern Korea	Primorsky Krai	Yamato Bank
			Previous[b]	Revised									
Soleidae	*Aesopia cornuta*	W	Present										
	Aseraggodes kaianus	W	Present	+						+			
	Aseraggodes kobensis	W	Present	+			+	+	(+)	+			
	Brachirus annularis	W	Present	+						+			
	Liachirus melanospilus	W	Present										
	Heteromycteris japonica	W	Present	+			+	+	(+)				
	Pseudaesopis japonica	W	Present	+			+	+	(+)	+	+		
	Soleichthys heterorhinos	W	Present										
	Zebrias zebrinus	W	Present	+			+	+	(+)	+			
Cynoglossidae	*Cynoglossus abbreviatus*	W	Present	+						+			
	Cynoglossus arel	W	Present										
	Cynoglossus bilineatus	W	Present										
	Cynoglossus interruptus	W	Present	+			+	+	+	+			
	Cynoglossus itinus	W	Present	+				+	+				
	Cynoglossus joyneri	W	Present	+			+	+	+	+	+		
	Cynoglossus nigropinnatus	W	Present										
	Cynoglossus ochiaii	W	Present	+			+	+	(+)				
	Cynoglossus robustus	W	Present	+				+	+	+			
	Cynoglossus semilaevis	W	Present	+						+			
	Paraplagusia japonica	W	Present	+		+	+	+	+	+	+		
	Symphurus longirostris	W	Present	+			+	+					
	Symphurus orientalis	W	Present	+				+	(+)				
Total number of species[c]			89	73	16	19	37	55	47	43	23	15	3

+, records supported by vouchers such as museum specimens and/or photos

(+), records lacking vouchers, but distribution presumed based on occurrence in adjacent water body (including East China Sea)

[a] *W* warm-water species mainly distributed in Kuroshio waters, *C* cold-water species mainly in Oyashio waters

[b] Data from Kawano et al. (2014), Parin et al. (2014), Kim et al. (2020), and Sonoyama et al. (2020)

[c] Including *Hippoglossoides elassodon/Hippoglossoides robustus* species complex if recorded from area

records exist for the following species, all included in this area by Parin et al. (2014): *Atheresthes evermanni*, *Eopsetta grigorjewi*, *Hippoglossus stenolepis*, *Limanda aspera*, *Microstomus achne*, *Platichthys bicoloratus*, *Reinhardtius hippoglossoides*, *Verasper moseri*, and *Verasper variegatus* (all Pleuronectidae).

The "*Hokkaido*" area, located in the northeastern part of the sea, is connected to the Sea of Okhotsk in the north via the Soya Strait and to the Pacific Ocean in the south via the Tsugaru Strait (Fig. 6.1). A total of 19 species in three families are recognized (Table 6.1; Appendix), 17 in Pleuronectidae (90%), and one each in Paralichthyidae and Cynoglossidae (each 5%). Despite being included in Kawano et al. (2014), records for the following species could not be confirmed: *Pseudorhombus pentophthalmus* and *Tarphops oligolepis* (Paralichthyidae); *Atheresthes evermanni*, *Dexistes rikuzenius*, *Glyptocephalus kitaharae*, *Lepidopsetta billineata*, *Liopsetta pinnifasciata*, *Pleuronectes quadrituberculatus*, *Pseudopleuronectes obscurus*, *Reinhardtius hippoglossoides*, *Verasper moseri*, and *Verasper variegatus* (all Pleuronectidae); and *Pseudaesopis japonica* (Soleidae).

The "*Tohoku-Hokuriku*" area, the eastern to southern part of the sea, is connected to the Pacific Ocean in the north via the Tsugaru Strait (Fig. 6.1). A total of 37 species in six families (about half of all species) are recognized herein (Table 6.1; Appendix): 18 species in Pleuronectidae (48.6%), five species each in Cynoglossidae and Paralichthyidae (each 13.5%), four species each in Bothidae and Soleidae (each 10.8%), and one species in Poecilopsettidae (2.7%). Records of the following species, included in Kawano et al. (2014), could not be confirmed: *Lepidoblepharon ophthalmolepis* (Citharidae); *Tarphops elegans* (Paralichthyidae); *Arnoglossus tenuis*, *Crossorhombus kobensis*, *Engyprosopon grandisquama*, and *Psettina tosana* (all Bothidae); *Atheresthes evermanni*, *Hippoglossoides elassodon* species complex, *Hippoglossus stenolepis*, *Lepidopsetta billineata*, *Liopsetta pinnifasciata*, *Reinhardtius hippoglossoides*, and *Verasper moseri* (all Pleuronectidae); *Samariscus japonicus* (Samaridae); *Aesopia cornuta* (Soleidae); and *Cynoglossus robustus* (Cynoglossidae).

The "*Kinki-San'in*" area, located in the south to southwestern part of the sea, is connected to the Seto Inland Sea in the west via the Kanmon Strait (Fig. 6.1). A total of 55 species in six families (about three-fourths of all species) are recognized herein (Table 6.1; Appendix): 19 species in Pleuronectidae (34.5%), 11 species in Bothidae (20.0%), eight species each in Cynoglossidae and Paralichthyidae (each 14.5%), four species in Soleidae (7.3%), three species in Samaridae (5.5%), and one species each in Citharidae and Poecilopsettidae (each 1.8%). Records of the following species included in Kawano et al. (2014) could not be confirmed: *Lepidoblepharon ophthalmolepis* (Citharidae); *Pseudorhombus dupliciocellatus* (Paralichthyidae); *Arnoglossus japonicus*, *Bothus pantherinus*, *Bothus myriaster*, *Engyprosopon macroptera*, and *Parabothus coarctatus* (all Bothidae); *Lepidopsetta bilineata*, *Pseudopleuronectes schrenki*, and *Reinhardtius hippoglossoides* (all Pleuronectidae); *Samariscus latus* (Samaridae); *Aesopia cornuta*, *Aseraggodes kaianus*, *Liachirus melanospilus*, and *Soleichthys heterorhinos* (all Soleidae); and *Cynoglossus arel*, *Cynoglossus bilineatus*, and *Cynoglossus nigropinnatus* (all Cynoglossidae).

The "*Kyushu*" area, located in the southernmost part of the sea, is connected to the Seto Inland Sea in the east via the Kanmon Strait (Fig. 6.1). Because specimens examined by the author and voucher specimens supporting published lists were much fewer than for the other Japanese areas, the present species list for this area includes many presumptive species (Table 6.1). A total of 47 species (including 23 presumptive) in eight families are included, as follows: 13 species in Pleuronectidae (27.7%), 10 species in Bothidae (21.3%), eight species in Paralichthyidae (17.0%), seven species in Cynoglossidae (14.9%), four species in Soleidae (8.5%), three species in Samaridae (6.4%), and one species each in Citharidae and Poecilopsettidae (each 2.1%) (Table 6.1; Appendix). Despite being listed by Kawano et al. (2014)

and Takeuchi et al. (2015), records of the following species could not be confirmed: *Arnoglossus japonicus* (Bothidae), *Aesopia cornuta* and *Aseraggodes kaianus* (Soleidae), and *Cynoglossus arel* (Cynoglossidae).

The "*Southern Korea*" area, forming the southernmost part of the sea together with the Kyushu area, is connected to both the East China and Yellow seas (Fig. 6.1). Based on published lists supported by voucher specimens (e.g., Lindberg and Fedorov 1993; Kim and Youn 1994; Kim and Ryu 2016), a total of 43 species in eight families are recognized herein (Table 6.1; Appendix): 16 species in Pleuronectidae (37.2%), eight species in Bothidae (18.6%), six species in Cynoglossidae and (14.0%), five species in Soleidae (11.6%), four species in Paralichthyidae (9.3%), two species in Samaridae (4.7%), and one species each in Citharidae and Poecilopsettidae (each 2.3%). Records could not be confirmed for the following species: *Pseudorhombus oculocirris* and *Tarphops elegans* (Paralichthyidae); *Arnoglossus japonicus*, *Bothus myriaster*, *Crossorhombus kobensis*, and *Psettina iijimae* (all Bothidae); *Lepidopsetta mochigarei*, *Pseudopleuronectes obscurus*, and *Verasper moseri* (all Pleuronectidae); *Aesopia cornuta* and *Heteromycteris japonica* (Soleidae); and *Cynoglossus gracilis* (Cynoglossidae).

The "*Eastern Korea*" area is defined herein as the east coast of the Korean Peninsula, north of Pohang (Fig. 6.1). On the basis of literature covering the Southern Korea area, a total of 24 species (including two presumptive) in eight families are recognized (Table 6.1; Appendix): 19 species in Pleuronectidae (79.2%), two species each in Cynoglossidae and Paralichthyidae (8.3%), and one species in Soleidae (4.2%). A fauna of flatfishes in this area is characterized by mostly pleuronectids with a small number of other families. Records could not be confirmed for the following species: *Bothus myriaster* (Bothidae); *Lepidopsetta billineata*, *Liopsetta pinnifasciata*, and *Verasper moseri* (all Pleuronectidae); and *Aseraggodes kobensis* (Soleidae).

The "*Primorsky Krai*" area, in the northwestern part of the sea (Fig. 6.1), is characterized by a relatively low flatfish diversity, comprising only 15 species (all in Pleuronectidae) (Table 6.1; Appendix). Despite being included in the comprehensive list given by Parin et al. (2014), records could not be confirmed for the following species: *Paralichthys olivaceus* (Paralichthyidae); *Eopsetta grigorjewi*, *Hippoglossus stenolepis*, *Microstomus achne*, *Platichthys bicoloratus*, *Pleuronectes quadrituberculatus*, *Pleuronichthys* spp., *Pseudopleuronectes yokohamae* (all Pleuronectidae); and *Cynoglossus itinus* and *Symphurus orientalis* (Cynoglossidae).

The "*Yamato Bank*" area, located in the central Sea of Japan, is an underwater mountain range (236 m depth at its shallowest) comprising the Yamato Bank and seamounts scattered in deep water off the southern Yamato Bank (Fig. 6.1). Only three pleuronectid species, also listed in Shinohara et al. (2011) on the basis of museum specimens, are recognized herein (Table 6.1; Appendix).

6.3.2 Faunal Characteristics

It is well established that the community structures of shallow-water fishes in the Sea of Japan change drastically between southern Hokkaido and northern Tohoku, and off the east coast of the Korean Peninsula (e.g., Nishimura 1965a; Kafanov et al. 2000), due to the influence of environmental factors, such as the path of the Tsushima Warm Current flowing from the south, the path of the North Korean Cold Current flowing along the continental coast, and different climatic conditions. Additionally, these and other environmental factors have also resulted in a wide transition zone of warm- and cold-water fishes, especially along the coast of Honshu Island, Japan. There are various theories about a zoozeographic boundary for fishes in the Sea of Japan [see Nishimura 1965a; Kafanov et al. 2000].

Similar patterns can be seen in the species diversity of flatfishes. Warm-water species (e.g., Bothidae, Cynoglossidae, Paralichyidae, and a few species of Pleuronectidae) are dominant in the *Kyushu*, *Kinki-San'in*, *Tohoku-Hokuriku*, and *Southern Korea* areas, which are strongly influenced by the Tsushima Warm Current, whereas a less diverse fauna, comprising mostly cold-water species (Pleuronectidae), dominate the *Eastern Korea*, *Primorsky Krai*, and *Tatar* areas (all strongly influenced by cold water currents), and the *Hokkaido* area (Tsushima Warm Current flows along the coast but exposed to a cold climate). In addition, a gradual shift in fauna from warm- to cold-water species, and vice versa, has been observed in the waters between the *Kinki-San'in* (20% and 80%, respectively) and *Tohoku-Hokuriku* (27% and 73%, respectively) areas (Fig. 6.1). A comparison of the fauna of these areas based on more fine-scaled data should result in clearer transition patterns being observed.

Although some pleuronectid species, such as *Cleisthenes pinetorum*, *Clidoderma asperrimum*, *Glyptocephalus stelleri*, and *Pseudopleuronectes herzensteini*, are distributed throughout the Sea of Japan (Table 6.1), most have a more or less limited distribution, toward to the north (warm-water species) or south (cold-water species). Interestingly, the distributional limits vary among species, even if closely related. For example, the abundant bothid *Engyprosopon multisquama* is widely distributed from Kyushu to Tohoku on the Japanese coast, whereas the congeners *E. grandisquama* and *E. longipelvis* are less common and have a northern limit not extending beyond the Noto Peninsula (Appendix). Such small but significant differences in distribution patterns may provide clues to understanding the evolution of fishes in the Sea of Japan.

The reconstructed flatfish faunal list resulting from this most recent assessment of species has a certain similarity to the lists proposed by previous studies, notwithstanding the unsupported records for 17 species (see above). The occurrence of such species in the Sea of Japan should remain questionable until confirmed by voucher specimens—which treatment should also apply to the distributional ranges for each of the recognized species.

6.3.3 Temporal Changes in Flatfish Community Structures in Wakasa Bay

Minami et al. (1977) conducted a benthic sledge survey from June 1971 to October 1972 to investigate the benthic fish community in the western part of Wakasa Bay (also called Tango Sea), located on the southern coast of the Sea of Japan (*Kinki-San'in* area) (Fig. 6.1). Recently, the author and colleagues conducted a similar survey (from April 2014 to March 2018) in approximately the same areas as those previously surveyed (off the mouth of the Yura River in depths of 5–60 m). A comparison of the overall results of the two survey programs found an increase in the number of flatfish species from 14 in 1971–1972 to 18 in 2014–2018 (Table 6.2). Among the new records, the paralichthyid *Pseudorhombus oligodon* was particularly notable, having been commonly collected during the later surveys. Additionally, significant fluctuations in abundance were also noted for the cynoglossid *Cynoglossus joyneri* (ca. 100 individuals in 1971–1972 vs. <5 in 2014–2018) and the soleid *Aseraggodes kobensis* (1 in 1971–1972 vs. >50 in 2014–2018).

The paralichthyid *Tarphops oligolepis* is small-sized species mainly inhabiting sandy coastal shores. Because of its abundance, some fundamental biological studies on the species had been undertaken in the Tango Sea [e.g., Minami 1983 (early life history); Kamisaka et al. 1999 (reproductive biology)]. However, the species inexplicably disappeared from the sandy beach (<10 m depth) off the Yura River during 2013–2015 (Tashiro et al. 2017). Although a small number of individuals have been recorded from that area since summer 2016, the cause of this phenomenon is still unclear.

6.4 Conclusion

In recent years, there has been a shift in the community structure of fishes in the Sea of Japan, with an increase in numbers of southern

Table 6.2 Flatfishes collected during benthic sledge surveys in western Wakasa Bay in 1971–1972 and 2014–2018

Family	Species	1971–1972	2014–2018
Paralichthyidae	*Paralichthys olivaceus*	+	+
	Pseudorhombus cinnamoneus	+	
	Pseudorhombus oculocirris		+
	Pseudorhombus oligodon		+
	Pseudorhombus pentophthalmus	+	+
	Tarphops elegans	+	
	Tarphops oligolepis	+	+
Bothidae	*Arnoglossus tenuis*		+
	Engyprosopon multisquama		+
Pleuronectidae	*Glyptocephalus kitaharae*	+	
	Platichthys bicoloratus	+	+
	Pseudopleuronectes yokohamae	+	+
	Pleuronichthys lighti	+	+
Soleidae	*Aseraggodes kobensis*		+
	Heteromycteris japonica	+	+
	Pseudaesopis japonica		+
	Zebrias zebrinus		+
Cynoglossidae	*Cynoglossus interruptus*	+	+
	Cynoglossus itinus		+
	Cynoglossus joyneri	+	+
	Cynoglossus robustus	+	
	Paraplagusia japonica	+	+

Data for 1971–1972 from Minami et al. (1977)

species (warm-water species). Although a causal relationship with global warming has sometimes been suggested (Nishida et al. 2005; Kawano et al. 2014), dispersal linked to expanded distribution may be a natural consequence of evolving species, and most neritic fishes inhabiting adjacent seas can actively or passively enter the Sea of Japan without difficulty. In fact, many incidental cases of warm-water species in the Sea of Japan have been recorded over the years (e.g., Nishimura 1965a; Tashiro et al. 2017; Matsunuma et al. 2019). Because of the young age of the Sea of Japan, thereby resulting in "unexplored" waters, it is likely that some species have been trying to establish viable populations in the sea for a long time. Accordingly, there may be little meaning in discussing changes in community structure and species diversity related to global warming, based on simple comparisons of species numbers. However, the community structure of fishes in the Sea of Japan may have changed over the past few decades as a result of human activities, including not only direct causes such as overfishing and coastal development but also land-based activities. In order to maintain fish species diversity in the Sea of Japan and continue with associated applied research, the overall fish fauna needs to be identified and confirmed as soon as possible.

This review has adopted a relatively negative view of published fish species lists unsupported by voucher specimens, due to the necessity for scientific research to be "reproducible". On the other hand, such studies have summarized a very large amount of information from a wide range of sources and have stimulated an interest in species diversity among many subsequent researchers, including myself.

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Appendix: Checklist of Flatfishes in the Sea of Japan

The systematic arrangement of families follows Nakabo (2013). Scientific names generally follow Nakabo (2013), except for Pleuronectidae, which follow Vinnikov et al. (2018). Specimens examined by the author are deposited at the Kyoto University, Kyoto and Maizuru (FAKU), the Hokkaido University Museum, Hakodate (HUMZ), the National Museum of Nature and Science, Tsukuba (NSMT), and the Seikai National Fisheries Research Institute (SNFR) (see original publications for cited vouchers shown in double quotation marks). Standard length is abbreviated as SL.

Order Pleuronectiformes

Family Citharidae

***Citheroides macrolepidotus* Hubbs, 1915 [Japanese name: Kokebirame] (Fig. 6.2a)**
Kinki-San'in: FAKU 138113, 106.4 mm SL, off Mishima I., Yamaguchi, 15 June 2015; >5 additional specimens deposited in FAKU and SNFR [see also Shinohara et al. 2011 ("ZIN 45093," Fukui)]. ***Kyushu***: FAKU 134665, 95.2 mm SL, off Tsushima I., Nagasaki, October 30, 2011; two additional specimens deposited in FAKU. ***Southern Korea***: See Kim and Ryu (2016) (e.g., "PKU 281–286," off Jeju I.).

Family Paralichthyidae

***Paralichthys olivaceus* (Temminck and Schlegel, 1846) [Japanese name: Hirame] (Fig. 6.2b)**
Hokkaido: HUMZ 96446, 201.3 mm SL, Ishikari Bay, Hokkaido, 14 September 1982; >10 additional specimens deposited in HUMZ. ***Tohoku-Hokuriku***: NSMT-P 73321, two specimens, 127.9–177.8 mm SL, Akita, October 16, 1931; and four additional specimens deposited in HUMZ. ***Kinki-San'in***: FAKU 136969, 160.7 mm SL, Wakasa Bay, Kyoto, March 4, 2015; and >10 additional specimens deposited in FAKU and HUMZ. ***Kyushu***: FAKU 137390, 227.9 mm SL, off Genkai I., Fukuoka, 18 April 2015; >5 additional specimens deposited in FAKU and NSMT. ***Southern Korea***: See Kim and Ryu (2016) (e.g., "PKU 6511," Yeosu). ***Eastern Korea***: See Lindberg and Fedorov (1993) ("ZIN 12378," Wonsan) and Kim and Ryu (2016) (e.g., "PKU 56317–56325," Sokcho).

***Pseudorhombus arsius* (Hamilton, 1822) [Japanese name: Tenjikugarei] (Fig. 6.2c)**
Kinki-San'in: FAKU 136988, 285.3 mm SL, Kunda Bay, Miyazu, Kyoto, March 7, 2015. ***Kyushu***: FAKU 137382, 166.2 mm SL, off Meinohama, Fukuoka, April 19, 2015; >10 additional specimens deposited in FAKU.

***Pseudorhombus cinnamoneus* (Temminck and Schlegel, 1846) [Japanese name: Ganzoubirame] (Fig. 6.2d)**
Tohoku-Hokuriku: HUMZ 62207, 224.9 mm SL, off Sado I., Niigata, September 23, 1976. ***Kinki-San'in***: FAKU 137408, 91.1 mm SL, Wakasa Bay, Kyoto, 2011–2012 (detailed data unknown); >5 additional specimens deposited in FAKU and HUMZ. ***Kyushu***: FAKU 101780, 183.1 mm SL, off Tsushima I., Nagasaki, July 31, 1973. ***Southern Korea***: See Lindberg and Fedorov (1993) ("ZIN 23735," Busan) and Kim and Ryu (2016) (e.g., "PKU 8598," Namhae).

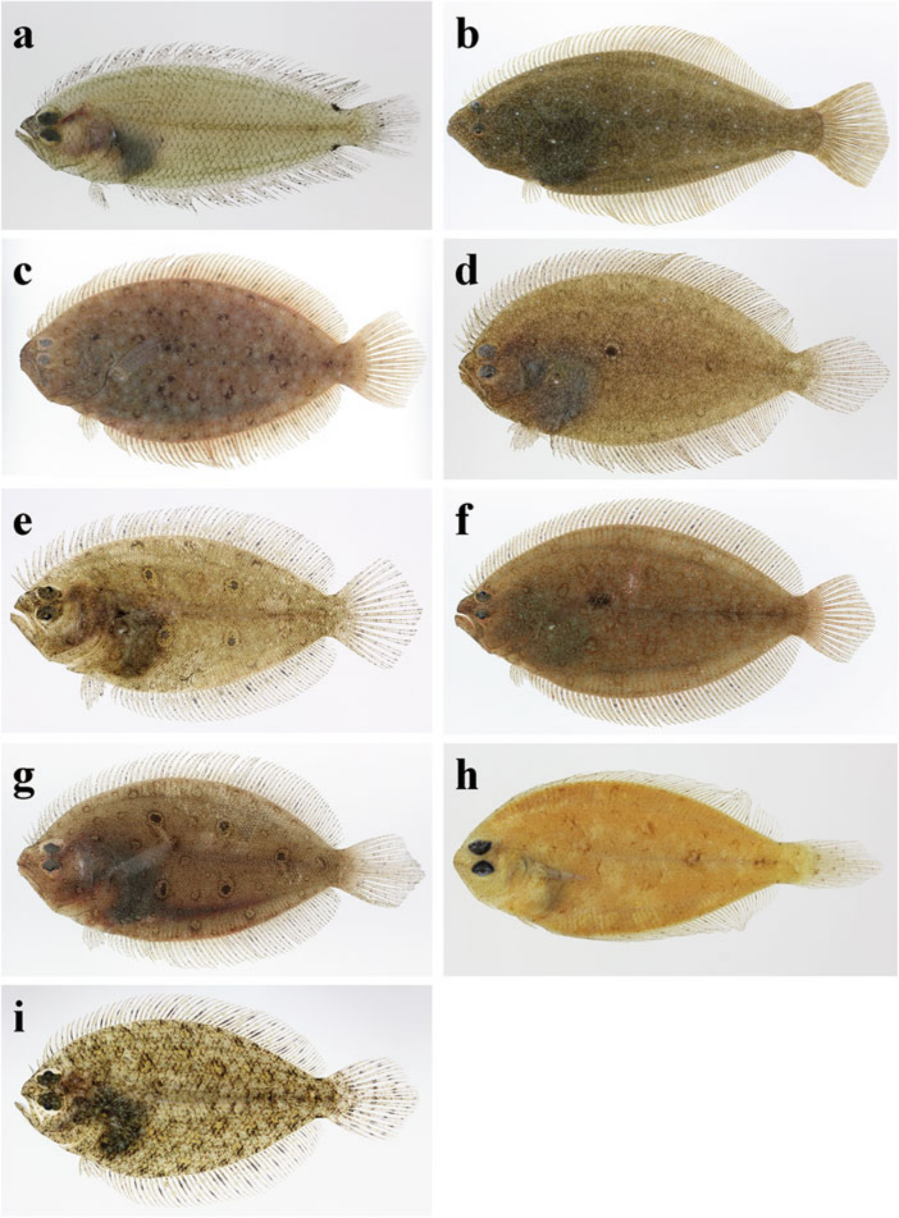

Fig. 6.2 Families Citharidae and Paralichthyidae. (**a**) *Citheroides macrolepidotus*, FAKU 138113; (**b**) *Paralichthys olivaceus*, FAKU 136969; (**c**) *Pseudorhombus arsius*, FAKU 136988; (**d**) *Pseudorhombus cinnamoneus*, FAKU 137408; (**e**) *Pseudorhombus oculocirris*, FAKU 145574; (**f**) *Pseudorhombus oligodon*, FAKU 136982; (**g**) *Pseudorhombus pentophthalmus*, FAKU 136887; (**h**) *Tarphops elegans*, FAKU 145534, preserved condition; (**i**) *Tarphops oligolepis*, FAKU 144933

***Pseudorhombus oculocirris* Amaoka, 1969 [Japanese name: Heraganzoubirame] (Fig. 6.2e)**
Tohoku-Hokuriku: See Honma et al. (1990) ("photo," Kashiwazaki, Niigata). ***Kinki-San'in***: FAKU 145574, 62.5 mm SL, off Maizuru, Kyoto, September 25, 2017; >10 additional specimens deposited in FAKU. **Remarks**: Records of this species based on voucher specimens from Southern Korea by Lee and Lee (2007) need to be reexamined.

***Pseudorhombus oligodon* (Bleeker, 1854) [Japanese name: Nan'yougarei] (Fig. 6.2f)**
Kinki-San'in: FAKU 136982, 196.9 mm SL, Maizuru Bay, Maizuru, Kyoto, March 12, 2015; >10 additional specimens deposited in FAKU. ***Kyushu***: FAKU 137491, 204.1 mm SL, off Meinohama, Fukuoka, April 19, 2015; one additional specimen deposited in FAKU.

***Pseudorhombus pentophthalmus* Günther, 1862 [Japanese name: Tamaganzoubirame] (Fig. 6.2g)**
Tohoku-Hokuriku: FAKU 137085, two specimens, 70.3–73.9 mm SL, Tsugaru, Aomori, September 5, 2000; >10 additional specimens deposited in FAKU and HUMZ. ***Kinki-San'in***: FAKU 136887, 149.9 mm SL, Wakasa Bay, Kyoto, February 2015; >10 additional specimens in FAKU, HUMZ, and SNFR. ***Kyushu***: FAKU 114739–114741, three specimens, 99.1–126.3 mm SL, off Nokonoshima I., Fukuoka, 27 September 1981; three additional specimens deposited in FAKU. ***Southern Korea***: See Lindberg and Fedorov (1993) ("ZIN 23825," Busan) and Kim and Ryu (2016) (e.g., "PKU 3264–3267," Yeosu). ***Eastern Korea***: See Kim and Youn (1994) ("CNUC 19681," Pohang).

***Tarphops elegans* Amaoka, 1969 [Japanese name: Yumearamegarei] (Fig. 6.2h)**
Kinki-San'in: FAKU 145534, 72 mm SL, off Hamada, Shimane, July 25, 1973; >10 additional specimens deposited in FAKU.

***Tarphops oligolepis* (Bleeker, 1858–1859) [Japanese name: Aramegarei] (Fig. 6.2i)**
Tohoku-Hokuriku: FAKU 137086, nine specimens, 33.5–56.0 mm SL, off Ajigasawa, Aomori, September 5, 2000; >10 additional specimens deposited in FAKU and HUMZ. ***Kinki-San'in***: FAKU 144933, 52.2 mm SL, off Maizuru, Kyoto, May 22, 2017; >10 additional specimens deposited in FAKU and SNFR. ***Kyushu***: FAKU 101548, 33.1 mm SL, off Tsushima I., Nagasaki, 1973–1974 (detailed data unknown); three additional specimens deposited in NSMT. ***Southern Korea***: See Kim et al. (2009) ("MRIC 2927," Jeju I.).

Family Bothidae

***Arnoglossus polyspilus* (Günther, 1880) [Japanese name: Nan'youdarumagarei]**
Kinki-San'in: See Sonoyama et al. (2020) ("SNFR 11126," off Yamaguchi). ***Southern Korea***: See Kim et al. (2010) ("JNU 20040618," off Jeju I.).

***Arnoglossus tenuis* Günther, 1880 [Japanese name: Nagadarumagarei] (Fig. 6.3a)**
Kinki-San'in: FAKU 141371, Maizuru Bay, Kyoto, May 26, 2016; FAKU 134821, three specimens, 60.1–73.8 mm SL, off Senzaki, Yamaguchi, October 6, 2011; >10 additional specimens deposited in FAKU and HUMZ.

***Arnoglossus yamanakai* Fukui, Yamada and Ozawa, 1988 [Japanese name: Tohkainagadarumagarei] (Fig. 6.3b)**
Kinki-San'in: FAKU 136241, 40.4 mm SL, off Ine, Kyoto, September 10, 2014; FAKU 145489, 99.7 mm SL, off Oumi-jima I., Yamaguchi, June 20, 2017; one additional specimen deposited in FAKU. ***Kyushu***: FAKU 134667, 95.0 mm SL, off Tsushima I., Nagasaki, November 28, 2008.

***Asterorhombus intermedius* (Bleeker, 1865) [Japanese name: Seitenbirame] (Fig. 6.3c)**
Tohoku-Hokuriku: HUMZ 231988, 29.5 mm SL, off Sado I., Niigata, September 16, 2020.

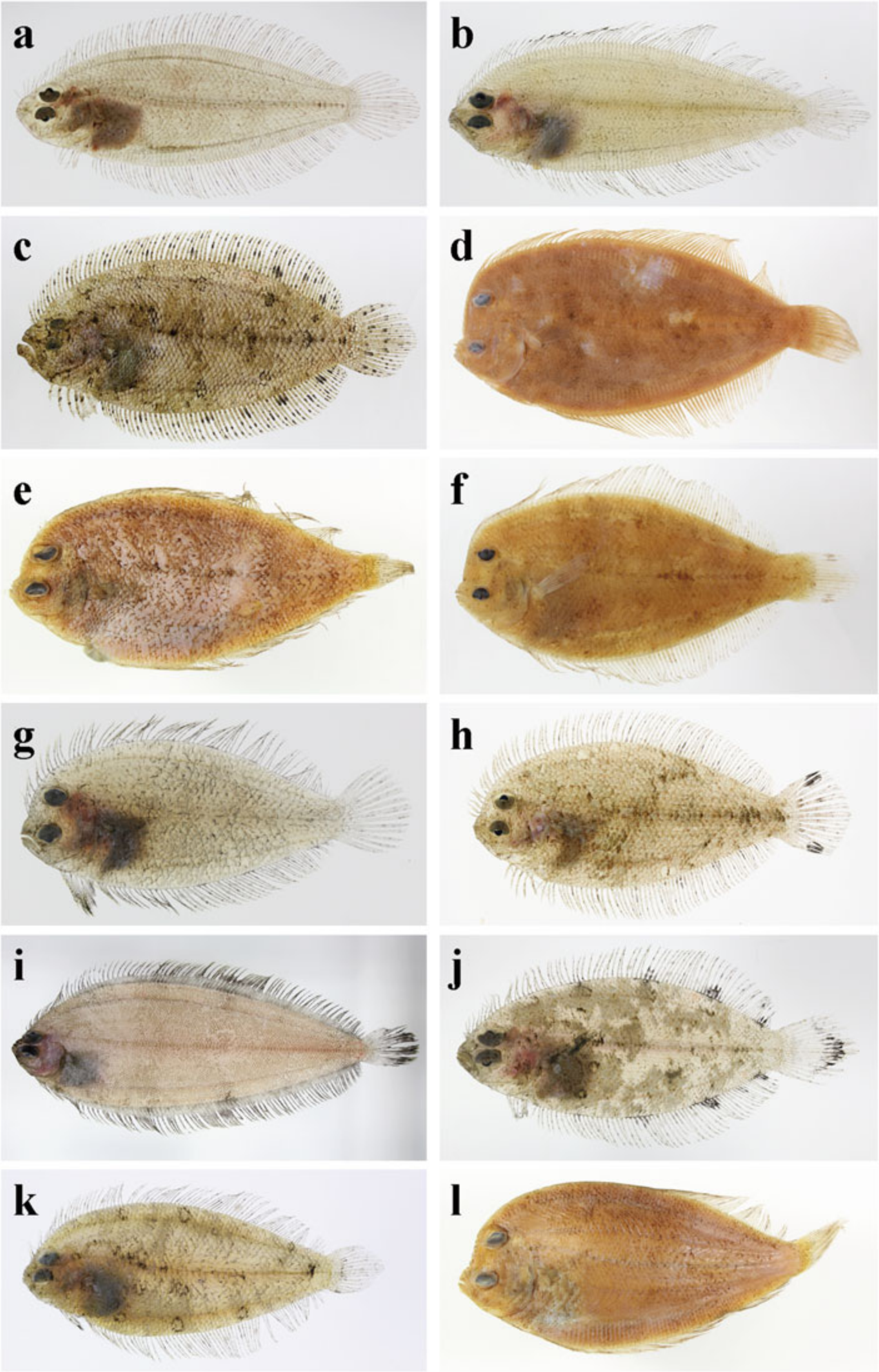

Fig. 6.3 Family Bothidae. (**a**) *Arnoglossus tenuis*, FAKU 141371; (**b**) *Arnoglossus yamanakai*, FAKU 145489; (**c**) *Asterorhombus intermedius*, FAKU 144467; (**d**) *Crossorhombus kanekonis*, FAKU S198, preserved condition; (**e**) *Crossorhombus kobensis*, NSMT-P 94323, preserved condition; (**f**) *Engyprosopon grandisquama*, FAKU 145532, preserved condition; (**g**) *Engyprosopon longipelvis*, FAKU 138918; (**h**) *Engyprosopon multisquama*, FAKU 143517; (**i**) *Laeops kitaharae*, FAKU 136454; (**j**) *Psettina iijimae*, FAKU 136867; (**k**) *Psettina tosana*, FAKU 138915; (**l**) *Tosarhombus octoculatus*, NSMT-P 94322, preserved condition

Kinki-San'in: FAKU 144467, 137 mm SL, Miyazu Bay, Kyoto, April 20, 2017 [see also Fujiwara et al. 2018 ("KAUM-I. 97427," off Yamaguchi)]. ***Southern Korea***: See Han et al. (2012) (e.g., "JNU 20090605," off Jeju I.).

***Crossorhombus kanekonis* (Tanaka, 1918) [Japanese name: Kanekodarumagarei] (Fig. 6.3d)**
Kyushu: FAKU S198, 145.8 mm SL, off Tsushima I., Nagasaki, summer of 1973.

***Crossorhombus kobensis* (Jordan and Starks, 1906) [Japanese name: Kobedarumagarei] (Fig. 6.3e)**
Kyushu: NSMT-P 94323, 107.3 mm SL, off Tsushima I., Nagasaki, July 1987; two additional specimens deposited in NSMT.

***Engyprosopon grandisquama* (Temminck and Schlegel, 1846) [Japanese name: Darumagarei] (Fig. 6.3f)**
Kinki-San'in: FAKU 145532, 106 mm SL, off Hamada, Shimane, 1970s; >10 additional specimens deposited in FAKU [see also Sonoyama et al. 2020 (e.g., "HH Pi 812," off Shimonoseki, Yamaguchi)]. ***Kyushu***: FAKU S199, 96.0 mm SL, off Tsushima I., Nagasaki, summer of 1973; three additional specimens in FAKU and NSMT. ***Southern Korea***: See Lee and Choi (2010) ("KNUM 2670," off Tongyeong, Gyeongsangnam-do).

***Engyprosopon longipelvis* Amaoka, 1969 [Japanese name: Himedarumagarei] (Fig. 6.3g)**
Kinki-San'in: FAKU 132825, 35.0 mm SL, off Ine, Kyoto, November 5, 2010; FAKU 138918, 50.7 mm SL, off Oumi-jima I., Yamaguchi, July 30, 2015; >10 additional specimens deposited in FAKU.

***Engyprosopon multisquama* Amaoka, 1963 [Japanese name: Chikamedarumagarei] (Fig. 6.3h)**
Tohoku-Hokuriku: HUMZ 136030, 45.0 mm SL, off Sakata, Yamagata, September 14, 1994; two additional specimens deposited in HUMZ. ***Kinki-San'in***: FAKU 143517, 74.2 mm SL, Miyazu, Kyoto, December 29, 2016; >10 additional specimens deposited in FAKU [see also Sonoyama et al. 2020 ("SNFR 12551," Nagato, Yamaguchi)].

***Japonolaeops dentatus* Amaoka, 1969 [Japanese name: Hinadarumagarei]**
Kinki-San'in: See Sonoyama et al. (2020) ("SNFR 11178," off Yamaguchi). ***Southern Korea***: See Kim et al. (2011) (e.g., "JNU 304-1–3," Jeju I.).

***Kamoharaia megastoma* (Kamohara, 1936) [Japanese name: Wanigarei]**
Southern Korea: See Jang et al. (2018) ("NIFS00003," off Jeju I.).

***Laeops kitaharae* (Smith and Pope, 1906) [Japanese name: Yarigarei] (Fig. 6.3i)**
Tohoku-Hokuriku: SNFR 18878, 63.4 mm SL, off Niigata, August 28, 2012. ***Kinki-San'in***: FAKU 136454, 133.6 mm SL, off Ine, Kyoto, November 20, 2014; FAKU 134689, 96.2 mm SL, off Nagato, Yamaguchi, October 7, 2011; >10 additional specimens deposited in FAKU and HUMZ. ***Southern Korea***: See Kim and Ryu (2016) (e.g., "PKU 23130," off Jeju I.).

***Parabothus kiensis* (Tanaka, 1918) [Japanese name: Kishudarumagarei]**
Southern Korea: See Kim et al. (2009) as *Parabothus kinesis* [sic] ("MRIC 1627," Jeju I.).

***Psettina iijimae* (Jordan and Starks, 1904) [Japanese name: Iijimadarumagarei] (Fig. 6.3j)**
Tohoku-Hokuriku: FAKU 132892, 45.5 mm SL, off Murakami, Niigata, December 5, 2012. ***Kinki-San'in***: FAKU 136867, 45.4 mm SL, off Maizuru, Kyoto, January 21, 2015; FAKU 133191, 84.9 mm SL, off Hagi, Yamaguchi, April 6, 2011; >5 additional specimens deposited in FAKU and SNFR.

***Psettina tosana* Amaoka, 1963 [Japanese name: Tosadarumagarei] (Fig. 6.3k)**
Kinki-San'in: FAKU 136873, 55.3 mm SL, off Maizuru, Kyoto, January 21, 2015; FAKU 138915, 86.3 mm SL, off Cape Kawajiri, Yamaguchi, July 30, 2015; >10 additional specimens deposited in FAKU and SNFR. ***Kyushu***: FAKU 57354, 63.8 mm SL, off Tsushima I., Nagasaki, July 17, 1990; five additional specimens deposited in FAKU. ***Southern Korea***: See Lee and Lee (2007) ("BKNU 2241–2242," off Saryang I.).

***Tosarhombus octoculatus* Amaoka, 1969 [Japanese name: Yatsumedarumagarei] (Fig. 6.3l)**
Kyushu: NSMT-P 94322, 108.8 mm SL, off Tsushima I., Nagasaki, July 1987.

Family Pleuronectidae

***Acanthopsetta nadeshnyi* Schmidt 1904 [Japanese name: Urokomegarei] (Fig. 6.4a)**
Hokkaido: HUMZ 42778, 224.5 mm SL, off Okushiri I., Hokkaido, June 6, 1975; >10 additional specimens deposited in HUMZ. ***Tohoku-Hokuriku***: FAKU 141021, 181.8 mm SL, off Itoigawa, Niigata, April 5, 2016; >10 additional specimens deposited in FAKU and HUMZ. ***Kinki-San'in***: FAKU 36270–36272, three specimens, 188.1–237.6 mm SL, off Kami, Hyogo, December 19–21, 1968. ***Eastern Korea***: See Kim and Ryu (2016) (e.g., "PKU 6250–6252," Goseong, Gangwon) and Voronina and Volkova (2019) (e.g., "ZIN 12339," East Korea Bay). ***Primorsky Krai***: See Voronina and Volkova (2019) (e.g., "ZIN 12343," Vladivostok). ***Tatar***: See Shinohara et al. (2011) (e.g., "ZIN 45190," 51°30′N, 140°45′E). ***Yamato Bank***: HUMZ 53804, 201.4 mm SL, 39°16.7′N, 135°2.7′E, May 31, 1976.

***Atheresthes evermanni* Jordan and Starks, 1904 [Japanese name: Aburagarei] (Fig. 6.4b)**
Kinki-San'in: NSMT-P 76630, 438.5 mm SL, Shinonsen, Hyogo, April 9, 2007. ***Eastern Korea***: See Park et al. (2020) (e.g., "NFRDI-FI-IS-0008430," Goseong, Gangwon).

***Cleisthenes pinetorum* Jordan and Starks, 1904 [Japanese name: Souhachi] (Fig. 6.4c)**
Hokkaido: HUMZ 231163, 299.7 mm SL, Esashi, Hokkaido, May 16, 2020; >10 additional specimens deposited in HUMZ. ***Tohoku-Hokuriku***: HUMZ 59119, 141.9 mm SL, off Sado I., Niigata, September 23, 1976; >10 additional specimens deposited in FAKU and HUMZ. ***Kinki-San'in***: SNFR 15990, 165.9 mm SL, off Mishima I., Yamaguchi, May 27, 1995; >10 additional specimens deposited in FAKU, HUMZ, and SNFR. ***Kyushu***: See Shinohara et al. (2011) ("NSMT-P 66141," off Tsushima I., Nagasaki). ***Southern Korea***: See Kim and Ryu (2016) (e.g., "PKU 54331–54385," Yeosu). ***Eastern Korea***: See Kim and Ryu (2016) (e.g., "PKU 51337–51349," Goseong, Gangwon) and Voronina and Volkova (2019) (e.g., "ZIN 12363," Wonsan). ***Primorsky Krai***: See Voronina and Volkova (2019) ("ZIN 12361," Vladivostok). ***Tatar***: See Shinohara et al. (2011) ("ZIN 45084," 51°16′N, 142°10′E) and Voronina and Volkova (2019) ("ZIN 12362," Kholmsk).

***Clidoderma asperrimum* (Temminck and Schlegel, 1846) [Japanese name: Samegarei] (Fig. 6.4d)**
Hokkaido: HUMZ 97169, off Yoichi, Hokkaido, October 22, 1982. ***Tohoku-Hokuriku***: See Uozu Aquarium (2014) ("photo," off Toyama). ***Kinki-San'in***: FAKU 139321, 370.1 mm SL, off Kyotango, Kyoto, October 16, 2015; >5 additional specimens deposited in FAKU [see also Sonoyama et al. 2020 ("KPM-NR 198290 (photo only)," off Hagi, Yamaguchi)]. ***Southern Korea***: See Kim and Ryu (2016) (e.g., "PKU 54131–54139," Tongyeong). ***Eastern Korea***: See Kim and Ryu (2016) (e.g., "PKU 8304–8305," Sokcho). ***Primorsky Krai***: See Ivankova (2007) ("TINRO-tsentr P-172," 43°57'4"N, 135°59'9"E). ***Tatar***: See Lindberg and Fedorov (1993) (e.g., "ZIN 45582," Moneron I.).

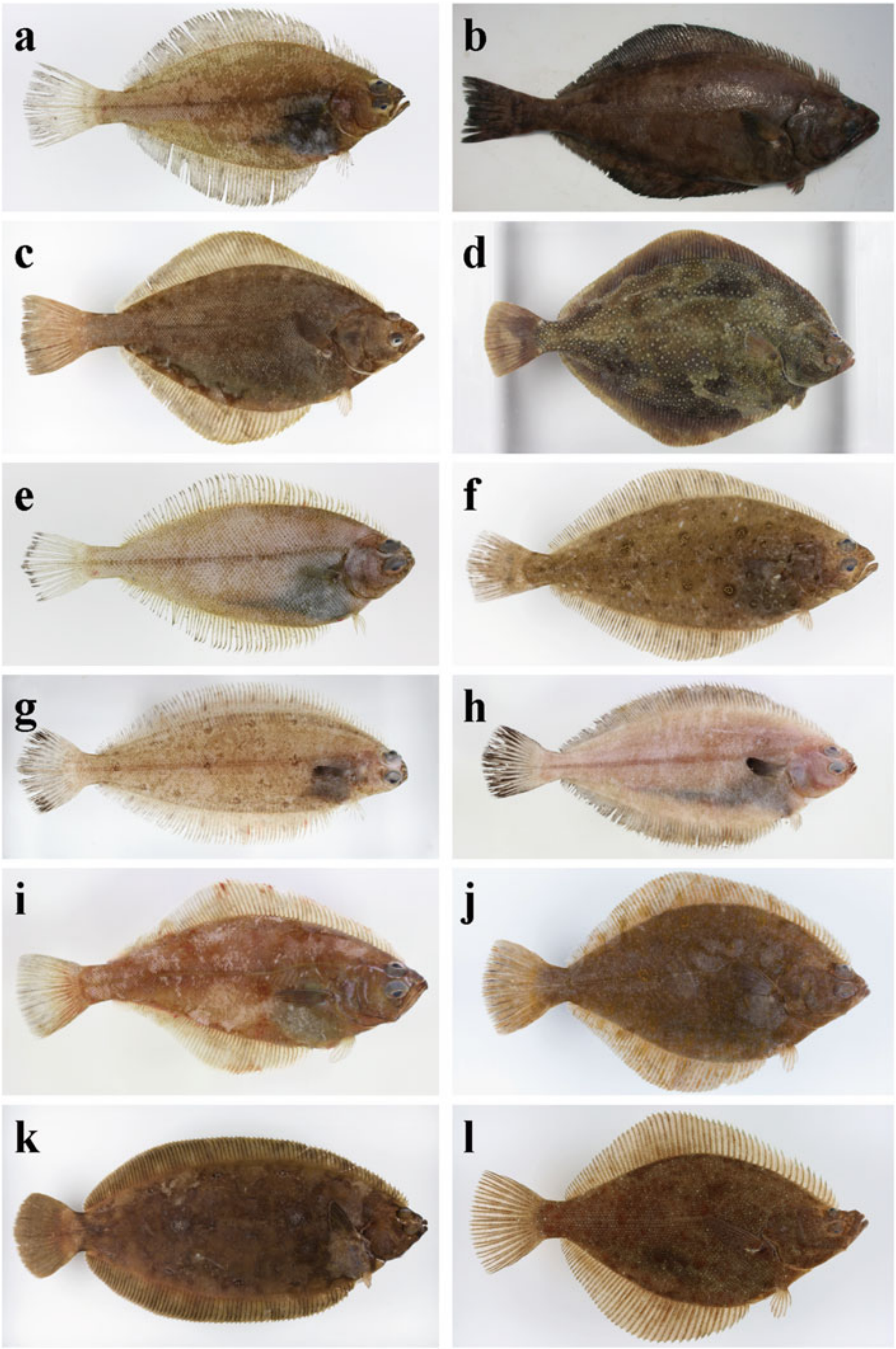

Fig. 6.4 Family Pleuronectidae (I). (**a**) *Acanthopsetta nadeshnyi*, FAKU 141021; (**b**) *Atheresthes evermanni*, NSMT-P 76630, photo courtesy of NSMT; (**c**) *Cleisthenes pinetorum*, HUMZ 231163; (**d**) *Clidoderma asperrimum*, FAKU 139321; (**e**) *Dexistes rikuzenius*, FAKU 137998; (**f**) *Eopsetta grigorjewi*, HUMZ 230351; (**g**) *Glyptocephalus kitaharae*, FAKU 136872; (**h**) *Glyptocephalus stelleri*, FAKU 136513; (**i**) *Hippoglossoides dubius*, FAKU 136514; (**j**) *Lepidopsetta mochigarei*, HUMZ 230360; (**k**) *Microstomus achne*, HUMZ 230350; (**l**) *Myzopsetta punctatissima*, HUMZ 231164

***Dexistes rikuzenius* Jordan and Starks, 1904 [Japanese name: Migigarei] (Fig. 6.4e)**
Tohoku-Hokuriku: HUMZ 59113, 120.3 mm SL, off Sado I., Niigata, September 23, 1976; >10 additional specimens deposited in HUMZ. ***Kinki-San'in***: FAKU 137998, 145.8 mm SL, Wakasa Bay, Kyoto, June 18, 2015; SNFR 15989, 178.7 mm SL, off Mishima I., Yamaguchi, May 27, 1995; >10 additional specimens deposited in FAKU. ***Southern Korea***: See Kim and Ryu (2016) (e.g., "PKU 509," Jeju I.). ***Eastern Korea***: See Kim and Ryu (2016) ("PKU 8341," Sokcho).

***Eopsetta grigorjewi* (Herzenstein. 1890) [Japanese name: Mushigarei] (Fig. 6.4f)**
Hokkaido: HUMZ 230351, 270.1 mm SL, Esashi, Hokkaido, May 18, 2019; >10 additional specimens deposited in HUMZ. ***Tohoku-Hokuriku***: HUMZ 52528, 138.4 mm SL, off Sado I., Niigata, March 25, 1976; >10 additional specimens deposited in FAKU and HUMZ. ***Kinki-San'in***: FAKU 125497, 121.0 mm SL, Wakasa Bay, Kyoto, November 6, 1981; >10 additional specimens deposited in FAKU, HUMZ, and SNFR. ***Kyushu***: FAKU 101775, 178.3 mm SL, off Tsushima I., Nagasaki, July 31, 1973; >10 additional specimens deposited in FAKU and NSMT-P. ***Southern Korea***: See Kim and Ryu (2016) (e.g., "PKU 54447–54485," Yeosu). **Eastern Korea**: See Kim and Ryu (2016) (e.g., "PKU 8238–8244," Sokcho).

***Glyptocephalus kitaharae* (Jordan and Starks, 1904) [Japanese name: Yanagimushigarei] (Fig. 6.4g)**
Tohoku-Hokuriku: FAKU 139223, 151.5 mm SL, off Tsugaru, Aomori, June 12, 2015; >10 additional specimens deposited in FAKU, HUMZ, and SNFR. ***Kinki-San'in***: FAKU 136872, 140.0 mm SL, Wakasa Bay, Kyoto, January 21, 2015; >10 additional specimens deposited in FAKU and HUMZ. **Southern Korea**: See Kim and Youn (1994) ("CNUC 19089," Yeosu).

***Glyptocephalus stelleri* (Schmidt 1904) [Japanese name: Hireguro] (Fig. 6.4h)**
Hokkaido: HUMZ 68358, 212.5 mm SL, off Shakotan Peninsula, May 15, 1977; >10 additional specimens deposited in HUMZ. ***Tohoku-Hokuriku***: FAKU 140507, 262.4 mm SL, off Niigata, February 17, 2016; >10 additional specimens deposited in FAKU and HUMZ. ***Kinki-San'in***: FAKU 136513, 213.3 mm SL, off Obama, Fukui, November 22, 2014; FAKU 138149, 253.6 mm SL, off Yamaguchi, June 15, 2015; >10 additional specimens deposited in FAKU and HUMZ. ***Kyushu***: See Shinohara et al. (2011) ("NSMT-P 66148," off Tsushima I.). ***Southern Korea***: See Kim and Ryu (2016) (e.g., "PKU 9917," Ulsan). ***Eastern Korea***: See Kim and Ryu (2016) (e.g., "PKU 56821–56829," Goseong, Gangwon) and Voronina and Volkova (2019) (e.g., "ZIN 12347," Wonsan). ***Primorsky Krai***: See Voronina and Volkova (2019) (e.g., "ZIN 12352," Vladivostok). ***Tatar***: See Shinohara et al. (2011, 2014) ("ZIN 45084," 51°16′N, 142°10′E) and Voronina and Volkova (2019) ("ZIN 12437," Kholmsk). ***Yamato Bank***: HUMZ 53776, 200.2 mm SL, 39°17.1′N, 135°3.5′E, May 29, 1976.

***Hippoglossoides dubius* Schmidt 1904 [Japanese name: Akagarei] (Fig. 6.4i)**
Hokkaido: HUMZ 67696, 179.9 mm SL, off Shakotan Peninsula, May 18, 1977; >10 additional specimens deposited in HUMZ. ***Tohoku-Hokuriku***: FAKU 140505, 308.9 mm SL, off Sado I., Niigata, February 17, 2016; >10 additional specimens deposited in FAKU and HUMZ. ***Kinki-San'in***: FAKU 136514, 202.4 mm SL, off Obama, Fukui, November 22, 2014; SNFR 19410, 177.8 mm SL, off Yamaguchi, June 12, 2012; >10 additional specimens deposited in FAKU and SNFR. ***Eastern Korea***: See Kim and Ryu (2016) (e.g., "PKU 9907," Goseong, Gangwon). ***Primorsky Krai***: See Shinohara et al. (2011) (e.g., "ZIN 17902," 42°40′N, 133°00′E). ***Tatar***: See Shinohara et al. (2011) (e.g., "ZIN 17906," 51°00′N, 140°51′E) and Voronina and Volkova (2019) (e.g., "ZIN 12366," Kholmsk). ***Yamato Bank***: See Shinohara et al. (2011) (e.g.,

"HUMZ 53662," 39°7.9′N, 135°4.6′E). **Remarks**: HUMZ 53662 is currently missing.

***Hippoglossoides elassodon* Jordan and Gilbert, 1880/*Hippoglossoides robustus* Gill and Townsend, 1897 [Japanese name: Umagarei/ Dorogarei]**
Hokkaido: See Lindberg and Fedorov (1993) as *H. robustus* ("ZIN 19157," Otaru). ***Tatar***: See Lindberg and Fedorov (1993) as *H. elassodon* (e.g., "ZIN 18533," 58°58′N, 141°04′E), and as *H. robustus* (e.g., "ZIN 19062," between De Kastri and Alexandrovsk). **Remarks**: Because the taxonomy of *H. elassodon* and *H. robustus* remains uncertain (Parin et al. 2014), the two species are treated herein as a species complex "*Hippoglossoides elassodon/ Hippoglossoides robustus*."

***Hippoglossoides stenolepis* Schmidt 1904 [Japanese name: Ohyo]**
Hokkaido: See Yabe et al. (1991) (e.g., "HUMZ 55902" 44°27′N, 140°19′E). **Remarks**: HUMZ 55902 is currently missing.

***Lepidopsetta mochigarei* Snyder, 1911 [Japanese name: Asabagarei] (Fig. 6.4j)**
Hokkaido: HUMZ 230360, 264.1 mm SL, Esashi, Hokkaido, May 18, 2019; >10 additional specimens deposited in FAKU, HUMZ, and NSMT. ***Tohoku-Hokuriku***: FAKU 140071, 276.3 mm SL, off Oga, Akita, July 31, 2015; >5 additional specimens deposited in FAKU and HUMZ. ***Kinki-San'in***: FAKU 100254, 296.1 mm SL, Wakasa Bay, Kyoto, 1978 (detailed date unknown); >10 additional specimens in FAKU and HUMZ. ***Eastern Korea***: See Kim and Youn (1994) (e.g., "CNUC 19162," Pohang) and Kim and Ryu (2016) (e.g., "PKU 3849," Gangneung). ***Primorsky Krai***: See Lindberg and Fedorov (1993) (e.g., "ZIN 12892," Vladivostok). ***Tatar***: See Orr and Matarese (2000) (e.g., "USNM 77126," 47°38.2′N, 141°39.0′E). **Remarks**: *Lepidopsetta bilineata* (Ayres, 1855), closely related to *L. mochigarei*, is probably not distributed in the Sea of Japan (Orr and Matarese 2000).

***Limanda aspera* (Pallas, 1814) [Japanese name: Koganegarei]**
Southern Korea: See Lindberg and Fedorov (1993) ("ZIN 23847," Busan). ***Eastern Korea***: See Kim and Youn (1994) ("CNUC 19713–19714," Pohang). ***Primorsky Krai***: See Lindberg and Fedorov (1993) (e.g., "ZIN 17820," Peter the Great Bay). ***Tatar***: See Lindberg and Fedorov (1993) (e.g., "ZIN 25124," 51°28′N, 140°58′E).

***Limanda sakhalinensis* Hubbs, 1915 [Japanese name: Karafutogarei]**
Tatar: See Lindberg and Fedorov (1993) (e.g., "ZIN 17833," De Kastri).

***Liopsetta pinnifasciata* (Kner, 1870) [Japanese name: Tougarei]**
Primorsky Krai: See Lindberg and Fedorov (1993) (e.g., "ZIN 25516," Vladivostok). ***Tatar***: See Lindberg and Fedorov (1993) (e.g., "ZIN 19914," Tatar Strait).

***Microstomus achne* (Jordan and Starks, 1904) [Japanese name: Babagarei] (Fig. 6.4k)**
Hokkaido: HUMZ 230350, Esashi, Hokkaido, September 18, 2019 [Also see Lindberg and Fedorov 1993 ("ZIN 19152," Otaru)]. ***Tohoku-Hokuriku***: HUMZ 59112, 147.5 mm SL, off Sado I., Niigata, September 23, 1976; >10 additional specimens deposited in FAKU and HUMZ. ***Kinki-San'in***: FAKU 137373, 236.1 mm SL, off Sakaiminato, Tottori, April 23, 2015; >10 additional specimens deposited in FAKU and HUMZ [see also Sonoyama et al. 2020 (e.g., "KPM-NR 198989 (photo only)," off Hagi, Yamaguchi)]. ***Southern Korea***: See Kim and Ryu (2016) (e.g., "PKU 5675," off Jeju I.). ***Eastern Korea***: See Kim and Ryu (2016) (e.g., "PKU 4322," Uljin).

***Myzopsetta punctatissima* (Steindachner, 1879) [Japanese name: Sunagarei] (Fig. 6.4l)**
Hokkaido: HUMZ 231164, 251.3 mm SL, Esashi, Hokkaido, May 16, 2020; >10 additional specimens deposited in HUMZ. ***Tohoku-Hokuriku***: NSMT-P 73354, 215.2 mm SL, off Nikaho, Akita, October 20, 1932 [see also in

Uozu Aquarium 2014 ("photo," Toyama)]. ***Kinki-San'in***: FAKU 136103, 198.1 mm SL, Wakasa Bay, Kyoto, July 16, 2014. ***Southern Korea***: See Lindberg and Fedorov (1993) ("ZIN 23738," Busan). ***Primorsky Krai***: See Lindberg and Fedorov (1993) (e.g., "ZIN"). ***Tatar***: See Lindberg and Fedorov (1993) (e.g., "ZIN 45642," Tatar Strait).

Platichthys bicoloratus **(Basilewsky, 1855) [Japanese name: Ishigarei] (Fig. 6.5a)**
Hokkaido: HUMZ 231151, 314.9 mm SL, Esashi, Hokkaido, April 12, 2020; >5 additional specimens deposited in HUMZ. ***Tohoku-Hokuriku***: FAKU 140508, 275.7 mm SL, off Niigata, February 17, 2016; >10 additional specimens deposited in FAKU. ***Kinki-San'in***: FAKU 137144, 311.8 mm SL, Miyazu, Kyoto, March 21, 2015; >10 additional specimens deposited in FAKU [see also Sonoyama et al. 2020 ("HH-Pi 1206," Houhoku, Shimonoseki, Yamaguchi)]. ***Southern Korea***: See Kim and Ryu (2016) (e.g., "PKU 3397–3399," Gangjin). ***Eastern Korea***: See Kim and Ryu (2016) (e.g., "PKU 20552," Goseong, Gangwon).

Platichthys stellatus **Pallas, 1787 [Japanese name: Numagarei] (Fig. 6.5b)**
Hokkaido: HUMZ 231150, 243.7 mm SL, Esashi, Hokkaido, April 12, 2020; >10 additional specimens deposited in FAKU and HUMZ. ***Tohoku-Hokuriku***: FAKU 96118, 170.4 mm SL, Ushitsu, Noto, Ishikawa, May 1, 2008; >5 additional specimens deposited in FAKU and NSMT. ***Kinki-San'in***: FAKU 131762, 245.4 mm SL, Maizuru, Kyoto, February 23, 2009; >10 additional specimens deposited in FAKU. ***Eastern Korea***: See Kim and Youn (1994) (e.g., "CNUC 19234–19237," Pohang). ***Primorsky Krai***: See Voronina and Volkova (2003) (e.g., "ZIN 17963," Peter the Great Bay). ***Tatar***: See Voronina and Volkova (2003) (e.g., "ZIN 19173," De Kastri). **Remarks**: Interspecific hybrid individuals of *P. bicoloratus* and *P. stellatus* have been frequently obtained from the Sea of Japan (e.g., HUMZ 231149, 256.8 mm SL, Esashi, Hokkaido, April 12, 2020; Fig. 6.5c).

Pleuronectes quadrituberculatus **Pallas, 1814 [Japanese name: Tsunogarei]**
Southern Korea: See Kim and Youn (1994) ("CNUC 19416," Busan). ***Tatar***: See Lindberg and Fedorov (1993) (e.g., "ZIN 17996," De Kastri).

Pleuronichthys cornutus **(Temminck and Schlegel, 1846) [Japanese name: Nagaremeitagarei] (Fig. 6.5d)**
Hokkaido: See Suzuki et al. (2009) as paratype ("HUMZ 98252," Yoichi, Hokkaido) and nontype ("HUMZ 109423," Taisei, Hokkaido) of *P. japonicus*. ***Tohoku-Hokuriku***: See Suzuki et al. (2009) as paratypes (e.g., "FAKU 91921," off Niigata) and nontypes (e.g., "NMCI-P 1608," Hanami, Noto, Ishikawa) of *P. japonicus*; >10 additional specimens deposited in FAKU and HUMZ (e.g., FAKU 132223, 146.4 mm SL, off Tsutsuishi, Niigata, October 17, 2009). ***Kinki-San'in***: See Suzuki et al. (2009) as holotype ("FAKU 90216," off Hamada, Shimane), paratypes ("FAKU 90161," off Hamada, Shimane), and nontypes of *P. japonicus*; >10 additional specimens deposited in FAKU and SNFR (e.g., FAKU 136721, 163.4 mm SL, Wakasa Bay, Kyoto, December 2014). **Remarks**: *Pleuronichthys japonicus* Suzuki et al. 2009 was considered a junior synonym of *P. cornutus* by Yokogawa et al. (2014).

Pleuronichthys lighti **Wu, 1929 [Japanese name: Meitagarei] (Fig. 6.5e)**
Tohoku-Hokuriku: SNFR 18811, 105.6 mm SL, off Niigata, August 24, 2012 [see also Suzuki et al. 2009 as *P. cornutus* (e.g., "FAKU 91642," off Niigata)]. ***Kinki-San'in***: FAKU 137165, 173.5 mm SL, Wakasa Bay, Kyoto, March 26, 2015; >10 additional specimens deposited in FAKU, HUMZ, and SNFR [see also Suzuki et al. 2009 as *P. cornutus* (e.g., "FAKU 92140–92149," off Hamada, Shimane)]. ***Kyushu***: FAKU 137499, 177.1 mm SL, off Meinohama, Fukuoka, April 19, 2015; 3 additional specimens deposited in FAKU. ***Southern Korea***: See Suzuki et al. (2009) as *P. cornutus* (e.g., "pl. 126-1 in Chyung (1977)," Yeosu). **Remarks**: The taxon

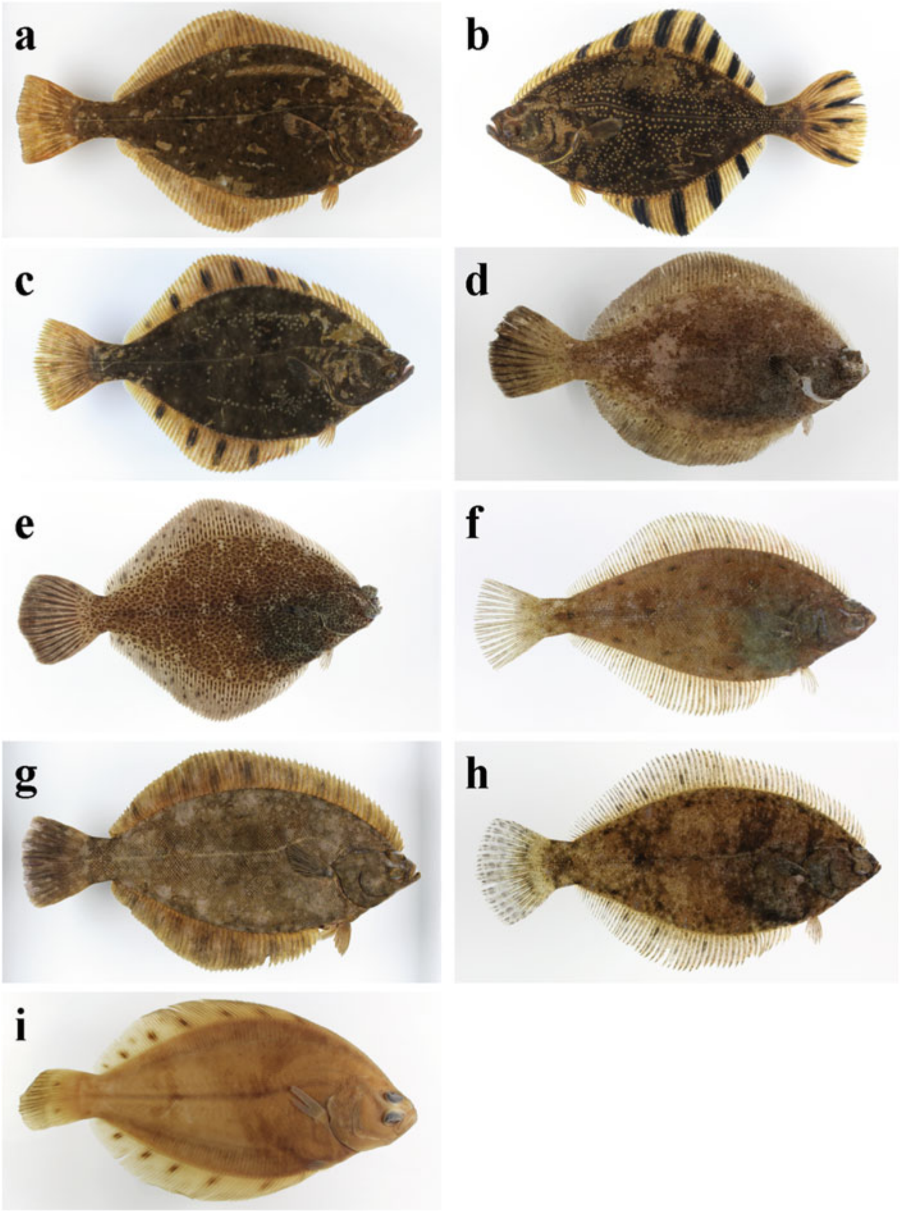

Fig. 6.5 Family Pleuronectidae (II). (**a**) *Platichthys bicoloratus*, HUMZ 231151; (**b**) *Platichthys stellatus*, HUMZ 231150; (**c**) hybrid individual of *Platichthys bicoloratus* and *Platichthys stellatus*, HUMZ 231149; (**d**) *Pleuronichthys cornutus*, FAKU 136721; (**e**) *Pleuronichthys lighti*, FAKU 137165; (**f**) *Pseudopleuronectes herzensteini*, FAKU 137996; (**g**) *Pseudopleuronectes schrenki*, HUMZ 230747; (**h**) *Pseudopleuronectes yokohamae*, FAKU 137040; (**i**) *Verasper variegatus*, NSMT-P 73272, preserved condition

treated as *P. cornutus* in Suzuki et al. (2009) was recognized as *P. lighti* by Yokogawa et al. (2014). Kim and Ryu (2016) recorded *P. japonicus* from the southern Korean region ("PKU 6238–6239, 6557–6559," Jeju I.) after its synonymization with *P. cornutus*. A specimen photograph which they identified as *P. japonicus* is likely to have been *P. lighti*.

Pseudopleuronectes herzensteini **(Jordan and Snyder, 1901) [Japanese name: Magarei] (Fig. 6.5f)**
Hokkaido: HUMZ 107662, 133.6 mm SL, off Otaru, April 15, 1986; >10 additional specimens deposited in FAKU and HUMZ. ***Tohoku-Hokuriku***: HUMZ 52756, 134.7 mm SL, off Sado I., Niigata, March 25, 1976; >10 additional specimens deposited in FAKU, HUMZ, and SNFR. ***Kinki-San'in***: FAKU 137996, 163.2 mm SL, Wakasa Bay, Kyoto, June 18, 2015; >10 additional specimens deposited in FAKU and HUMZ [see also Sonoyama et al. 2020 ("SNFR 16005," off Yamaguchi)]. ***Southern Korea***: See Kim and Youn (1994) ("CNUC 19226," Busan). ***Eastern Korea***: See Kim and Ryu (2016) (e.g., "PKU 20553," Goseong, Gangwon). ***Primorsky Krai***: See Voronina and Volkova (2019) ("ZIN 8730," Vladivostok). ***Tatar***: See Lindberg and Fedorov (1993) (e.g., "ZIN 19072," 51°23′N, 142°00′E).

Pseudopleuronectes obscurus **Herzenstein, 1890 [Japanese name: Kurogarei]**
Eastern Korea: See Kim and Ryu (2016) ("PKU 8393," Sokcho). ***Primorsky Krai***: See Voronina and Volkova (2019) (e.g., "ZIN 8726," Vladivostok). ***Tatar***: See Lindberg and Fedorov (1993) (e.g., "ZIN 31672," Antonovo; "ZIN 19059," De Kastri).

Pseudopleuronectes schrenki **(Schmidt 1904) [Japanese name: Kurogashiragarei] (Fig. 6.5g)**
Hokkaido: HUMZ 230747, 271.2 mm SL, Kaminokuni, Hokkaido, August 1, 2019; >10 additional specimens deposited in FAKU, HUMZ, and NSMT. ***Southern Korea***: See Kim and Youn (1994) ("CNUC 19742," Busan). ***Eastern Korea***: See Kim and Youn (1994) ("CNUC 19738," Yangyang). ***Primorsky Krai***: See Lindberg and Fedorov (1993) (e.g., "ZIN 17842," Posyet). ***Tatar***: See Voronina and Volkova (2019) ("ZIN 12377b," Kholmsk).

Pseudopleuronectes yokohamae **(Günther, 1877) [Japanese name: Makogarei] (Fig. 6.5h)**
Hokkaido: HUMZ 230359, 245.2 mm SL, Esashi, Hokkaido, May 18, 2019; >5 additional specimens deposited in HUMZ. ***Tohoku-Hokuriku***: FAKU 137076, 72.0 mm SL, Himi, Toyama, 25 June 1997; >10 additional specimens deposited in FAKU and HUMZ. ***Kinki-San'in***: FAKU 137040, 136.8 mm SL, Miyazu, Kyoto, January 2015; >10 additional specimens deposited in FAKU and HUMZ. ***Kyushu***: FAKU 137493, 158.4 mm SL, off Meinohama, Fukuoka, April 19, 2015; three additional specimens deposited in FAKU. ***Southern Korea***: See Kim and Ryu (2016) (e.g., "PKU 7723," Namhae). ***Eastern Korea***: See Kim and Ryu (2016) (e.g., "PKU 4323," Uljin).

Verasper moseri **Jordan and Gilbert, 1898 [Japanese name: Matsukawa]**
Primorsky Krai: See Voronina and Volkova (2003) ("ZIN 45193," 42°52′N, 132°23′E).

Verasper variegatus **(Temminck and Schlegel, 1846) [Japanese name: Hoshi-garei] (Fig. 6.5i)**
Tohoku-Hokuriku: NSMT-P 73272, 2 specimens, 124.8–154.1 mm SL, Oga, Akita, November 14, 1931. ***Kinki-San'in***: FAKU 16975, 274.9 mm SL, Maizuru, Kyoto, November 6, 1951; three additional specimens deposited in FAKU. ***Southern Korea***: See Kim and Youn (1994) (e.g., "CNUC 19623–19625," Koheung) and Lindberg and Fedorov (1993) ("ZIN 23733," Busan). ***Primorsky Krai***: See Lindberg and Fedorov (1993) ("ZIN 10466," Vladivostok).

Family Poecilopsettidae

Poecilopsetta plinthus **(Jordan and Starks, 1904) [Japanese name: Kawaragarei] (Fig. 6.6a)**
Tohoku-Hokuriku: FAKU 135590, 91.6 mm SL, off Niigata, August 25, 2013. ***Kinki-San'in***: FAKU 138112, 98.6 mm SL, off Nagato, Yamaguchi, June 15, 2015; four additional specimens deposited in FAKU and HUMZ. ***Southern Korea***: See Kim and Ryu (2016) (e.g., "PKU 8599," Namhae).

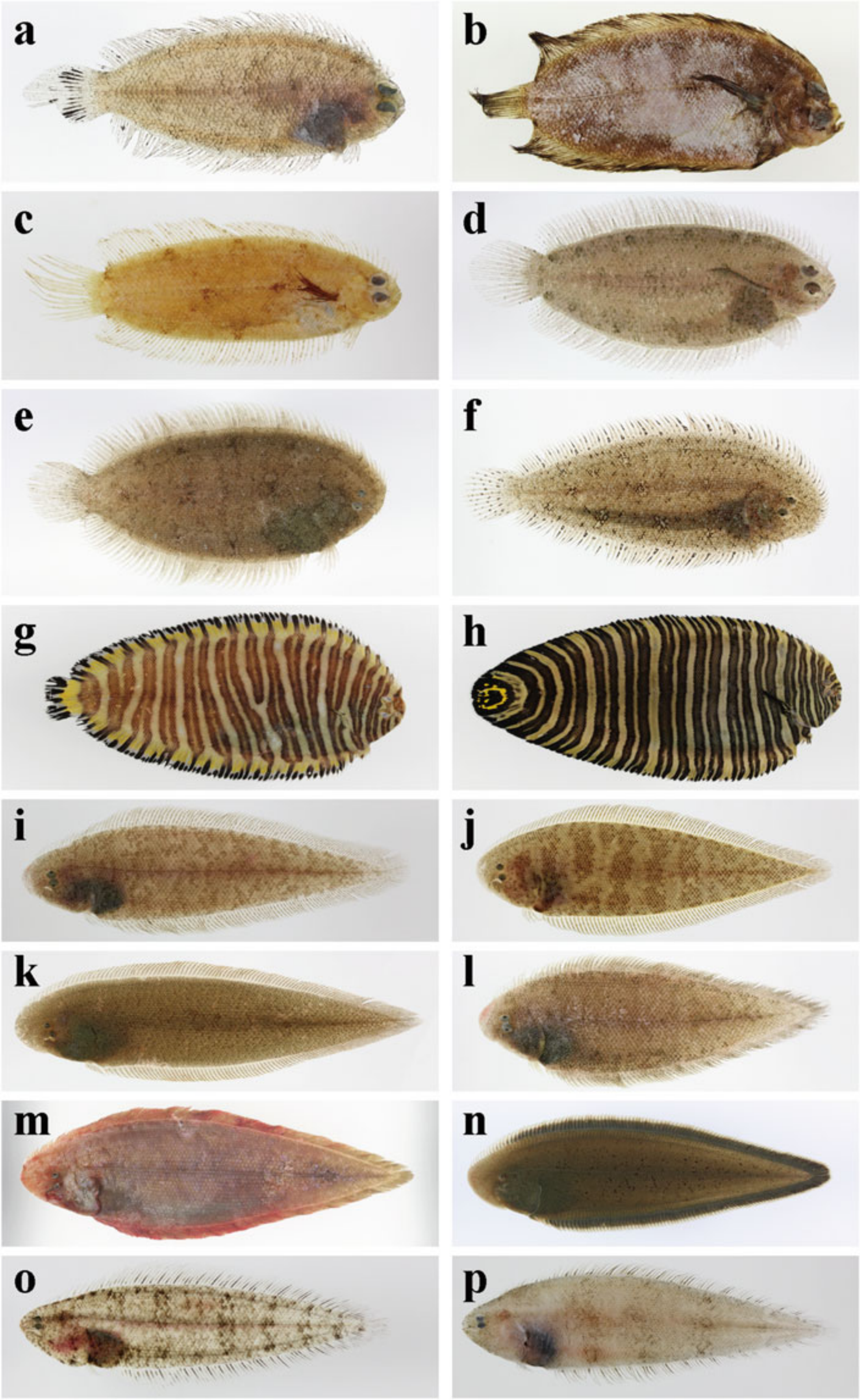

Fig. 6.6 Families Poecilopsettidae, Samaridae and Cynoglossidae. (**a**) *Poecilopsetta plinthus*, FAKU 138112; (**b**) *Plagiopsetta glossa*, NSMT-P 50613, preserved condition; (**c**) *Samariscus japonicus*, FAKU 58183, preserved condition; (**d**) *Samariscus xenicus*, FAKU 142395; (**e**) *Aseraggodes kobensis*, FAKU 136871; (**f**) *Heteromycteris japonica*, FAKU 136666; (**g**) *Pseudaesopis japonica*, FAKU 136720; (**h**) *Zebrias zebrinus*, FAKU 137215; (**i**) *Cynoglossus interruptus*, FAKU 136977; (**j**) *Cynoglossus itinus*, FAKU 145198; (**k**) *Cynoglossus joyneri*, FAKU 141526; (**l**) *Cynoglossus ochiaii*, FAKU 139735; (**m**) *Cynoglossus robustus*, FAKU 139705; (**n**) *Paraplagusia japonica*, FAKU 136970; (**o**) *Symphurus longirostris*, FAKU 139635; (**p**) *Symphurus orientalis*, FAKU 145360

Family Samaridae

Plagiopsetta glossa **Franz, 1910 [Japanese name: Berogarei] (Fig. 6.6b)**
Kinki-San'in: See Suzuki et al. (2000) ("OMNH-P7820," Shinonsen, Hyogo). ***Kyushu***: NSMT-P 50613, two specimens, 82.3–95.6 mm SL, off Tsushima, Nagasaki, July 1987; one additional specimen deposited in NSMT. ***Southern Korea***: See Park et al. (2007) (e.g., "NFRDI 20070104-01–10," off Jeju I.).

Samariscus japonicus **Kamohara, 1936 [Japanese name: Tsukinowagarei] (Fig. 6.6c)**
Kinki-San'in: FAKU 58183, 81.8 mm SL, off San'in (Yamaguchi to Tottori), July 1990; SNFR 19106, 34.2 mm SL, off Yamaguchi, June 12, 2012; two additional specimens deposited in SNFR. ***Southern Korea***: See Park et al. (2007) ("NFRDI 20070104-20," off Jeju I.).

Samariscus xenicus **Ochiai and Amaoka, 1962 [Japanese name: Kotsukinowagarei] (Fig. 6.6d)**
Kinki-San'in: FAKU 142395, 43 mm SL, Wakasa Bay, September 15, 2016; FAKU 134702, 43.3 mm SL, off Nagato, Yamaguchi, October 7, 2011; >10 additional specimens deposited in FAKU, HUMZ, and SNFR.

Family Soleidae

Aseraggodes kaianus **(Günther, 1880) [Japanese name: Moyouushinoshita]**
Southern Korea: See Park et al. (2007) ("NFRDI 20070104-35–37," off Jeju I.).

Aseraggodes kobensis **(Steindachner, 1896) [Japanese name: Tobisasaushinoshita] (Fig. 6.6e)**
Tohoku-Hokuriku: SNFR 118829, 88.6 mm SL, off Niigata, August 24, 2012; four additional specimens deposited in HUMZ and SNFR. ***Kinki-San'in***: FAKU 136871, 67.1 mm SL, Wakasa Bay, Kyoto, January 21, 2015; >10 additional specimens deposited in FAKU and HUMZ [see also Sonoyama et al. 2020 (e.g., "KPM-NR 198401 (photo only)," off Nagato, Yamaguchi)]. ***Southern Korea***: See Kim and Ryu (2016) (e.g., "PKU 1059," Busan).

Brachirus annularis **Fowler, 1934 [Japanese name: Wamonushinoshita]**
Southern Korea: See Kim et al. (2019) ("JNU 1503," between Jeju I. and Geomundo I.).

Heteromycteris japonica **(Temminck and Schlegel, 1846) [Japanese name: Sasaushinoshita] (Fig. 6.6f)**
Tohoku-Hokuriku: FAKU 137088, three specimens, 23.4–68.2 mm SL, off Tsugaru, Aomori, 5 September 2000; >10 additional specimens deposited in FAKU and HUMZ. ***Kinki-San'in***: FAKU 136666, 67.8 mm SL, Wakasa Bay, Kyoto, December 22, 2014; >10 additional specimens deposited in FAKU [see also Sonoyama et al. 2020 ("HH-Pi 1436," Houhoku, Shimonoseki, Yamaguchi)].

Pseudaesopis japonica **(Bleeker, 1860) [Japanese name: Setoushinoshita] (Fig. 6.6g)**
Tohoku-Hokuriku: FAKU 13804, 126.6 mm SL, off Uozu, Toyama, September 13, 1950; two additional specimens deposited in FAKU and HUMZ. ***Kinki-San'in***: FAKU 136720, 114.1 mm SL, off Ine, Kyoto, December 2014; >10 additional specimens deposited in FAKU and HUMZ [see also Sonoyama et al. 2020 ("HH-Pi 2620," off Izaki, Shimonoseki, Yamaguchi)]. ***Southern Korea***: See Kim and Ryu (2016) (e.g., "PKU 7762," Namhae). ***Eastern Korea***: See Kim and Ryu (2016) ("PKU 6913," Pohang).

Zebrias zebrinus **(Temminck and Schlegel, 1846) [Japanese name: Shimaushinoshita] (Fig. 6.6h)**
Tohoku-Hokuriku: HUMZ 61842, 174.5 mm SL, off Sado I., Niigata, October 19, 1976; >10 additional specimens deposited in FAKU and HUMZ. ***Kinki-San'in***: FAKU 137215, 174.7 mm SL, Miyazu, Kyoto, March 29, 2015; >10 additional specimens deposited in FAKU and NSMT. ***Southern Korea***: See Kim and Ryu

(2016) as *Zebrias fasciatus* (e.g., "PKU 563," Namhae). **Remarks**: *Zebrias fasciatus* (Basilewsky, 1855) was recently synonymized with *Zebrias zebrinus* by Wang et al. (2014).

Family Cynoglossidae

***Cynoglossus abbreviatus* (Gray, 1834) [Japanese name: Kouraiakashitabirame]**
Southern Korea: See Kim and Choi (1994) (e.g., "CNUC 18847," Yeosu).

***Cynoglossus interruptus* Günther, 1880 [Japanese name: Genko] (Fig. 6.6i)**
Tohoku-Hokuriku: HUMZ 135405, 130.1 mm SL, off Sakata, Yamagata, August 5, 1994; >10 additional specimens deposited in HUMZ. ***Kinki-San'in***: FAKU 136977, 97.8 mm SL, Wakasa Bay, Kyoto, March 9, 2015; >10 additional specimens deposited in FAKU, HUMZ, and SNFR. ***Kyushu***: FAKU 137523, 103.6 mm SL, off Meinohama, Fukuoka, April 19, 2015. ***Southern Korea***: See Kwun and Kim (2016) ("PKU 7469–7472," Changwon).

***Cynoglossus itinus* (Snyder, 1909) [Japanese name: Minamiakashitabirame] (Fig. 6.6j)**
Kinki-San'in: FAKU 145198, 91 mm SL, Wakasa Bay, Kyoto, June 29, 2017; >10 additional specimens deposited in FAKU. ***Kyushu***: NSMT-P 5479, 87.6 mm SL, Izumi Bay, Tsushima I., Nagasaki, August 1968.

***Cynoglossus joyneri* Günther, 1878 [Japanese name: Akashitabirame] (Fig. 6.6k)**
Tohoku-Hokuriku: FAKU 135929, 2 specimens, 47.4–52.9 mm SL, Mano Bay, Sado I., Niigata, May to July 2002; four additional specimens deposited in SNFR. ***Kinki-San'in***: FAKU 141526, 137 mm SL, Wakasa Bay, Kyoto, June 8, 2016; two additional specimens deposited in FAKU and SNFR. ***Kyushu***: FAKU 137406, off Genkai I., Fukuoka., 18 April 2015; >10 additional specimens deposited in FAKU. ***Southern Korea***: See Kim and Choi (1994) (e.g., "CNUC 18860," Wando). ***Eastern Korea***: See Kim and Ryu (2016) ("PKU 20555," eastern coast off Korea).

***Cynoglossus ochiaii* Yokogawa, Endo and Sakaji, 2008 [Japanese name: Okigenko] (Fig. 6.6l)**
Tohoku-Hokuriku: FAKU 13834, 13836, two specimens, 127.4–166.6 mm SL, off Uozu, Toyama, September 13, 1950. ***Kinki-San'in***: FAKU 139735, 179 mm SL, Wakasa Bay, Kyoto, December 9, 2015; FAKU 134700, 139.9 mm SL, off Oumi-jima I., Yamaguchi, November 18, 2018; >10 additional specimens deposited in FAKU and SNFR.

***Cynoglossus robustus* Günther, 1873 [Japanese name: Inunoshita] (Fig. 6.6m)**
Kinki-San'in: FAKU 139705, 400.7 mm SL, Wakasa Bay, Kyoto, December 2, 2015; one additional specimen deposited in FAKU. ***Kyushu***: FAKU 137395, 279.8 mm SL, off Genkai I., Fukuoka, April 18, 2015; three additional specimens deposited in FAKU. ***Southern Korea***: See Kim and Choi (1994) (e.g., "CNUC 18853–18855," Yeosu).

***Cynoglossus semilaevis* Günther, 1873 [Japanese name: Karaakashitabirame]**
Southern Korea: See Kim and Choi (1994) (e.g., "CNUC 19370–19375," Yeosu).

***Paraplagusia japonica* (Temminck and Schlegel, 1846) [Japanese name: Kuroushinoshita] (Fig. 6.6n)**
Hokkaido: HUMZ 109954, 180.0 mm SL, off Tomari, Hokkaido, November 13, 1986. ***Tohoku-Hokuriku***: FAKU 137015, two specimens, 132.9–150.9 mm SL, off Akita, August 4, 1997; >10 additional specimens deposited in FAKU and HUMZ. ***Kinki-San'in***: FAKU 136970, 222.1 mm SL, Wakasa Bay, Kyoto, March 4, 2015; >10 additional specimens deposited in FAKU. ***Kyushu***: FAKU 137084, three specimens, 69.6–160.8 mm SL, Karatsu, Saga, April 20, 1997; one additional specimen deposited in FAKU. ***Southern Korea***: See Kim and Choi (1994) (e.g., "CNUC 19173–19180,"

Yeosu). ***Eastern Korea***: See Kim and Choi (1994) (e.g., “CNUC 19815,” Samcheok).

Symphurus longirostris **Lee, Munroe and Kai, 2016 [Japanese name: Hashinagaazumagarei] (Fig. 6.6o)**
Tohoku-Hokuriku: FAKU 137988, 31.5 mm SL, off Niigata, March 6, 2015. ***Kinki-San’in***: FAKU 139635, 42.0 mm SL, Wakasa Bay, November 17, 2015; >10 additional specimens deposited in FAKU and HUMZ [see also Sonoyama et al. 2020 (“SNFR 19821,” off Yamaguchi)].

Symphurus orientalis **(Bleeker, 1879) [Japanese name: Azumagarei] (Fig. 6.6p)**
Kinki-San’in: FAKU 145360, 75.9 mm SL, off Mishima I., Yamaguchi.

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Fish Diversity of Subarctic Waters in Japan

7

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Abstract

The fish diversity of the subarctic waters in Japan is reviewed and its origin is discussed in this chapter. The subarctic waters in Japan, including Hokkaido and the Pacific coast of Tohoku District, are dominated mainly by cold currents, viz. Oyashio, Liman, and East Sakhalin currents, and by minor branches of the Tsushima Warm Current. Most of the species known in the region are cold-water inhabitants, also occurring in the Bering Sea, Arctic Ocean, and Gulf of Alaska; warm-water inhabitants are known from southern Hokkaido, as well as from the southern Sea of Okhotsk in summer. The number of warm-water inhabitants has been increasing in these decades, which can be attributed to habitat shifts following global warming. Hokkaido is an island surrounded by the Seas of Japan and Okhotsk and the Pacific Ocean, and these three regions are connected with narrow and shallow straits. The present distributions of deep-sea fishes are suggested to have been shaped by vicariance events, primarily sea level regression, during glacial periods in contrast with those of shallow-water species that are largely affected by current systems in the western North Pacific region.

Keywords

Fish fauna · Hokkaido · Cold-water inhabitants · Biogeography

7.1 Physical Characteristics

The subarctic region of the North Pacific Ocean is generally considered to be the area bounded by the Bering Strait to the north and the Subarctic Front to the south (Willis et al. 1988). The Subarctic Front is found at approximately 40° N between the cold, low salinity upper waters of the subarctic Pacific, and the warm, high salinity waters of the central North Pacific. In the western North Pacific, Hokkaido Island, except for its Pacific coast, is included in the subarctic region. The Pacific coast of Hokkaido and northern Honshu Islands are in the transition zone, a region of faunal mixing between the subarctic and subtropical fish faunas (Parin 1961) (Fig. 7.1).

Among the six marine climatic regimes in Japan's Exclusive Economic Zone (EEZ) (Nishimura 1992; Fujikura et al. 2010), the northern part of Japan, including Hokkaido and the Pacific coast of Tohoku District (referred as subboreal and cool-temperate zones), is dominated by cold currents, viz. Oyashio, Liman, and East Sakhalin currents (Fig. 7.1).

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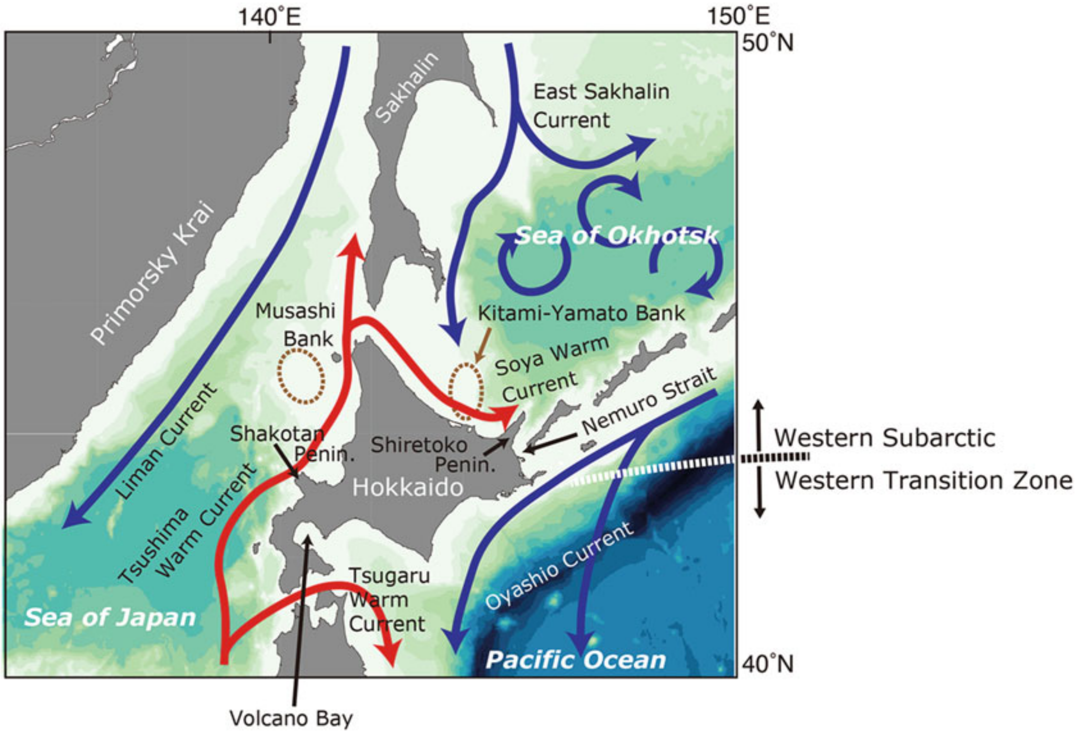

Fig. 7.1 Subarctic waters in Japan, showing current systems and major localities cited in the text

The Oyashio Current, one of the major cold currents, flows southward through Japanese waters from off Hokkaido along the Pacific coast. From the southern Sea of Japan, the Tsushima Warm Current flows along the Sea of Japan coast of Hokkaido northward to Cape Soya. However, most of the Tsushima Warm Current flows out through the Tsugaru Strait to the Pacific Ocean (the so-called Tsugaru Current). The southern part of Hokkaido, the Sea of Japan coast of Tohoku District, and the northern tip of the Pacific coast of Tohoku District belong to the warm temperate zone influenced by the Tsushima and Tsugaru currents. The Soya Current, a branch of the Tsushima Warm Current, flows along the Sea of Okhotsk. The current is induced by the sea level difference between the Seas of Japan and Okhotsk, which shows a remarkable seasonal variation, being strong in summer and weak in winter (Matsuyama et al. 2006). Owing to the Soya Current, warm-water inhabitants that moved north from the Sea of Japan are frequently recorded in the Sea of Okhotsk in summer (e.g., Takata et al. 2009; Ogimoto et al. 2014). The Sea of Okhotsk coast of Hokkaido is covered with sea ice in winter, being the southern limit of sea ice in the Northern Hemisphere. Due to high nutrient input from melting sea ice, winter vertical mixing, and seasonal upwelling of water, the southern part of the Sea of Okhotsk possesses a rich and unparalleled marine ecosystem (Sakurai 2007, 2013).

Hokkaido is an island surrounded by the Seas of Japan and Okhotsk and the Pacific Ocean (Fig. 7.1). The Seas of Japan and Okhotsk are connected by the Soya (La Pérouse) Strait (maximum depth ~70 m), and the Sea of Japan with the Pacific by the Tsugaru Strait (maximum depth ~140 m). The Kuril Islands separate the Sea of Okhotsk and the Pacific, with the passes between adjacent islands being relatively shallow—most not exceeding 100 m, except for the Krusenstern Strait (1920 m depth) and the Bussol Strait (2318 m depth) (Nishimura 1983). For some deep-sea fishes, such as *Bathyraja smirnovi*, *Bothrocara hollandi*, and *Davidijordania poecilimon*, the shallow straits act as physical barriers resulting in fine genetic population structures among the Seas of Japan and Okhotsk and the Pacific Ocean (Kodama et al. 2008; Kai et al. 2015; Misawa et al. 2020). Furthermore, the presumed vicariant species *Cottiusculus schmidti* and *Cottiusculus nihonkaiensis* are separated by the Tsugaru Strait and are presently forming a hybrid zone across the strait (Kai and Nakabo 2009; Kai and Yamanaka 2019). Similarly, *Careproctus rastrinus*, *Careproctus trachysoma*, and *Careproctus pellucidus* are found in the Sea of Okhotsk, Sea of Japan, and Pacific coast of northern Japan, respectively (Kai et al. 2011a, b; Orr et al. 2015), a distribution likely determined by vicariant events, such as sea level regression, at the shallow straits between these bodies of water. Later, Yashiki et al. (2020) suggested hybridization between *C. rastrinus* and *C. pellucidus*.

Two major offshore banks off Hokkaido, Kitami-Yamato Bank in the southern Sea of Okhotsk and Musashi Bank in the northern Sea of Japan, boast rich fishing grounds (Fig. 7.1). One commercially important fish in Hokkaido, *Sebastolobus macrochir* settles around Kitami-Yamato Bank and neighboring Abashiri Bay in the Sea of Okhotsk, and rarely migrates across the entire distribution area after settlement (Sakaguchi et al. 2014). Musashi Bank is well known as one of the nursery grounds of Walleye Pollock, *Gadus chalcogrammus* (see Uchida and Watanobe 2008), and Sôhachi, *Cleisthenes pinetorum* (see Nagasawa 1990). Accordingly, many fisheries surveys have been conducted on both banks (e.g., Hikita 1950; Amaoka et al. 1983; Yabe et al. 1991; Tohkairin et al. 2015).

7.2 Fish Fauna of Hokkaido

The fish fauna of subarctic waters in Japan, including Hokkaido and northern Honshu islands, has been variously investigated. Several local reports on fish fauna were published in the mid-1900s (e.g., Hikita 1950; Kobayashi 1962), but no comprehensive reports on the fish fauna covering the region were available until the study of Ueno (1971), who listed over 690 species from Hokkaido and adjacent areas, including the Pacific coast of Honshu Island, southern Sakhalin, and the Kuril islands. In a monograph of fisheries in Hokkaido, Maeda and Tsutsui (2003) listed 720 species from Hokkaido, including freshwater species. More recently, Amaoka et al. (2011) listed 651 species from Hokkaido, and in its updated version, Amaoka et al. (2020) listed 823 species with photo(s) and a brief description for each species, including freshwater species. According to Amaoka et al. (2020), the ratio of warm-water inhabitants recorded from Hokkaido was 44% in 2020, up from 39% in Amaoka et al. (2011). The growing number of species recorded in Hokkaido is partly attributed to habitat shifts of warm-water inhabitants following global warming (Amaoka et al. 2020). Miyazaki et al. (2015) summarized the species with range extensions to Hokkaido from the year 2000, implicating the effects of global warming.

The marine fish fauna of Hokkaido is herein summarized in Table 7.1 on the basis of Maeda and Tsutsui (2003), Nakabo (2013), Amaoka et al. (2020), Motomura (2021), and the Fish Collection of Kyoto University. There are 771 marine species in 51 orders of fishes and two *incertae sedis* families of Ovalentaria (Embiotocidae and Pomacentridae), if the classification of Nelson et al. (2016) is accepted. The order with the greatest number of species in the region is Scorpaeniformes with 291 species. The representative families of Scorpaeniformes are Cottidae (60 species), Zoarcidae (48 species), Liparidae (43 species), Stichaeidae (39 species), Sebastidae (25 species), and Agonidae (22 species). Most of the species of these families also occur in the Bering Sea, Arctic Ocean, and Gulf of Alaska.

The members of Cottidae are primarily inhabitants of cold waters, mostly known from the North Pacific (Mecklenburg et al. 2002). More than 120 marine cottoid species are known from the eastern North Pacific (Allen and Smith 1988) and 88 from Alaskan waters (Mecklenburg et al. 2002; Stevenson 2006, 2015; Maslenikov et al. 2013). Currently 83 species are known from Japan (Motomura 2021), and Hokkaido, with two

Table 7.1 The numbers of species by orders known from Hokkaido, Japan

Order	Total	Sea of Okhotsk		Pacific coast		Sea of Japan	
Scorpaeniformes	291	216	(0.74)	193	(0.66)	149	(0.51)
Pleuronectiformes	40	26	(0.65)	33	(0.83)	32	(0.80)
Tetraodontiformes	35	5	(0.14)	28	(0.80)	19	(0.54)
Perciformes	32	4	(0.13)	26	(0.81)	17	(0.53)
Scombriformes	29	3	(0.10)	26	(0.90)	16	(0.55)
Rajiformes	22	17	(0.77)	15	(0.68)	7	(0.32)
Myctophiformes	22	6	(0.27)	21	(0.95)	0	(0.00)
Gobiiformes	22	2	(0.09)	17	(0.77)	12	(0.55)
Carangiformes	22	4	(0.18)	22	(1.00)	10	(0.45)
Gadiformes	19	13	(0.68)	18	(0.95)	4	(0.21)
Anguilliformes	18	5	(0.28)	16	(0.89)	2	(0.11)
Lophiiformes	17	5	(0.29)	16	(0.94)	4	(0.24)
Stomiiformes	14	3	(0.21)	13	(0.93)	2	(0.14)
Aulopiformes	13	5	(0.38)	11	(0.85)	1	(0.08)
Beryciformes	11	4	(0.36)	11	(1.00)	0	(0.00)
Beloniformes	11	3	(0.27)	11	(1.00)	7	(0.64)
Carcharhiniformes	9	4	(0.44)	7	(0.78)	7	(0.78)
Lampriformes	9	1	(0.11)	9	(1.00)	4	(0.44)
Syngnathiformes	9	0	(0.00)	7	(0.78)	5	(0.56)
Callionymiformes	9	1	(0.11)	7	(0.78)	7	(0.78)

Numbers in parentheses show the ratio of number of species in each region to the total number of species

thirds of these species is a hotspot of cottoid diversity in the western North Pacific. Marine species are generally found on shallow reefs, soft sediments, and in kelp forests near shore and continental shelf, but sometimes found farther offshore and on deep reefs (Love 2011). On the basis of the phylogenetic hypothesis from morphological evidence, Yabe (2011) considered that shallow coastal species having narrow distributional areas were derived from deep offshore species having wide distributional ranges. For example, among the genera related to *Alcichthys* (*Pseudoblennius*, *Furcina*, *Ocynectes*, and *Vellitor*), *Alcichthys alcicornis*, known from the Seas of Japan and Okhotsk and the Pacific coast of Japan, is considered the most primitive species inhabiting deeper waters (~269 m depth) (Yabe 2011; Nakabo and Kai 2013). The species of the derived genera *Pseudoblennius*, *Furcina*, *Ocynectes*, and *Vellitor* are known from the shallow coastal areas of very restricted regions. Interestingly, Yabe (2011) pointed out that the derived species have generally small bodies and more southerly distributions. This hypothesis is partly supported by the recent molecular phylogenetic study by Knope (2013). In addition, Knope and Scales (2013) have shown that reduction of body size is one of the adaptive morphological shifts to shallow waters.

Eelpouts, family Zoarcidae, are benthic fishes comprising more than 240 species, most of them known from the North Pacific, North Atlantic, and Arctic oceans (Mecklenburg et al. 2002; Anderson and Fedorov 2004). Around Hokkaido, the number of eelpout species are higher in the Sea of Okhotsk (40 species) than the Sea of Japan (18 species) and the Pacific Ocean (17 species). The species compositions of the Sea of Japan and the Pacific coast are quite different, sharing only four species. In contrast, 14 species are shared between the Seas of Okhotsk and Japan, and 12 species between the Sea of Okhotsk and the Pacific coast. Nishimura (1967) considered that the deep-sea fishes of the Sea of Japan, especially eelpouts, have been derived from the ancestral species occurring in the Sea of Okhotsk and the Bering Sea, because morphologically similar species are known from respectively the Sea of Japan and the latter regions. For example, *Petroschmidtia toyamensis*, endemic to the Sea of Japan, is most closely related with *Petroschmidtia albonotata*, endemic to the Sea of Okhotsk, being well supported from both morphological and genetic evidences (Toyoshima 1985; Kai unpublished data). *Gymnelopsis japonicus* and *Lycodes yamatoi* were formerly considered as endemic species to the Sea of Japan, and their relatives, *Gymnelopsis ochotensis* and *Lycodes matsubarai*, respectively, were known only from the Sea of Okhotsk. However, the former two species are now considered as synonymous under the latter two species (Anderson 1982; Nazarkin and Shinohara 2012). On the basis of variations on mitochondrial DNA, Sakuma et al. (2014) demonstrated that genetic differentiations between the Seas of Japan and Okhotsk populations of *L. matsubarai*, as well as difference demographic history between them, and suggested that the population in the Sea of Okhotsk had a larger effective population size than that in the Sea of Japan.

Members of the family Liparidae (snailfishes), comprising over 430 species in ~30 genera worldwide, exhibit great diversity in morphology, as well as in geographic and habitat range (Chernova et al. 2004; Nelson et al. 2016; Fricke et al. 2021), occurring worldwide in warm temperate to cold water habitats ranging from intertidal to depths exceeding 8000 m (Nelson et al. 2016; Gerringer et al. 2017). Many species of snailfishes are uncommon or rare and several are only known from holotypes (Sakurai and Shinohara 2008), and large number of new species are still being described (e.g., Stein 2012; Gerringer et al. 2017; Orr 2020; Orr et al. 2020). The speciation and phenotypic evolutionary rates are estimated to be high in high-latitude and deep-sea fishes, especially in snailfishes (Rabosky et al. 2013). Currently, 69 species of snailfishes are known from Japanese waters, 47 of which being recorded from subarctic waters (Nakabo and Kai 2013; Kai et al. 2021; Motomura 2021; Murasaki et al. 2021). Around Hokkaido, three species, *Careproctus longidigitus*, *Careproctus shigemii*, and *Elassodiscus nyctereutes*, were recently described (Kai and Matsuzaki 2019; Kai et al. 2020; Matsuzaki et al. 2020). Snailfishes are considered to have direct development without planktonic stage, a characteristic likely to have influenced the high diversity and endemism of the family (Chernova et al. 2004).

The second most diverse order in the region is Pleuronectiformes with 40 species (Table 7.1). Of these, 35 species belong to family Pleuronectidae, which includes mostly cold-water inhabitants. In fact, 35% of these also occur in the Bering Sea. Most of the Japanese species are commercially important, such as *Cleisthenes pinetorum*, *Hippoglossoides dubius*, *Glyptocephalus stelleri*, and *Lepidopsetta mochigarei*. *Verasper variegatus* has a high commercial value; however, it is categorized as NT (Near Threatened) in the Red List compiled by the Ministry of the Environment, Japan (2017).

The third, fourth, and fifth most diverse orders are Tetraodontiformes, Perciformes, and Scombriformes, respectively (Table 7.1). They are mainly distributed in temperate or warm waters and dispersed by warm ocean currents of the Tsushima Warm Current and its branches. In fact, only 3–7% of the species known from Hokkaido also occur in the Bering Sea. The sixth and seventh most diverse orders, Gobiiformes and Carangiformes, are also primarily comprised of warm-water species, all being absent from the Bering Sea. These species dispersed from southern Japan via warm currents have been known from the earlier reports, before global warming was especially evident. For example, Sakurai et al. (1972) reported *Decapterus tabl* and *Alectis ciliaris* (Carangiformes), *Tetrosomus reipublicae* and *Mola mola* (Tetraodontiformes), and *Trichiurus japonicus* (Scombriformes) from eastern Hokkaido.

Other less divergent orders are Rajiformes and Myctophiformes (Table 7.1). Within Rajiformes, the family with the greatest number of species around Hokkaido is Arhynchobatidae with 17 species. Members of Arhynchobatidae occur in all oceans but are most abundant in polar and cool temperate regions (Last et al. 2016), mainly inhabiting continental slopes and abyssal plains to more than 3000 m depth. The low dispersal ability of Rajiformes owing to their large benthic egg capsules and the absence of a pelagic larval stage often has resulted in fine-scale population structure within species (Misawa et al. 2019). Such characteristics have influenced their high diversity, as is the case with snailfishes. In contrast, morphologically defined species sometimes show little or no genetic divergence, requiring further taxonomic revisions (Orr et al. 2011; Spies et al. 2011; Misawa et al. 2020).

Myctophiformes around Hokkaido is composed of two families: Neoscopelidae (2 species) and Myctophidae (20 species). Within the order, 21 species are known from the Sea of Okhotsk and 6 from the Pacific coast. However, no myctophiform species are known from the Sea of Japan, except for pelagic larva possibly transported accidentally by the Tsushima Warm Current (Nishimura 1983). Most species of the deep-sea fauna of the Sea of Japan are boreal, only recently evolving into a deep-sea mode of life—so-called secondary deep-sea species (Sutton et al. 2017). The absence of "true" deep-sea fishes in the Sea of Japan has been considered a result of the short period of time available for colonization. Because the Sea of Japan is a semi-enclosed sea, connected with neighboring waters by shallow and narrow straits, it was almost isolated during the last glacial maximum due to sea level regression (Tada 1994). Subsequently, the circulation pattern has been invigorated by the surface production of cold water resulting from winter surface cooling in the post-glacial period, and this has ventilated the deeper waters and allowed reinvasion of deep areas (Tyler 2002; Chap. 3).

7.3 Endemic Species

Some endemic species are reported from subarctic waters in Japan. The southern Sea of Okhotsk off Hokkaido is known to possess a high endemism of fishes. Two liparid fishes, *Careproctus bathycoetus* (Fig. 7.2a) and *Careproctus homopterus*, are only known from the holotypes collected from the region (Gilbert and Burke 1912; Kido 1988; Chernova et al. 2004). Because the two species of *Careproctus* inhabit deeper waters (3294 m and 805 m, respectively), more comprehensive surveys in deeper areas make it likely that additional individuals will be added. Although several specimens have been recorded, the distributions of the cottids *Icelus ecornis* and *Icelus mandibularis* (Fig. 7.2b) and *Careproctus segaliensis* are restricted to the southern Sea of Okhotsk (Yabe 1983; Tsutsui and Yabe 1996; Tohkairin et al. 2015). In addition, four species of the genus *Careproctus*—*Careproctus longidigitus* (Fig. 7.2c), *Careproctus shigemii* (Fig. 7.2d), *Careproctus parvidiscus* (Fig. 7.2e), and *Careproctus rausuensis*—have been collected from the more restricted region of the Shiretoko Peninsula, southern Sea of Okhotsk (Fig. 7.1) (Imamura and Nobetsu 2002; Machi et al. 2012; Kai and Matsuzaki 2019; Matsuzaki et al. 2020; Kai et al. 2020). The cottoid *Ricuzenius nudithorax* (Fig. 7.2f) is known only from the holotype collected from the Shiretoko Peninsula (Bolin 1936), and in addition, Nobetsu (2003) recorded a specimen of an unidentified genus and species of Cottidae from the region. The Shiretoko Peninsula, located at the southernmost part of the Sea of Okhotsk, is surrounded by steep volcanic cliffs that fall off to the deep sea without a distinct continental shelf. It is true that the southern Sea of Okhotsk can be characterized as having high endemism, but numerous records of rare species from the region may be due to the easy accessibility to the deep area of the Shiretoko Peninsula. The origin of endemism and patterns of speciation around the southern Sea of Okhotsk remains to be demonstrated by rigorous phylogenetic studies of the genera involved.

Along the Pacific coast of Hokkaido, two species are known to have a very limited distributional area: *Artediellus neyelovi* (Cottidae) from the Pacific coast of southwestern Hokkaido and *Neolumpenus unocellatus* (Stichaeidae) from the Pacific coast of eastern Hokkaido (Miki et al. 1987; Muto et al. 1994). The latter is only known from the holotype obtained from the stomach contents of *Gadus macrocephalus*. Similarly, *Xenolumpenus longipterus* (Stichaeidae) had been known only from the holotype and a paratype collected from the Sea of Japan coast of southern Hokkaido (Shinohara and Yabe 2009), but Zemnukhov

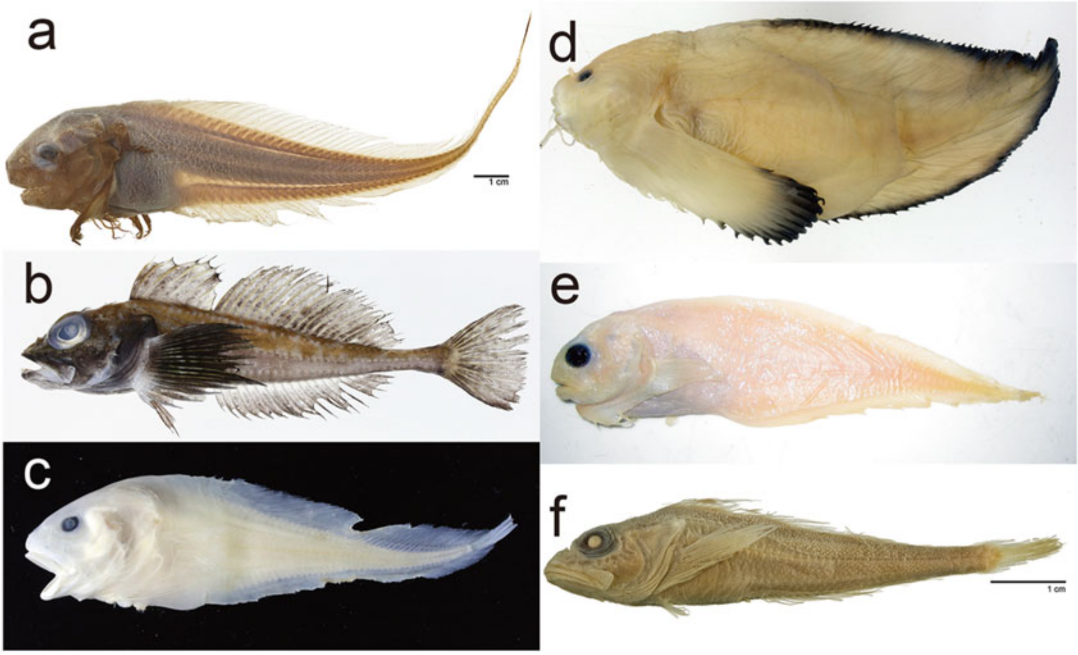

Fig. 7.2 Endemic species known from subarctic waters in Japan. (**a**) *Careproctus bathycoetus*, USNM 73337 (the Smithsonian Institution, National Museum of Natural History, Suitland, USA), 155.7 mm SL, holotype. (Photo by S. Raredon). (**b**) *Icelus mandiburalis*, FAKU 146891 (Kyoto University), 157.4 mm SL; (**c**) *Careproctus longidigitus*, FAKU 146739, 195.9 mm SL, holotype; (**d**) FAKU 146746, 203.5 mm SL, holotype; (**e**) *Careproctus parvidiscus*, HUMZ 164407 (the Hokkaido University Museum), 167.7 mm SL, holotype; (**f**) *Ricuzenius nudithorax*, USNM 102104, 60.7 mm SL, holotype. (Photo by S. Raredon)

et al. (2013) reported two additional species collected from the Sea of Japan coast of Russia and the southern Sea of Okhotsk.

Recent advances in scientific technical diving in mesophotic coral ecosystems have documented the presence of unidentified species (Pinheiro et al. 2016). In subarctic waters of Japan, scientific technical diving has revealed the fish diversity of previously unexplored rocky reefs (e.g., Tsuruoka et al. 2006, 2009a, b; Yamazaki et al. 2015), leading to the discovery of *Icelus sekii* in Hokkaido at the depth of 20 m (Tsuruoka et al. 2006).

7.4 Distributional Pattern

7.4.1 Shallow-Water Fishes

After the comprehensive faunal study of Ueno (1971), Yabe et al. (1991) investigated the fish fauna of northern Hokkaido, including Musashi Bank, and listed 104 species, 83% of them being cold-water inhabitants. They concluded that the fish fauna of the region was largely affected by the cold East Sakhalin and Liman currents, rather than the weak Tsushima Warm Current. Similarly, the Pacific coast of eastern Hokkaido is strongly dominated by the cold Oyashio Current, and Matsuura et al. (1993) showed that 93% of the recorded fishes from the region were cold-water inhabitants. The fish fauna of the southern Sea of Okhotsk, including the Nemuro Strait between Hokkaido and the Kunashiri Islands (Fig. 7.1), was investigated by Hikita (1951) and Shinohara et al. (2012). The latter reported 138 species, 78% of them being cold-water inhabitants. Nobetsu (2003) reported several warm-water inhabitants from the Shiretoko Peninsula (north of Nemuro Strait) and concluded that they were dispersed by the Soya Warm

Current, a branch of Tsushima Warm Current, in summer. In fact, Kubo (1981) noted that the coastal area of the Shiretoko Peninsula is strongly affected by the Soya Warm Current in summer. Off the Pacific coast of southern Hokkaido, the number of cold-water inhabitants is more limited, as demonstrated by several studies (Hikita 1951; Amaoka et al. 1989). Hikita (1951) noted that 85 out of the 141 species (60%) that occurred in Volcano Bay were warm-water inhabitants, owing to the influence of the warm Tsugaru Warm Current, a branch of the Tsushima Warm Current flowing from the East China Sea through the Sea of Japan. Along the Sea of Japan coast of Hokkaido, the Shakotan Peninsula likely hinders the extension and establishment of warm-water inhabitants (Miyazaki et al. 2015). Nakabo (2013) considered that Volcano Bay and the Shakotan Peninsula are the northern distributional limit of warm-water inhabitants occurring on the continental shelf (Fig. 7.1).

7.4.2 Deep-Sea Fishes

The deep-sea fishes that occur in the subarctic waters of Japan exhibit a wide range of divergence from fish populations or species in the Bering Sea and Arctic Ocean. Watling et al. (2013) proposed a classification of the lower bathyal biogeographic provinces of the world by incorporating high-resolution hydrographic and organic-matter flux data. According to them, the Seas of Japan and Okhotsk and the Pacific off Hokkaido are included in the "Northern Pacific Boreal" province with the Aleutian Ridge, Gulf of Alaska, Mathematicians Seamounts in the eastern Pacific, and the Emperor Seamounts. However, recent molecular studies have indicated more small-scale structure. For example, Kai et al. (2011a, b) and Orr et al. (2015) demonstrated that snailfishes of the *Careproctus rastrinus* species complex comprised nine species, most of them parapatrically distributed (Fig. 7.3a). In the western North Pacific including Japan, four species are recognized: *Careproctus rastrinus* from the Sea of Okhotsk, *Careproctus trachysoma* and *Careproctus acanthodes* from the Sea of Japan, and *Careproctus pellucidus* from the Pacific coast of Japan. Kai et al. (2011a) suggested that colder climates from the late Pliocene and the isolation of marginal seas during the Pleistocene may have driven the divergence of the *C. rastrinus* species complex from an ancestral species widely distributed in the North Pacific. A similar pattern of divergence can be seen in zoarcid species of subgenus *Furcimanus* sensu Stevenson and Sheiko (2009), comprising six species (*Lycodes diapterus*, *Lycodes beringi*, *Lycodes hubbsi*, *Lycodes nakamurae*, *Lycodes pectoralis*, and *Lycodes nishimurai*). On the basis of mitochondrial COI sequences deposited in INSDIC (International Nucleotide Sequence Database Collaboration), six haplotype groups are recognized here, most of which are almost parapatrically distributed (Fig. 7.3b). Four haplotype groups are recognized around Japan; one from the Sea of Okhotsk, the other mainly from the Pacific coast, and the remaining two from the northern and southern Sea of Japan, respectively. This distributional pattern is similar to that of the *Careproctus rastrinus* species complex, suggesting the divergence resulted from isolation among marginal seas. Four nominal species of *Furcimanus* are known from Japan (*L. hubbsi*, *L. nakamurae*, *L. nishimurai*, and *L. pectoralis*), and a taxonomic study will be required to determine the relationships between the nominal species and haplotype groups. Two psychrolutid species, *Malacocottus zonurus* and *Malacocottus gibber*, are also parapatrically distributed in the western North Pacific (Stevenson 2015) (Fig. 7.3c). The former is known from the Pacific coast of Japan, Sea of Okhotsk, Bering Sea, and the Gulf of Alaska to Washington State, and the latter only from the Sea of Japan, suggesting the vicariance event following the isolation of the Sea of Japan during the glacial periods led to its speciation. However, no genetic divergence between the two species in the mitochondrial control region were found by Adachi et al. (2009).

Divergence patterns in the lumpsuckers of the *Eumicrotremus asperrimus* species complex (Fig. 7.3d) and in *Aptocyclus ventricosus* (Fig. 7.3e) have been considered the result of

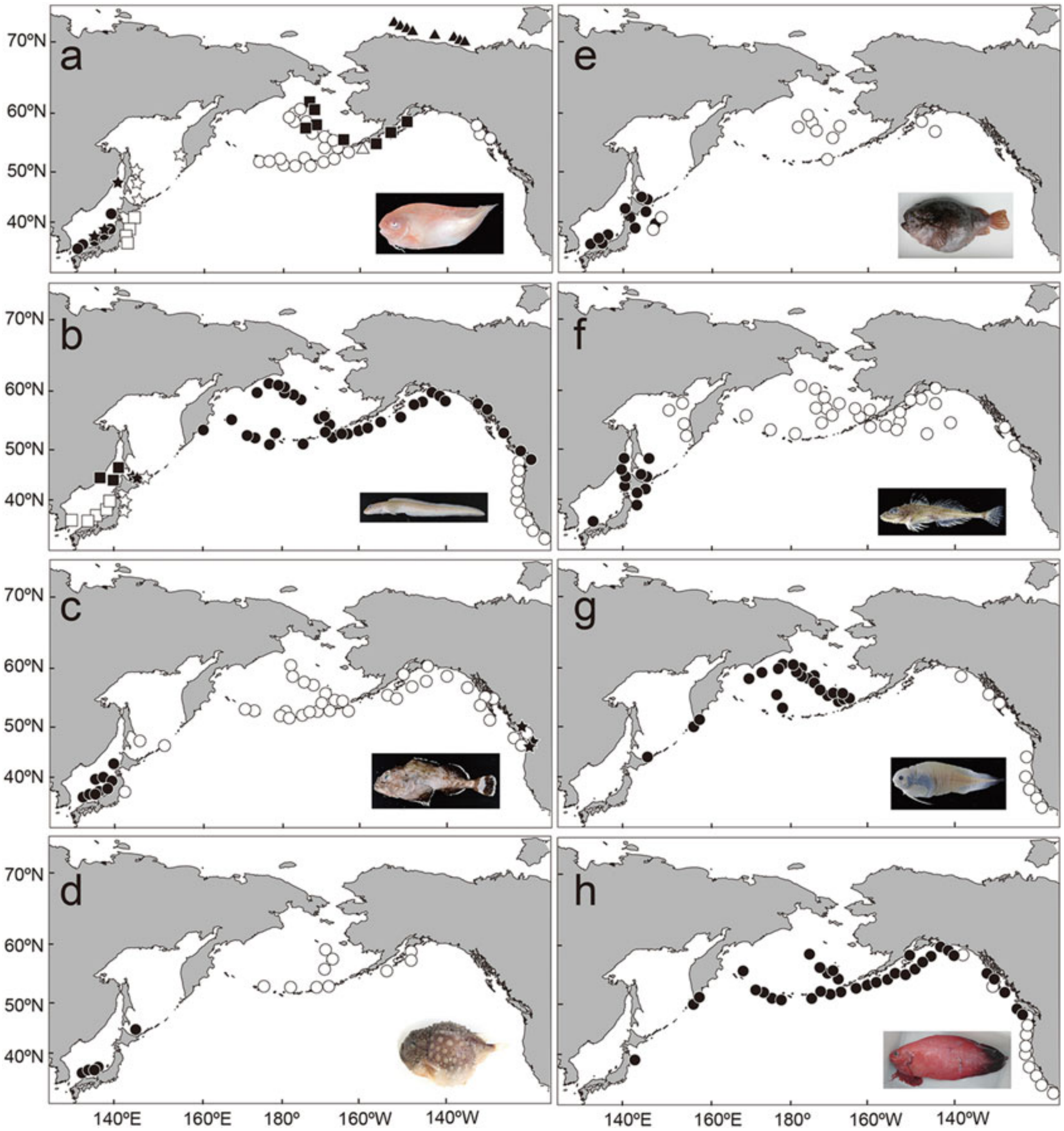

Fig. 7.3 Distributional patterns of closely related species group. (**a**) *Careproctus rastrinus* species complex (Liparidae): *open squares C. pellucidus*, *open stars C. rastrinus*, *closed circles C. trachysoma*, *closed stars C. acanthodes*, *open circles C. scottae*, *closed squares C. phasma*, *open triangle C. spectrum*, *closed triangles C. lerikimae*. (Modified from Orr et al. 2015). (**b**) Species of subgenus *Furcimanus* (Zoarcidae) defined by COI sequence variations: data from Stevenson and Sheiko (2009) and INSDIC, LC606411–LC606467, KC748102, KC751829–KC751832, KC879734, KC879735, KF019352, KF930085, KY570340, KY570341, JQ354202, JQ354203, FJ156952–FJ156963, FJ164767–FJ164775, HQ704755, MK560615; (**c**) two species of *Malacocottus*: *open circles M. zonurus*, *closed circles M. gibber*, *closed stars M. kincaidi*. (Modified from Stevenson 2015). (**d**) Two haplotype groups of *Eumicrotremus asperrimus*. (Modified from Kai et al. 2015). (**e**) Two haplotype groups of *Aptocyclus ventricosus*. (Modified from Okazaki et al. 2020). (**f**) Two species of *Icelus*: *open circles I. spiniger*, *closed circles I. cataphractus*. (Modified from Nelson 1984). (**g**) Two species of *Elassodiscus*: *open circles E. caudatus*, *closed circles E. nyctereutes*. (Modified from Kai et al. 2020). (**h**) Two species of *Careproctus*: *open circles C. ambustus*, *closed circles C. melanurus*. (Modified from Orr et al. 2020, photo by J.W. Orr)

vicariance events following gene flow between marginal seas. DNA sequence data of Kai et al. (2015) divided the *E. asperrimus* species complex into two distinct clades (now recognized as *Eumicrotremus asperrimus* and *Eumicrotremus gyrinops*, see Stevenson et al. 2017), corresponding to the eastern North Pacific (the Bering Sea, Aleutian Islands, and Gulf of Alaska) and the western North Pacific (the Seas of Japan and Okhotsk) regions. Within the western North Pacific clades, two haplotype groups were detected, one consisting only of specimens from the Sea of Okhotsk, the other of specimens from both the Sea of Japan and the Sea of Okhotsk (Kai et al. 2015). This suggests the vicariance of populations because of a low level of gene flow between the Seas of Japan and Okhotsk. Similarly, two haplotype groups were recovered within the widely distributed North Pacific *A. ventricosus*: one group consisting of western and one of eastern North Pacific individuals, except for some specimens collected from offshore of Tohoku, northern Japan (Okazaki et al. 2020) (Fig. 7.3e). The geographic distribution of haplotypes suggests that ocean currents in the North Pacific have shaped the population structure of the species after historical vicariant events between the Kuril Islands and Kamchatka Peninsula. Two cottoid species, *Icelus cataphractus* and *Icelus spiniger*, are similar to each other, having been taxonomically confused until clarified by Nelson (1984). The distributional ranges of two species overlap in the Sea of Okhotsk (Fig. 7.3f). No genetic studies for the species of *Icelus* have been conducted, but their present distributions suggest historical vicariant events between the Kuril Islands and Kamchatka Peninsula and the subsequent dispersal of *I. spiniger* to the northern Sea of Okhotsk.

In contrast, the distributional boundaries between several sister species have been known in the eastern North Pacific. *Elassodiscus caudatus* was formerly regarded to be distributed widely in the North Pacific, known from the Kuril Islands, Bering Sea, Gulf of Alaska southward to California (Mecklenburg et al. 2002). However, the recent morphological and molecular study of Kai et al. (2020) has revealed that two species were confused within previously recognized "*E. caudatus*": the newly described *Elassodiscus nyctereutes* known from the Sea of Okhotsk and Bering Sea and *E. caudatus* known from the Gulf of Alaska and eastern North Pacific (Fig. 7.3g). This parapatric distribution suggests that the Alaska Peninsula may have acted as a vicariant boundary for their speciation. A similar study is known for two other snailfishes: *Careproctus melanurus* and *Careproctus ambustus* (see Orr et al. 2020). Although the two species were previously confused and recognized as "*C. melanurus*," Orr et al. (2020) demonstrated genetic and morphological divergences between the two species. Their new species, *C. ambustus*, ranges from Japan, through Alaska, to the west coast of Vancouver Island, British Columbia, where its distribution overlaps with *C. melanurus*, which ranges from southern Alaska and British Columbia to Baja California (Fig. 7.3h). The distributional overlap is located in an intermediate or transitional zoogeographic province within the Boreal Eastern Pacific zoogeographic region (Allen and Smith 1988; Pietsch and Orr 2019). The distributions of *Lycodes beringi* and *L. diapterus* exhibit a similar pattern, overlapping latitudinally in British Columbia (Fig. 7.3b).

The origin and distribution of the subarctic fishes in Japan are the result of past vicariant events among marginal seas and subsequent dispersal with ocean currents in the North Pacific. For the further understandings of the speciation events, comparative studies of various presumed cognate pairs of species using molecular data will be required.

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8

Diversity and Distribution Patterns of Deep-Sea Demersal Fishes of Japan: A Perspective from Grenadiers

Naohide Nakayama

Abstract

In order to illuminate spatial patterns in species diversity and distribution of deep-sea demersal fishes of Japan, this study explored the biogeography of grenadiers (Actinopterygii: Gadiformes: Macrouridae) occurring in the northwestern Pacific Ocean around the Japanese Archipelago. Grenadiers were well represented in the study area (76 species in 18 genera), and the total regional fauna contributed about 21% of the global species diversity (63% of the global generic diversity) of the family. The rich representation is attributable to a wide variety of oceanographic conditions of the study area, the geographical proximity of the archipelago to the East Indies (center of the diversity of the group), and extensive collecting efforts over the last 175 years. The taxonomic compositions drastically changed along depth and latitudinal gradients. Hierarchal cluster analyses revealed the presence of the upper bathyal (<1100 m) and lower bathyal (1100–2000 m) assemblages, with the former further subdivided into the four regional faunas: Sea of Japan, Kyushu-Palau Ridge, East China Sea + Pacific Ocean off southern Japan, and Pacific Ocean off northern Japan + southern Okhotsk Sea. The faunal heterogeneity between the four regions can be explained by differences in physical factors such as water temperatures and current flows, discontinuous distributions of shelf and upper slope habitats between the regions, and paleoceanographic history since the Last Glacial Maximum.

Keywords

Biodiversity · Biogeography · Cluster analysis · Macrouridae · Gadiformes · Kuroshio Current · Oyashio Current

8.1 Introduction

The deep sea (>200 m depth) is by far the largest habitat for fishes, occupying 93% of the total volume of the world's oceans. Despite recent advances in technology, this vast environment is hard to explore owing to its remote location and the high hydrostatic pressure. Because of the difficulties in accessibility, the diversity and distribution patterns of deep-sea fishes are still poorly understood compared with shallow water taxa. However, we have rather good knowledge on taxonomy and distribution of deep-sea demersal fishes in the northwestern Pacific Ocean off the Japanese Archipelago, due to extensive collecting efforts since the late-nineteenth century [e.g., Temminck and Schlegel 1843, 1846;

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Günther 1877; Steindachner and Döderlein 1887; Jordan and Starks 1904; Kamohara 1950; Okamura et al. 1982; Amaoka et al. 1983; Okamura and Kitajima 1984; Okamura 1985; Shinohara et al. 1996, 2001, 2005, 2009, 2011, 2014, 2020; Shinohara and Matsuura 1997; Furuhashi et al. 2010; see Nakayama 2016 for a brief review].

Comprising at least 370 species in about 27 genera, grenadiers of the gadiform family Macrouridae (sensu stricto; excluding species of bathygadids, macrouroidids, and trachyrincids) are among the most dominant deep-sea demersal fishes both in terms of species diversity and abundance (Marshall 1979; Gage and Tyler 1992; Iwamoto and Merrett 1997; Merrett and Headrich 1997; Iwamoto and Graham 2001; Shao et al. 2008; Iwamoto et al. 2015; Nakayama 2020). The group is well represented in all major oceans, with the highest diversity in tropical and subtropical waters (Marshall 1965; Marshall and Iwamoto 1973; Iwamoto 1990; Iwamoto et al. 2015), particularly in the Indo-West Pacific. Most species are tightly associated with the sea floor (demersal, or more precisely, benthopelagic), whereas a few species exclusively inhabit pelagic layers of the open oceans (Marshall 1965; Marshall and Iwamoto 1973; Iwamoto 1990, 2008). Depth distributions of demersal grenadiers are generally restricted to the bathyal zone along the continental slope (200–2000 m), and only a limited number of species occur in much deeper (abyssal, 2000–6000 m; hadal, >6000 m) or shallower (shelf or sublittoral, <200 m) zones (Marshall and Iwamoto 1973; Marshall 1979; Iwamoto 1990; Nakayama 2020). Horizontal distributions of bathyal species are also highly restricted especially in low- and mid-latitude regions, and there are very few examples of trans-oceanic distributions (Iwamoto 1990; Briggs 1995). Considering the high taxonomic diversity and the relatively narrow spatial distribution of most species (both vertical and horizontal), grenadiers are suitable for exploring biogeographical patterns of deep-sea demersal fishes.

Taxonomy of grenadiers has received great attention in Japan, since Temminck and Schlegel (1846) described the first species, *Macrourus japonicus* (= *Coelorinchus japonicus*), from the East China Sea off Nagasaki. Since then, during the last 175 years, a huge body of work has been published (see Nakayama 2020, and references cited therein), including comprehensive reviews or monographs by Jordan and Gilbert (in Jordan and Starks 1904), Gilbert and Hubbs (1916), Okamura (1970), and Nakayama (2020). Collecting sites of previous works almost entirely cover the continental shelves and slopes along the archipelago (see Nakayama 2020: fig. 4), providing sufficient occurrence data to delineate distribution limits of most species in the area. Consequently, the taxonomy of grenadiers of Japan and adjacent waters is stable compared with other areas in the Indo-West Pacific, and distributions of most species are known to very high resolution. Using these data, this study discusses biogeography of the regional grenadier fauna to illuminate the distribution patterns of deep-sea demersal fishes of Japan.

8.2 Materials and Methods

8.2.1 Study Area

The study area encompasses the northwestern Pacific Ocean off the Japanese Archipelago (23.9333–45.8000° N, 121.0000–150.6000° E), including the East China Sea, Sea of Japan, southern Okhotsk Sea, Kyushu-Palau Ridge, and Shichito-Iojima Ridge (Fig. 8.1). The area includes vicinities of the northeastern part of Taiwan and South Korea.

8.2.2 Data Sources and Treatment

This study analyzed species occurrence records confirmed by Nakayama (2020), who thoroughly reviewed the taxonomy of grenadiers of Japan and adjacent waters. Taxonomic diversity of the

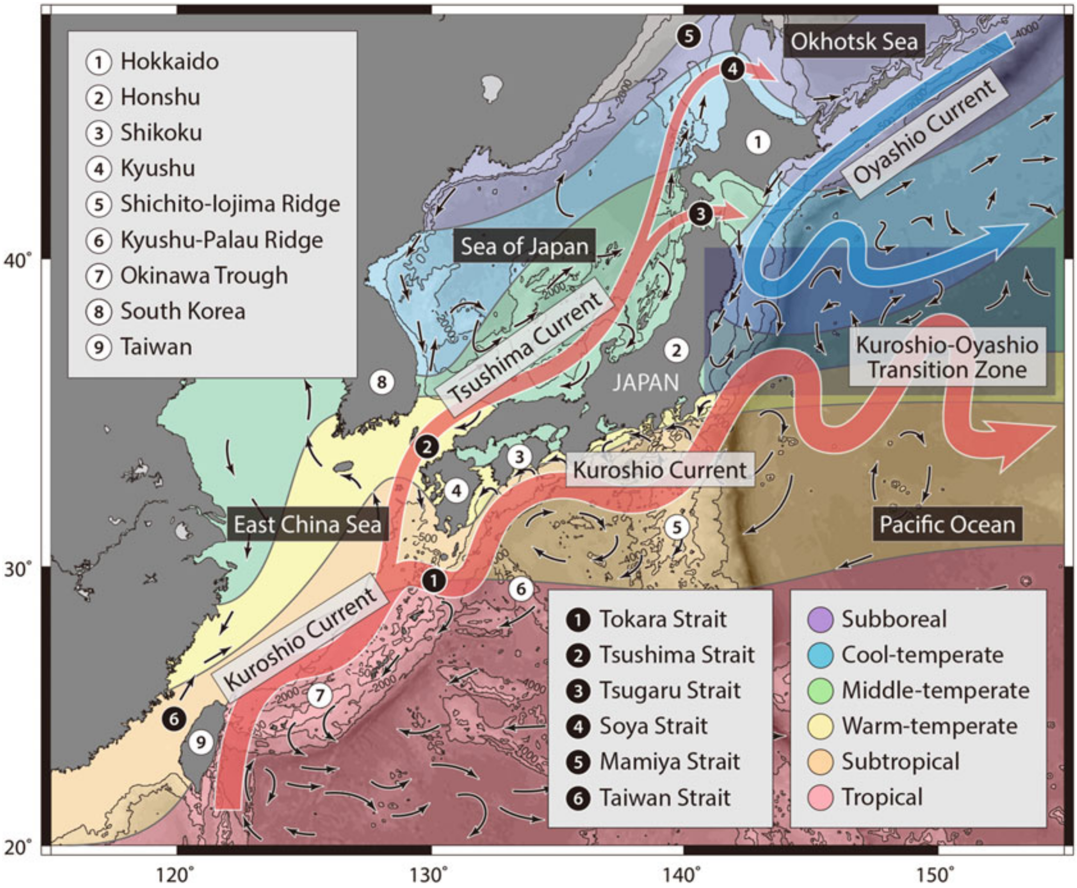

Fig. 8.1 Map of the northwestern Pacific Ocean showing the study area in Japan and adjacent waters. (After Nakayama 2020: figs. 2, 3)

total regional fauna was briefly summarized based on that study. Records without precise locality data and those based on putative midwater captures of juveniles were excluded for the present analyses. The dataset used here comprises 5876 records (catalog entries) based on the museum specimens that he examined and 296 records from previous literature that he verified (see Nakayama 2020, and references cited therein). The mean value was calculated for depth of capture when the original data were expressed as a range (e.g., from minimum to maximum, or from on-bottom to off-bottom). Regarding coordinates of capture, only those for a start position (on-bottom or net-in) were used when data were also recorded at an end position.

8.2.3 Elucidating Bathymetric and Biogeographical Boundaries

Because horizontal boundaries of marine organisms can be influenced by depth (Zezina 1997; Macpherson 2003; Macpherson et al. 2010), this study analyzed biogeographical characteristics in the following two steps: (1) vertical distribution analyses to explore the presence of significant vertical separation of the total regional fauna; and (2) horizontal distribution analyses to delimit biogeographical regions within the study area. In cases where capture depth data were uncertain, records, particularly those associated with specimens obtained at fish landing sites or markets, were excluded for the vertical distribution analyses. However, such records were included in the horizontal distribution analyses, unless otherwise stated, when original localities were unambiguous.

In the vertical distribution analyses, depth intervals were set at 100 m from 0 to 2000 m, and thereafter at intervals of 1000 m down to a depth greater than 7000 m. The taxonomic compositions were compared between these depth strata to describe trends in faunal changes along depth gradients, with particular reference to the five major genera (Figs. 8.2 and 8.3a; Table 8.1), viz., *Coelorinchus*, *Coryphaenoides*, *Hymenocephalus*, *Nezumia*, and *Ventrifoss*a. In addition, a hierarchical cluster analysis was performed to investigate the presence of vertical separation of the total regional fauna; the abyssal and hadal zones ($\geq$2000 m) were excluded due to scant collecting efforts in such depths. Based on a presence/absence data matrix of species and 100-m depth strata (generated from Fig. 8.2), a dendrogram was constructed using unweighted pair-group method using arithmetic averages (UPGMA) and Jaccard similarity coefficient (Fig. 8.3b); a similarity profile (SIMPROF) test (Clarke et al. 2008) was conducted to identify statistically significant cluster groupings at the 95% confidence level.

Targeting the shelf and upper bathyal zones (>1100 m), the taxonomic compositions were compared (with particular reference to the five major genera) between the following 15 local areas (Fig. 8.4a, c; Table 8.2): (1) East China Sea off northeastern Taiwan; (2) East China Sea off Nansei Islands (southern Okinawa Trough); (3) East China Sea off Kyushu (northern Okinawa Trough); (4) Pacific Ocean off Kyushu and Shikoku, including Hyuga-nada and Tosa Bay; (5) Pacific Ocean off Kinki and Tokai districts, including Kumano-nada and Enshu-nada; (6) Pacific Ocean off Kanto District, including Suruga and Sagami bays, Izu Islands (north of Miyake-jima Island; 34.0600° N), and off Boso Peninsula; (7) Pacific Ocean off Kitakanto and southern Tohoku districts, including Kashima-nada and Sendai Bay; (8) Pacific Ocean off Sanriku coast; (9) Pacific Ocean off Hokkaido; (10) southern Okhotsk Sea; (11) Genkai-nada and east of Korean Peninsula; (12) Sea of Japan off southern Honshu; (13) Sea of Japan off northern Honshu; (14) Sea of Japan off Hokkaido; and (15) Kyushu-Palau Ridge. In addition, a hierarchical cluster analysis was performed to elucidate positions of biogeographical boundaries within the study area. A dendrogram was generated using UPGMA and Jaccard similarity coefficient (Fig. 8.4b), based on a presence/absence data matrix of species and local areas (Table 8.3); significance of cluster groupings was evaluated using a SIMPROF test at the 95% confidence level. A record of *Coryphaenoides rudis* collected by a local fisher from Suruga Bay (in Area 6; capture depth uncertain) was excluded from the horizontal distribution analyses because the species appeared to be restricted to the lower bathyal zone ($\geq$1000 m) in the study area (1100–1481 m; see Nakayama 2020).

8.2.4 Data Analyses and Visualization

Cluster analyses were performed in R 4.1.0 (R Core Team 2021) using the packages "*clustsig*" (Whitaker and Christman 2014) and "*vegan*" (Oksanen et al. 2020). Maps were generated using the Generic Mapping Tools (GMT ver. 4.5.12; see Wessel et al. 2013), with temperature data from World Ocean Atlas 2018 (Boyer et al. 2018; Locarnini et al. 2019) and bathymetric data from ETOPO1 (Amante and Eakins 2009; NOAA National Geophysical Data Center 2009).

8.3 Results and Discussion

8.3.1 Taxonomic Diversity and Biogeographical Characteristics of Total Regional Fauna

The northwestern Pacific Ocean off the Japanese Archipelago yields a taxonomically rich fauna of grenadiers, with 76 species representing 18 genera reported to date (Nakayama 2020). Of these,

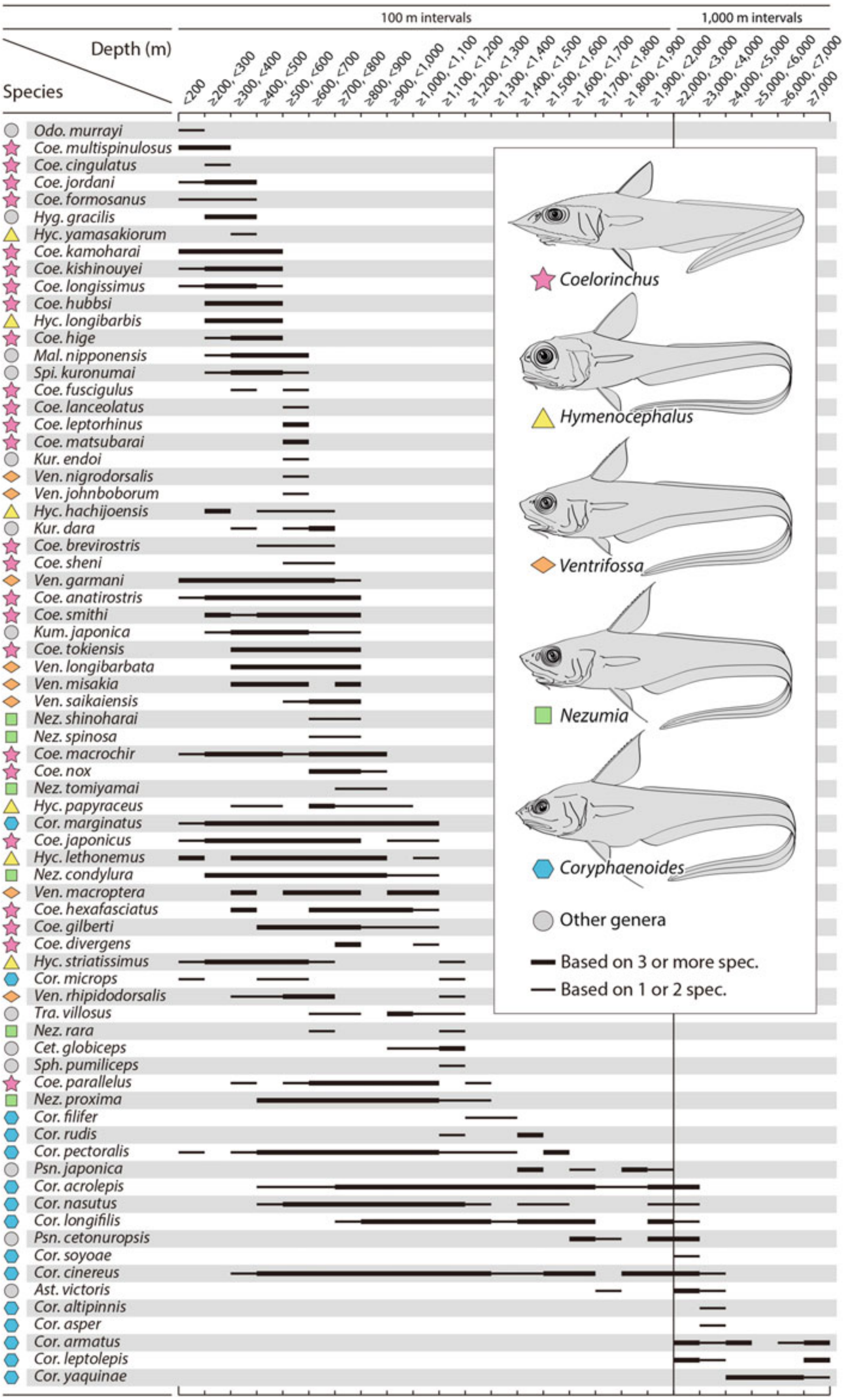

Fig. 8.2 Depth ranges of 73 species of grenadiers in Japan and adjacent waters. *Lucigadus nigromarginatus*, *Nezumia kamoharai*, and *Pseudonezumia* sp. cf. *septifer* are excluded due to uncertainty of depth of capture (see Sect. 8.2.2). The depth strata are separated by intervals of 100 m from 0 to 2000 m, and thereafter at intervals of 1000 m down to a depth greater than 7000 m

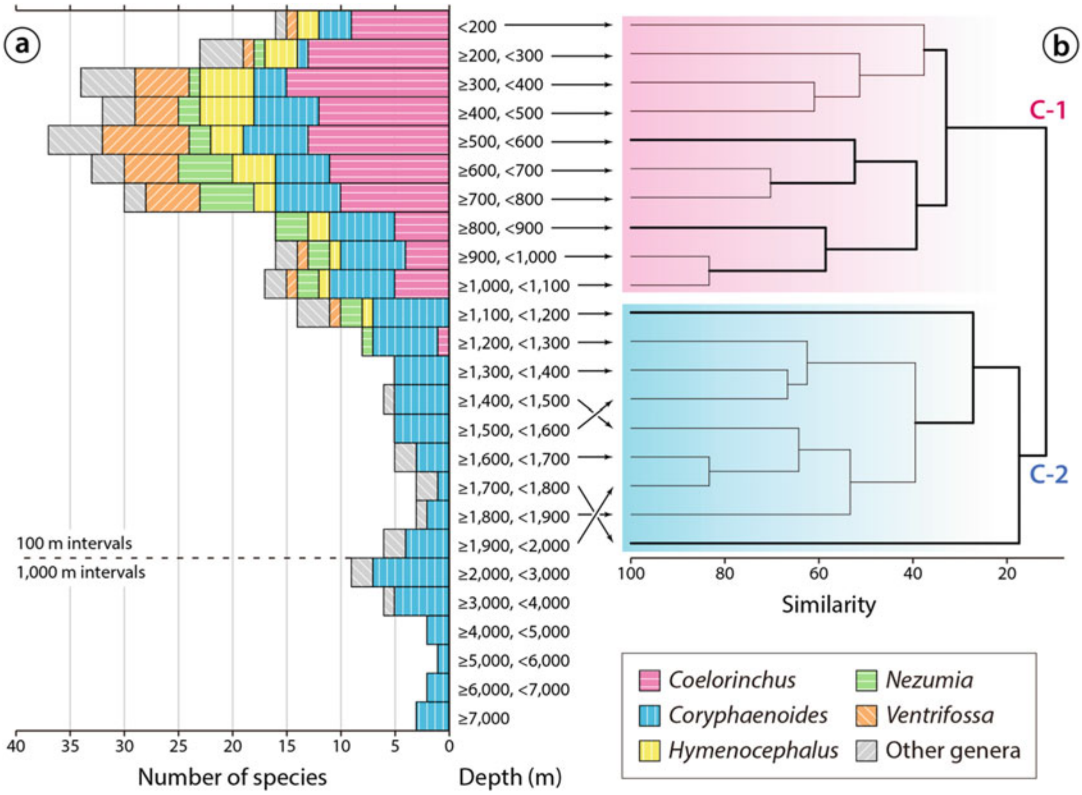

Fig. 8.3 Vertical distribution patterns of grenadiers in Japan and adjacent waters. (**a**) Vertical profile of the total number of species and percentage contribution of five major genera in each depth range. The depth strata are separated by intervals of 100 m from 0 to 2000 m, and thereafter at intervals of 1000 m down to a depth greater than 7000 m. (**b**) Dendrogram from UPGMA (unweighted pair-group method using arithmetic averages) hierarchical clustering of 19 different depth strata in the upper 2000 m, based on Jaccard's similarity coefficient calculated from presence/absence data of 73 species (data matrix was generated from Fig. 8.2). Bold lines indicate cluster groups where SIMPROF ($P < 0.05$) suggested that the structure is not random

25 species were of *Coelorinchus*, accounting for 33% of the total regional fauna. In terms of species diversity, *Coelorinchus* is by far the largest in the family with about 120 species worldwide (Nakayama 2020), most of which occur on the outer shelf and the upper slope between 150 and 800 m depth (Iwamoto 1990). It is considered predominantly an Indo-West Pacific group (Merrett and Iwamoto 2000), with its center of diversity in Southeast Asia (Nakayama and Endo 2017; Nakayama et al. 2020), particularly in the East Indies or the Indo-Malay-Philippine Archipelago. *Coryphaenoides* was the second-most speciose in the study area with 15 species (the number seems to be the highest in the world's oceans; N. Nakayama, pers. observ.), accounting for 20% of the total regional fauna. Comprising about 65 species worldwide, the genus is the second largest in the family (Nakayama and Endo 2016; Nakayama 2020), typically found on the slope between 700 and 2000 m depth (Iwamoto 1990), with seemingly high abundance in mid- and high-latitude regions (Nakayama 2020). Besides these two genera, *Hymenocephalus* (6 of the 27 known species occurred in the study area), *Nezumia* (7 of ca. 50 spp.), and *Ventrifossa* (8 of >25 spp.) also contributed well to the species richness of the study area (Nakayama 2020). With respect to global diversity patterns, *Coelorinchus*,

Table 8.1 Comparison of grenadier faunas in Japan and adjacent waters across depth strata (see also Figs. 8.2 and 8.3a), with reference to five major genera

Benthic zones	**–**	**Shelf**	**Slope (bathyal)**										
Depth strata	**Total**	**<200**	**≥200, <300**	**≥300, <400**	**≥400, <500**	**≥500, <600**	**≥600, <700**	**≥700, <800**	**≥800, <900**	**≥900, <1000**	**≥1000, <1100**	**≥1100, <1200**	**≥1200, <1300**
No. of spp.													
Coelorinchus	25	9	13	15	12	13	11	10	5	4	5	0	1
Coryphaenoides	15	3	1	3	6	6	5	6	6	6	6	7	6
Hymenocephalus	6	2	3	5	5	3	4	2	2	1	1	1	0
Nezumia	6[a]	0	1	1	2	2	5	5	3	2	2	2	1
Ventrifossa	8	1	1	5	4	8	5	5	0	1	1	1	0
Other genera	13[a]	1	4	5	3	5	3	2	0	2	2	3	0
Total no. of spp.	73	16	23	34	32	37	33	30	16	16	17	14	8
Total no. of gen.	16[a]	5	9	10	8	9	8	7	4	7	7	7	3
Benthic zones	**Slope (bathyal)**							**Rise + abyssal plain (abyssal)**				**Hadal**	
Depth strata	**≥1300, <1400**	**≥1400, <1500**	**≥1500, <1600**	**≥1600, <1700**	**≥1700, <1800**	**≥1800, <1900**	**≥1900, <2000**	**≥2000, <3000**	**≥3000, <4000**	**≥4000, <5000**	**≥5000, <6000**	**≥6000, <7000**	**≥7000**
No. of spp.													
Coelorinchus	0	0	0	0	0	0	0	0	0	0	0	0	0
Coryphaenoides	5	5	5	3	1	2	4	7	5	2	1	2	3
Hymenocephalus	0	0	0	0	0	0	0	0	0	0	0	0	0
Nezumia	0	0	0	0	0	0	0	0	0	0	0	0	0
Ventrifossa	0	0	0	0	0	0	0	0	0	0	0	0	0
Other genera	0	1	0	2	2	1	2	2	1	0	0	0	0
Total no. of spp.	5	6	5	5	3	3	6	9	6	2	1	2	3
Total no. of gen.	1	2	1	2	3	2	2	3	2	1	1	1	1

[a] *Lucigadus nigromarginatus*, *Nezumia kamoharai*, and *Pseudonezumia* sp. cf. *septifer* are excluded due to uncertainty of depth of capture (see Fig. 8.2 and Sect. 8.2.2)

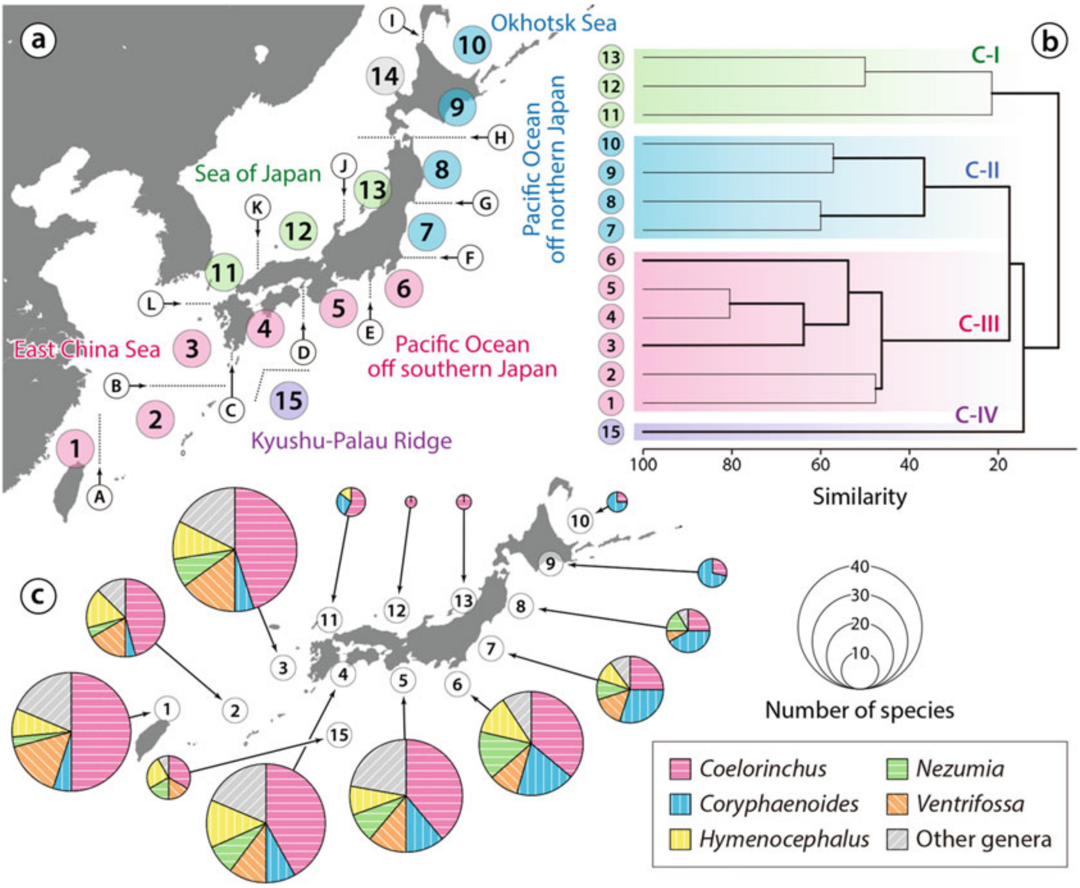

Fig. 8.4 (**a**) Horizontal distribution patterns of grenadiers occurring shallower than 1100 m depth in Japan and adjacent waters. (**a**) Map showing 15 local areas (1–15) involved in the analysis presented here; the boundaries of these areas, as shown in the map, are as follows: *A* Yonaguni-jima Island (123.0000° N), *B* Takara-jima Island (29.1497° N), *C* Cape Satamisaki (130.6592° E), *D* Kii Channel (134.9227° E), *E* Izu Peninsula (138.8452° E), *F* Choshi, Chiba Pref. (35.6963° N), *G* Oshika Peninsula (38.2926° N), *H* Tsugaru Strait (41.3500° N), *I* Cape Soyamisaki (141.9366° E), *J* Noto Peninsula (137.3455° E), *K* Hamada, Shimane Pref. (132.0598° E), *L* Jeju Island (33.4703° N). (**b**) Dendrogram from UPGMA (unweighted pair-group method using arithmetic averages) hierarchical clustering of 14 local faunas (excluding Area 14, where no species were recorded), based on Jaccard's similarity coefficient calculated from presence/absence data of 63 species (Table 8.3). *Bold lines* indicate cluster groups where SIMPROF ($P < 0.05$) suggested that the structure is not random. (**c**) *Pie charts* showing the total number of species and percentage contribution of five major genera in the 14 local faunas involved in the cluster analysis

Hymenocephalus, and *Ventrifossa* are especially diverse in the tropical and subtropical Indo-West Pacific (Merrett and Iwamoto 2000), with most species found on the upper slope (Iwamoto 1990; Schwarzhans 2014). By contrast, *Nezumia* is apparently rare in low-latitude regions, whereas the genus is abundant in temperate waters in the world's oceans (Iwamoto and Merrett 1997; Nakayama and Endo 2015; Nakayama 2020), with the richest diversity in the eastern Pacific Ocean (Merrett and Iwamoto 2000; Nakayama 2020). Other genera are small in number, and were poorly represented in the study area, with one or two species only (Nakayama 2020): *Asthenomacrurus* (1 of the 2 known species occurred in the study area), *Cetonurus* (1 of

Table 8.2 Comparison of grenadier faunas of 15 local areas in Japan and adjacent waters (see also Fig. 8.4), with reference to five major genera

	Regions (area no.)															
	Total	ECS			PSJ			PNJ			OS	SJ				KPR
	–	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)	(15)
No. of spp.																
Coelorinchus	24	19	11	18	16	14	12	5	3	2	1	4	1	2	0	4
Coryphaenoides	7	2	1	2	3	4	6	6	5	5	3	2	0	0	0	0
Hymenocephalus	6	3	4	4	5	3	4	2	0	0	0	1	0	0	0	3
Nezumia	7	1	1	3	3	3	5	2	2	0	0	0	0	0	0	2
Ventrifossa	8	6	4	6	4	4	3	3	1	0	0	0	0	0	0	2
Other genera	11	7	3	7	7	8	3	2	1	0	0	0	0	0	0	1
Total no. of spp.	63	38	24	40	38	36	33	20	12	7	4	7	1	2	0	12
Total no. of gen.	15	12	8	12	11	12	8	7	5	2	2	3	1	1	0	5

Area numbers correspond with those in Fig. 8.4a; Abbreviations: *ECS* East China Sea, *KPR* Kyushu-Palau Ridge, *OS* southern Okhotsk Sea, *PNJ* Pacific Ocean off northern Japan, *PSJ* Pacific Ocean off southern Japan, *SJ* Sea of Japan

Table 8.3 Presence (1) or absence (0) data matrix of 63 species of grenadiers × 14 areas (see Fig. 8.4a) in Japan and adjacent waters, based on records from the layer above 1100 m depth

	Regions (area no.)													
	ECS			PSJ			PNJ			OS	SJ			KPR
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(15)
Species														
Cetonurus globiceps	0	0	1	0	1	0	0	0	0	0	0	0	0	0
Coelorinchus anatirostris	1	1	1	1	1	1	0	0	0	0	0	0	0	0
Coelorinchus brevirostris	1	1	1	0	0	0	0	0	0	0	0	0	0	0
Coelorinchus cingulatus	1	0	1	1	0	0	0	0	0	0	0	0	0	0
Coelorinchus divergens	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Coelorinchus formosanus	1	1	1	1	0	0	0	0	0	0	1	0	0	0
Coelorinchus fuscigulus	1	1	1	0	0	0	0	0	0	0	0	0	0	0
Coelorinchus gilberti	0	0	0	1	1	1	1	1	1	0	0	0	0	1
Coelorinchus hexafasciatus	1	0	1	0	0	1	0	0	0	0	0	0	0	1
Coelorinchus hige	1	0	1	1	1	0	0	0	0	0	0	0	0	0
Coelorinchus hubbsi	0	1	0	1	1	1	1	0	0	0	0	0	0	0
Coelorinchus japonicus	1	1	1	1	1	1	1	0	0	0	0	0	0	0
Coelorinchus jordani	0	0	1	1	1	0	0	0	0	0	0	0	0	0
Coelorinchus kamoharai	1	1	1	1	1	1	1	1	0	0	1	0	0	0
Coelorinchus kishinouyei	1	0	0	1	1	1	0	0	0	0	0	0	0	0
Coelorinchus leptorhinus	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Coelorinchus longissimus	1	0	1	1	1	1	0	0	0	0	0	0	0	0
Coelorinchus macrochir	1	0	1	1	1	1	1	1	1	1	1	0	1	0
Coelorinchus matsubarai	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Coelorinchus multispinulosus	1	0	1	1	1	0	0	0	0	0	1	1	1	0
Coelorinchus nox	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Coelorinchus parallelus	1	1	1	1	1	1	0	0	0	0	0	0	0	0
Coelorinchus sheni	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Coelorinchus smithi	1	1	1	1	1	1	0	0	0	0	0	0	0	0
Coelorinchus tokiensis	0	1	1	1	1	1	0	0	0	0	0	0	0	1
Coryphaenoides acrolepis	0	0	0	0	1	1	1	1	1	1	0	0	0	0
Coryphaenoides cinereus	0	0	0	0	0	1	1	1	1	1	0	0	0	0
Coryphaenoides longifilis	0	0	0	1	1	1	1	1	1	0	0	0	0	0
Coryphaenoides marginatus	0	0	1	1	1	1	1	0	0	0	1	0	0	0
Coryphaenoides microps	1	0	0	0	0	0	0	0	0	0	1	0	0	0
Coryphaenoides nasutus	1	1	1	1	1	1	1	1	1	0	0	0	0	0
Coryphaenoides pectoralis	0	0	0	0	0	1	1	1	1	1	0	0	0	0
Hymenocephalus hachijoensis	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Hymenocephalus lethonemus	1	1	1	1	1	1	1	0	0	0	0	0	0	1
Hymenocephalus longibarbis	1	1	1	1	1	0	0	0	0	0	0	0	0	0
Hymenocephalus papyraceus	0	1	1	1	0	1	0	0	0	0	0	0	0	0
Hymenocephalus striatissimus	1	1	1	1	1	1	1	0	0	0	1	0	0	1
Hymenocephalus yamasakiorum	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Hymenogadus gracilis	1	1	1	1	1	0	0	0	0	0	0	0	0	0
Kumba japonica	1	0	1	1	1	1	1	1	0	0	0	0	0	1
Kuronezumia dara	1	0	1	1	1	0	0	0	0	0	0	0	0	0
Kuronezumia endoi	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Lucigadus nigromarginatus	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Malacocephalus nipponensis	1	1	1	1	1	1	0	0	0	0	0	0	0	0

(continued)

Table 8.3 (continued)

	Regions (area no.)													
	ECS			PSJ			PNJ			OS	SJ			KPR
Nezumia condylura	1	1	1	1	1	1	1	1	0	0	0	0	0	1
Nezumia kamoharai	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Nezumia proxima	0	0	1	1	1	1	1	1	0	0	0	0	0	0
Nezumia rara	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Nezumia shinoharai	0	0	0	1	0	1	0	0	0	0	0	0	0	0
Nezumia spinosa	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Nezumia tomiyamai	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Odontomacrurus murrayi	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Pseudocetonurus sp. cf. *septifer*	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Spicomacrurus kuronumai	1	0	1	1	1	0	0	0	0	0	0	0	0	0
Trachonurus villosus	0	1	1	1	1	1	0	0	0	0	0	0	0	0
Ventrifossa garmani	1	1	1	1	1	1	1	1	0	0	0	0	0	0
Ventrifossa johnboborum	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Ventrifossa longibarbata	1	1	1	1	1	1	1	0	0	0	0	0	0	0
Ventrifossa macroptera	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Ventrifossa misakia	0	0	1	1	1	1	1	0	0	0	0	0	0	1
Ventrifossa nigrodorsalis	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Ventrifossa rhipidodorsalis	1	1	1	1	1	0	0	0	0	0	0	0	0	0
Ventrifossa saikaiensis	1	1	1	0	0	0	0	0	0	0	0	0	0	0

Area numbers correspond with those in Fig. 8.4a; Abbreviations: *ECS* East China Sea, *KPR* Kyushu-Palau Ridge, *OS* southern Okhotsk Sea, *PNJ* Pacific Ocean off northern Japan, *PSJ* Pacific Ocean off southern Japan, *SJ* Sea of Japan

2 spp.), *Hymenogadus* (1 of 2 spp.), *Kumba* (1 of 9 spp.), *Kuronezumia* (2 of 8 spp.), *Lucigadus* (1 of 7 spp.), *Malacocephalus* (1 of 7 spp.), *Odontomacrurus* (monotypic), *Pseudocetonurus* (1 of 2 spp.), *Pseudonezumia* (2 of 5 spp.), *Sphagemacrurus* (1 of 6 spp.), *Spicomacrurus* (1 of 4 spp.), and *Trachonurus* (1 of 6 spp.). Considering that the family comprises at least 370 species in about 27 genera worldwide (Nakayama 2020), the study area contributes roughly 21% of the global species diversity of the family (63% of the global generic diversity).

The remarkable taxonomic diversity of grenadiers of Japan and adjacent waters is attributable to several factors, particularly to (1) a complexity of oceanographic conditions in the study area (Fig. 8.1), (2) the geographical proximity of the archipelago to the East Indies, and (3) extensive collecting efforts of Japanese deep-sea fishes since the late-nineteenth century. Japan is located in the mid-latitude region along the northwestern margin of the Pacific Ocean, surrounded on all sides by vast seas (i.e., Pacific Ocean, East China Sea, Sea of Japan, and Okhotsk Sea). Reflecting its geographical location, Japan's coast is washed by contrasting warm (Kuroshio and Tsushima currents) and cold (Oyashio and Okhotsk currents) currents. Due to their strong influence on the oceanographic characteristics of Japan and adjacent waters, the study area (despite its relatively small geographical coverage) encompasses six marine climatic regimes, viz., tropical, subtropical, warm-temperate, middle-temperate, cool-temperate, and subboreal (Nishimura 1992; Fujikura et al. 2010). The wide variety of climatic regimes enables both tropical-subtropical (e.g., *Coelorinchus*, *Hymenocephalus*, *Ventrifossa*, and many other genera) and temperate-subboreal (e.g., *Coryphaenoides* and *Nezumia*) groups to be diverse in such a small region. The high diversity of *Coelorinchus*, *Hymenocephalus,* and *Ventrifossa* is further attributable to the geographical proximity of the Japanese Archipelago to the East Indies, the latter of which hosts the highest species diversity of these genera (Merrett and Iwamoto 2000; Nakayama and Endo 2017; Nakayama et al. 2020; see also above). A close faunal similarity between Japan–Taiwan and the

East Indies was also suggested in other deep-sea benthic organisms such as galatheid squat lobsters (Macpherson et al. 2010). By contrast, the mid-latitude location of the Japanese Archipelago allows occurrence of boreal North Pacific species of *Coryphaenoides*, viz., *Coryphaenoides acrolepis*, *Coryphaenoides cinereus*, *Coryphaenoides filifer*, *Coryphaenoides longifilis*, and *Coryphaenoides pectoralis*. The southern distribution limits of these species in the western Pacific Ocean are located within the study area. The rich representation of *Coryphaenoides* is also due to underestimated species diversity of the genus in other regions or, in other words, extensive collecting efforts in Japanese waters over the last 175 years (see Sect. 8.1). Numerous trawl hauls have been conducted in the study area, not limited to the shelf and slope, but also the rise, abyssal plain, and hadal zone (e.g., Nakayama 2020: fig. 4). Of these, at least 54 hauls reached depths of 2000 m or greater, resulting in successful captures of abyssal and hadal representatives of *Coryphaenoides*, viz., *Coryphaenoides altipinnis*, *Coryphaenoides armatus*, *Coryphaenoides asper*, *Coryphaenoides leptolepis*, and *Coryphaenoides yaquinae*. Two of these species (*Cor. altipinnis* and *Cor. asper*) are so far known from Japanese waters, while additional investigations in adjacent regions of the western Pacific Ocean will add their new localities. While the other three species (*Cor. armatus*, *Cor. leptolepis*, and *Cor. yaquinae*) are widely distributed across several ocean basins (Gaither et al. 2016), their known localities are somewhat sporadic, particularly in the Southern Hemisphere (Wilson Jr and Waples 1983; Wilson Jr and Waples 1984; Endo and Okamura 1992; Nakayama 2020). The high diversity of grenadier genera in the study area may also be attributable to the above three points.

8.3.2 Vertical Distribution Patterns

The taxonomic compositions of grenadiers of Japan and adjacent waters showed considerable changes with depth (Figs. 8.2 and 8.3a; Table 8.1). The vertical distribution of the total regional fauna varied from a shelf depth of 70 m (*Coelorinchus kishinouyei*, from Sagami Bay off Izu Peninsula) to a hadal depth of 7387 m (*Cor. armatus*, *Cor. leptolepis*, and *Cor. yaquinae*, from Japan Trench off Miyako). The depth range of each species tended to be broader with increasing depth of occurrence (Fig. 8.2). Most species occurred on the upper slope, from which the taxonomic diversity decreased toward shallower and deeper depths (Figs. 8.2 and 8.3a; Table 8.1). Although the family is predominantly a deep-sea group, 16 species in five genera were recorded from the 0–199 m stratum. The greatest diversity was on the upper slope, particularly in the layer between 300 and 799 m, where 30 or more species in at least seven genera occurred in each 100-m stratum. More specifically, the diversity peaked in the 500–599 m stratum, where 37 species in nine genera were recorded. Grenadiers of the upper slope were further characterized by rich representation of four major genera, viz., *Coelorinchus*, *Hymenocephalus*, *Nezumia*, and *Ventrifossa* (Figs. 8.2 and 8.3a; Table 8.1). In Japan and adjacent waters, species of these genera were mainly restricted to the area shallower than 1300 m. Depth ranges of several minor genera, including *Hymenogadus*, *Kumba*, *Kuronezumia*, *Malacocephalus*, and *Spicomacrurus*, were also confined to the layer between 200 and 799 m (Fig. 8.2). By contrast, grenadiers of the lower slope were poorly diverse both at species and generic levels. The trend was especially noteworthy in the layer between 1200 and 1999 m, where fewer than nine species in 1–3 genera occurred in each 100-m stratum. Poor representation of grenadiers was similarly observed in the abyssal (rise and plain) and hadal zones, where fewer than 10 species in 1–3 genera occurred in each 1000-m stratum. *Coryphaenoides* was by far the dominant genus in deeper layers from the lower slope to the hadal zones, although the species composition obviously changed with depth (Fig. 8.2; e.g., several species, viz., *Cor. altipinnis*, *Cor. armatus*, *Cor. asper*, *Cor. leptolepis*, and *Cor. yaquinae*, were restricted to the abyssal and/or hadal zones, not occurring on the slope). Species of *Asthenomacrurus* and *Pseudonezumia* also exclusively occurred on the lower slope and/or the upper abyssal zone.

A hierarchical cluster analysis based on species occurrence across 19 depth strata (<2000 m; 100-m depth intervals) revealed the presence of two vertical assemblages of grenadiers in the study area (Fig. 8.3b): (1) the upper bathyal assemblage (C-1 in Fig. 8.3b) extended from the shelf to the upper slope above 1100 m; and (2) the lower bathyal assemblage (C-2) occurred in much deeper waters (1100–1999 m). As outlined above, the taxonomic diversity was notably richer in the shelf and upper slope than in the lower slope. The boundary between the two assemblages (1100 m) generally corresponded with marked changes in the taxonomic compositions along depth gradients. For example, more than 15 species constantly occurred in each 100-m stratum in the upper bathyal assemblage, whereas in the lower bathyal assemblage, the number was lower (Fig. 8.3a; Table 8.1). Furthermore, most species (48 spp. accounting for 66% of the total regional fauna) exclusively occurred in the upper bathyal assemblage (Fig. 8.2). The generic diversity was also richer in the upper bathyal than in the lower bathyal assemblages (usually 7–-10 vs. usually 1–3; Table 8.1).

8.3.3 Horizontal Distribution Patterns

In the following horizontal distribution analyses, species occurrence records from only the layer above 1100 m were analyzed, considering the faunal differences between the upper and lower bathyal assemblages (see Sect. 8.3.2). The treatment was also due to heterogeneous sampling effort in much deeper depths across local areas around the Japanese Archipelago (e.g., only a few trawl hauls were made in greater depths of the Kyushu-Palau Ridge).

The species compositions of the upper bathyal assemblage showed significant horizontal changes across the study area (Fig. 8.4c; Table 8.2). Grenadiers were well represented in the East China Sea (Areas 1–3) and the Pacific Ocean off southern Japan (4–6) both at species and generic levels, with at least 24 species in 8–12 genera occurring in each local area. The taxonomic diversity along the Pacific coast generally decreased with increasing latitude, and only seven species in two genera were recorded from the Pacific Ocean off Hokkaido (Area 9). Comprising 12 species in five genera, the local fauna of the Kyushu-Palau Ridge (Area 15) was not especially rich, despite its close geographical proximity to the East China Sea and the main islands of southern Japan. For example, many species typically found in the East China Sea and Pacific Ocean off southern Japan were not distributed in this oceanic elevation (see Table 8.3). Particularly, no species of *Coryphaenoides* have been recorded from the Kyushu-Palau Ridge, whereas *Coelorinchus matsubarai* was exclusively confined to the area in Japanese waters (although the species is also known from the Emperor Seamounts). By contrast, grenadier faunas of the Sea of Japan (Areas 11–14) and southern Okhotsk Sea (10) were evidently poor, with fewer than eight species in 1–3 genera occurring in each local area, except for the Area 14 (Sea of Japan off Hokkaido) where no species have been recorded. The poor representation of grenadiers in the Sea of Japan was especially noticeable in comparison with areas located at the same latitudes in the Pacific Ocean (7 spp. in 3 gen. in Area 11 vs. 33 spp. in 8 gen. in Area 6; only 1 sp. in Area 12 vs. 20 spp. in 7 gen. in Area 7; 2 spp. in 1 gen. in Area 13 vs. 12 spp. in 5 gen. in Area 8).

Patterns of latitudinal gradients in species diversity differed among the five major genera (Fig. 8.4c; Table 8.2). The total numbers of species of *Coelorinchus*, *Hymenocephalus* and *Ventrifossa* generally decreased with increasing latitude, except in the Sea of Japan and Kyushu-Palau Ridge. Patterns in *Coryphaenoides* and *Nezumia* were inverse, with the highest diversities in the Pacific Ocean off central Japan (Areas 6 and/or 7), and the total numbers of species gradually decreased southward. Furthermore, *Coelorinchus* was the best represented genus in local faunas through the East China Sea, Pacific Ocean off southern Japan, Kyushu-Palau Ridge, and Sea of Japan, whereas *Coryphaenoides* was most speciose through the Pacific Ocean off northern Japan and southern Okhotsk Sea.

A hierarchical cluster analysis based on species occurrence across 14 local areas around the Japanese Archipelago (Fig. 8.4b; Table 8.3; excluding the Area 14 where no grenadier species were recorded) suggested the presence of four faunal regions for the upper bathyal assemblage of grenadiers: (1) Sea of Japan (Areas 11–13; C-I in Fig. 8.4b); (2) Kyushu-Palau Ridge (15; C-IV); (3) Pacific Ocean off northern Japan and southern Okhotsk Sea (7–10; C-II); and (4) East China Sea and Pacific Ocean off southern Japan (1–6; C-III).

According to the dendrogram, the grenadier fauna of the Sea of Japan is readily separated from those of other regions in the study area. This is obviously associated with the poor representation of grenadiers in the region. The unique faunal characteristics can be attributable to a relatively recent origin of deep-sea fish fauna of the region. The Sea of Japan is a semi-closed marginal sea in the northwestern Pacific Ocean, connected to adjacent seas by four narrow and shallow straits (Fig. 8.1), viz., Tsushima Strait (maximum depth 130 m), Soya (or La Pérouse) Strait (55 m), Tsugaru Strait (140 m), and Mamiya (or Tatar) Strait (15 m). Due to the enclosed nature of the Sea of Japan, the hydrographic environment of the region has dramatically changed since the Late Pleistocene. In particular, high anoxic conditions dominated the deep-water layer of the Sea of Japan between 27 and 20 ka BP (Oba et al. 1991, 1995; Itaki et al. 2004), during which most deep-sea organisms were likely eliminated from the region. This anoxic condition resulted from the development of a well stratified water column caused by the combination of a large fresh water inflow from China and the lowest level in eustatic sea level in the Last Glacial Maximum (Oba et al. 1991, 1995; Itaki et al. 2004). The present-day grenadier fauna of the Sea of Japan appears to originate from about 12 ka BP, when the Tsushima Current became stronger and restarted to flow in the region through the Tsushima Strait (Oba et al. 1995; Ishiwatari et al. 1999; Itaki et al. 2004). This hypothesis is further supported in that most grenadiers recorded from the Sea of Japan are subtropical-temperate species with high abundance in the East China Sea (e.g., *Coelorinchus formosanus*, *Coelorinchus kamoharai*, *Coelorinchus multispinulosus*, *Coryphaenoides marginatus*, *Coryphaenoides microps*, and *Hymenocephalus striatissimus*).

The poor development of the grenadier fauna of the Sea of Japan may also be attributable to the present hydrographic characteristics of the region. The Sea of Japan is geographically connected to the East China Sea where grenadiers are dominant deep-sea demersal fishes in terms of taxonomic diversity (Okamura and Kitajima 1984; Shinohara et al. 2005) and abundance (Furuhashi et al. 2010). Considering the midwater occurrence of grenadiers in their early life stages (Stein 1980; Merrett 1989; Endo 2014) and the flow direction of the Tsushima Current, eggs and larvae would be transported to the Sea of Japan from the East China Sea. However, the deep layer in the former region (ca. >300 m) is occupied by the Japan Sea Proper Water (JSPW), which is characterized by uniformly low temperature (0.0–1.0 °C) (Uda 1934; Sudo 1986). Because JSPW is distinctly colder than at the same depth in other parts of southern Japan (Fig. 8.5b), deep waters of the Sea of Japan are likely unsuitable for settlement of most subtropical and warm-temperate species. In fact, occurrence in the region was very rare for most species, except *Coe. multispinulosus*. This species typically occurs on the outer shelf (<200 m) in the study area, commonly known from the southern margin of the Sea of Japan along Honshu (Yamada et al. 2007; Nakayama 2020). The shallow water temperature of the Sea of Japan is not especially low (Fig. 8.5a), likely allowing penetration of the species into the region. The Sea of Japan is also connected with the Pacific Ocean and Okhotsk Sea via the Tsugaru and Soya straits respectively. However, currents flowing in the two straits are directed eastward, possibly preventing westward transport of subboreal and cool-temperate species in early life stages (Figs. 8.1 and 8.5a).

Apart from the Sea of Japan, the Kyushu-Palau Ridge is highly distinctive in its unique grenadier fauna. As shown in the dendrogram, it (Area 15) is significantly different from a large cluster comprising the remaining areas across the East China Sea (1–3), Pacific Ocean off Japan (4–9), and

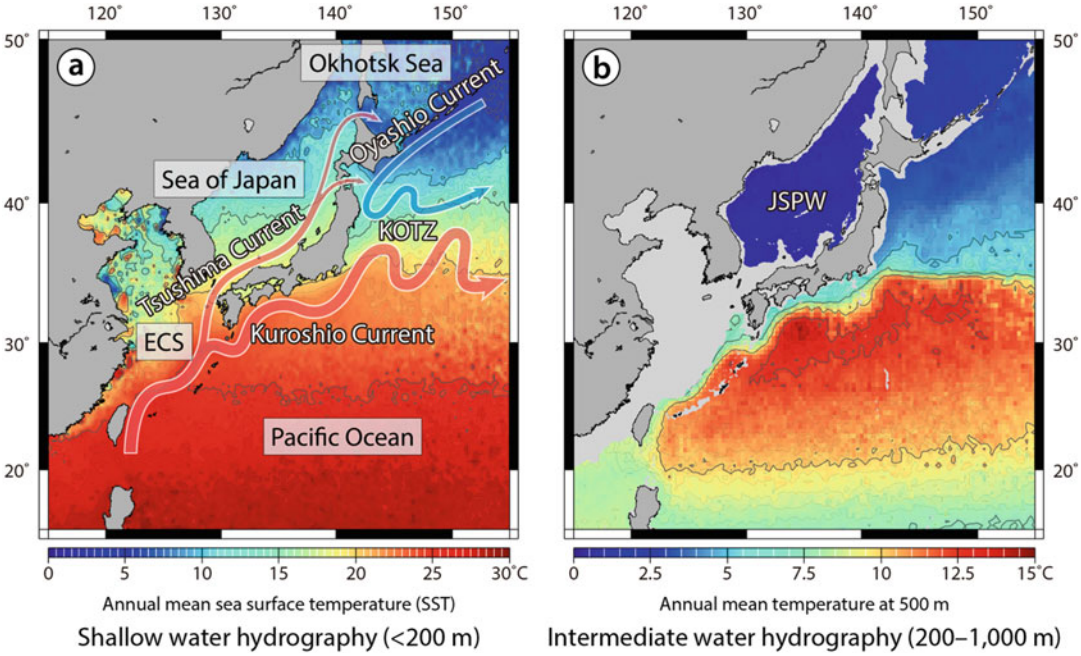

Fig. 8.5 Maps of the northwestern Pacific Ocean showing hydrographic characteristics of the study area. (After Matsuzaki and Itaki 2017: fig. 1; Nakayama 2020: fig. 3). (**a**) Annual mean sea surface temperature (SST); (**b**) Intermediate water temperature at a depth of 500 m. Abbreviations: *ECS* East China Sea, *JSPW* Japan Sea Proper Water, *KOTZ* Kuroshio-Oyashio Transition Zone

southern Okhotsk Sea (10). Despite their close geographical proximity, the species composition of Kyushu-Palau Ridge is quite different from those of the East China Sea and Pacific Ocean off southern Japan. The Kyushu-Palau Ridge is geologically isolated from other regions in the study area, being located on a different tectonic plate (Philippine Plate vs. Eurasian and North American plates), and surrounded by abyssal depths (>2000 m; Fig. 8.1). In most species of grenadiers, adults are primarily benthopelagic and closely associated with the sea floor (see Sect. 8.1). Therefore, the abyssal waters around the Kyushu-Palau Ridge are considered an effective biogeographical barrier for bathyal species to prevent migration between the ridge and other regions [see also Nakaya and Shirai (1992) for a similar discussion on scyliorhinid sharks and rajid skates]. In addition, larval dispersal between the Kyushu-Palau Ridge and the main islands of Japan is also likely restricted, considering the presence of the Kuroshio Current, which flows between the two regions (Figs. 8.1 and 8.5a). Moving across the current seems to be difficult for drifting larvae of grenadiers.

The remaining 10 local faunas were separated into two large clusters, of which one comprised those in the Pacific Ocean off northern Japan (Areas 7–9) and southern Okhotsk Sea (10), and the other included those in the East China Sea (1–3) and Pacific Ocean off southern Japan (4–6) (Fig. 8.4b). The boundary between the two clusters is geographically located in the Kuroshio-Oyashio Transition Zone, where hydrographic conditions at the surface, as well as in deeper layers, abruptly change across latitude (Fig. 8.5). The boundary generally corresponds with northern distribution limits of many subtropical-temperate species (Table 8.3; e.g., *Coe. japonicus*, *Coe. kishinouyei*, *Coelorinchus longissimus*, *Coelorinchus parallelus*, *Coelorinchus smithi*, *Cor. marginatus*, *Hymenocephalus longibarbis*, *Malacocephalus nipponensis*, *Trachonurus villosus*, *Ventrifossa* *longibarbata*, and *Ventrifossa rhipidodorsalis*). Undoubtedly, the above discussion further indicates that temperature plays an important role in determining the distribution of bathyal grenadier species in the study area.

8.4 Conclusions and Future Perspectives

The distribution patterns of grenadiers in Japan and adjacent waters can be explained by the combination of the geographical location of the archipelago (in relation to the East Indies), physical factors such as water temperature and current flows, discontinuous distributions of shelf and upper slope habitats, and paleoceanographic history since the Last Glacial Maximum. Because grenadiers are dominant deep-sea demersal fishes in the world's oceans, the knowledge on their distribution provides a fundamental basis for biogeographical discussion of other deep-sea taxa, especially for those having a similar early life history and adult lifestyle. Further investigations are necessary to elucidate whether similar patterns of distribution are found in other groups of deep-sea demersal fishes. In addition, more in-depth studies regarding the ecology, physiology, and early life history of grenadiers are required for better understanding the biogeography of the group.

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9

Fish Diversity of Estuaries Revealed by Environmental DNA

Manabu Kume and Edouard Lavergne

Abstract

Estuarine ecosystems are important habitats for many fish species. Large-scale patterns of estuarine fish communities can be affected by geographical factors, such as water temperature and latitude, which either limit or allow fish dispersal, and/or by environmental factors that select locally adapted species. Furthermore, increased human activity has also altered fish diversity through the modification of estuarine environments. In this study, we used environmental DNA metabarcoding to study a large-scale pattern of estuarine fish communities across 26 watersheds in the Japanese Archipelago, and assessed the effects of geographical, environmental, and anthropogenic factors in structuring these communities. Of the 197 fish species detected, 40 species were red-listed by the Japanese Ministry of Environment and seven were alien. Non-metric multidimensional scaling showed that both latitude and water temperature affected river mouth fish communities. Although other anthropogenic factors were not found to affect these communities, the bank artificialization rate was influenced. Furthermore, the relationship between the fish community and ocean currents was weak. The number of red-listed fish affected fish community structures, whereas that of alien species did not. The numbers of red-listed fish were negatively correlated with the bank artificialization rate and the rate of tetrapod formation. These findings provide useful information that may be used to conserve estuarine ecosystems.

Keywords

Environmental DNA metabarcoding · River mouth · Fish community · Red list · Bank artificialization

Abbreviations

BAR	Bank artificialization rate
DO	Dissolved oxygen
eDNA	Environmental DNA
NMDS	Non-metric multidimensional scaling
SR	Species richness
TFR	Tetrapod formation rate
TN	Total nitrogen
WT	Water temperature

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9.1 Introduction

Estuaries are important fish habitats for feeding, growing, and spawning. They also facilitate freshwater/seawater adaptation when the fish migrate upstream/downstream, (Potter et al. 2015). Flooding and ebb tides subject estuaries to spatiotemporal changes in their physicochemical environments (e.g., water depth, water temperature, and salinity), which result in the creation of various types of fluctuating habitats. The river mouth is particularly characterized by high level of primary production and complex hydrodynamics due to sustained terrestrial and marine nutrient supplies (McLusky and Elliott 2004; Kasai et al. 2010; Sugimoto et al. 2021). Thus, estuarine environments provide highly productive, fluctuating ecosystems for fish communities that are composed of many species with varying life history types, such as those from freshwater, estuarine, and marine environments, and those that are diadromous (Potter et al. 2015).

Large-scale patterns of estuarine fish communities can be influenced by geographic factors, including historical events, that either limit or allow fish dispersal (e.g., latitude and the presence of land-bridges) and/or by the selection of environmental factors selecting for locally adapted species (e.g., water temperature, salinity, and their fluctuations) (Pasquaud et al. 2015; Watanabe et al. 2017). However, human activities can cause the loss of estuarine biodiversity via multiple stressors (Teichert et al. 2016) such as habitat modification (urbanization and engineering construction; Yoshimura et al. 2005), eutrophication, water pollution, and the loss of tidal flats and seagrass/seaweed beds (Lotze et al. 2006; Airoldi et al. 2008). For example, modifications of river mouths (i.e., channelization and bank protection) reduce habitat complexity, and domestic and factory effluents cause eutrophication (Simpson and Sharples 2012). As a consequence, the amount of the coastal fishery catch in Japan has been decreasing since the mid-1980s (Ministry of Agriculture, Forestry and Fisheries 2019). This is the most likely due to overfishing, land reclamation, river water pollution, and the construction of concrete protections along the coasts and rivers. Thus, long-term assessment of estuarine fishes and studies on the effects of anthropogenic factors on estuarine fishes are required for the sustainable use of fishery resources.

In this chapter, we first demonstrate that eDNA metabarcoding reveals a large-scale pattern of fish diversity and distribution across 26 watersheds distributed over the Honshu, Shikoku, and Kyushu Islands in the Japanese Archipelago. We also characterize the species richness of native, red-listed, and alien fish along the geographical and environmental gradients. Second, we determine the geographical, environmental, and anthropogenic factors that determine estuarine fish community structures.

9.2 What Is eDNA?

Environmental DNA (eDNA) is a genetic material originating from cell fragments, feces, saliva, urine, and skin cells found in various environments (e.g., soil, sediment, water, or air). Recently, various aquatic organisms, including aquatic plants, aquatic insects, bivalves, salamanders, and fishes, have been detected by eDNA (Fukumoto et al. 2015; Matsuhashi et al. 2016; Doi et al. 2017b; Takahara et al. 2019). Thus, eDNA metabarcoding (Bohmann et al. 2015) has proven to be a powerful tool for monitoring fish communities and their composition in various aquatic environments, such as bays, rivers, and lagoons/estuaries (Yamamoto et al. 2017; Stoeckle et al. 2017; Nakagawa et al. 2018). The eDNA metabarcoding has also been found to be more useful for studying fish distribution and diversity than traditional fish sampling (e.g., electrofishing, traps and nets, and visual census) (Sard et al. 2019; Zou et al. 2020). Another advantage of this technique is its ability to sample a greater number of sites in less time than what is required for traditional techniques, thereby allowing for greater geographical coverage. Moreover, this method is nonintrusive and does not necessitate the sacrifice of any organism. Recently, fish abundance has been estimated (Yamanaka and Minamoto 2016; Doi et al. 2017a), and genetic diversity has been evaluated using eDNA (Uchii et al. 2016; Tsuji et al. 2020). Thus, eDNA is a technology that is expected to be applied to various approaches in the future. The methodology of eDNA metabarcoding is described in detail by Miya et al. (2020) and Minamoto et al. (2021).

9.3 Estuarine Fish Species Composition

Using eDNA metabarcoding with MiFish universal primer set (Miya et al. 2015), which targets a hypervariable region of the fish mitochondrial 12S rRNA gene (ca. 172 bp), we investigated the fish communities in 26 river estuaries (Table 9.1; Fig. 9.1; see the methods of Ahn et al. 2020 and Kume et al. 2021). A total of 197 fish species, belonging to 146 genera and 69 families, were detected in 52 water samples (collected in both high and low tides) from 26 river mouths using eDNA metabarcoding. Within the 26 rivers, we detected 25–60 fish species (Table 9.1; Appendix). Among these, *Mugil cephalus*, *Lateolabrax japonicus*, and *Tridentiger* spp. (present in all rivers) were detected very frequently (Table 9.2).

Previous studies have revealed that several factors, such as higher water temperature, longer time, and greater distance, increase the eDNA degradation rate (Nukazawa et al. 2018; Murakami et al. 2019; Kasai et al. 2020). Nevertheless, primary freshwater fishes inhabiting mid- to upper streams, such as *Rhynchocypris lagowskii steindachneri*, *Lethenteron* sp. S sensu Yamazaki et al. (2003), *Tachysurus nudiceps*, *Niwaella delicata*, and *Cottus pollux* were detected in the water samples that collected during the summer, which is the warmest season in Japan. Therefore, the eDNA of these fishes was thought to be transported from the upper reaches of freshwater to the river mouths. These results support the hypothesis that eDNA has a high degree of sensitivity in the detection of fish species.

It is known that eDNA is a powerful tool for detection of rare, endangered, and alien species (Bohmann et al. 2015; Balasingham et al. 2018). In our study, a total of 40 red-listed species, which were categorized in the Japanese Red List of the Ministry of Environment (2017, 2019) (20.3% of the number of total fish species detected) were found. Among these, *Lateolabrax japonicus*, *Anguilla japonica* (present in 20 rivers), and *Misgurnus anguillicaudatus* (12 rivers) were the most common (Table 9.2). Moreover, two locally endemic species with narrow distribution ranges, *Cobitis takatsuensis* and *Odontobutis hikimius* were detected in the Takatsu River. In addition, seven alien species (3.6%) were found (Nakabo 2013; Hosoya 2019), but at a lower frequency (Table 9.2). Importantly, the early detection of a *Micropterus dolomieu dolomieu* invasion was found in the Sagami River mouth (Kume et al. 2021). It was confirmed that the potential of the eDNA method enables a more accurate identification of the distribution range of species.

The eDNA metabarcoding showed evidence that many species might have recently changed their distribution ranges. In this study, five fish species were found in previously uncolonized river sites (Nakabo 2013; Hosoya 2019) possibly expanding their ranges to adjacent rivers of higher latitudes. Of those were *Platycephalus* sp. 2 sensu Nakabo (1993) from the Yoneshiro River, *Pterocaesio tile* from the Yahagi River, *Pseudolabrus sieboldi* and *Stethojulis interrupta terina* from the Naruse River, and *Omobranchus punctatus* from the Arakawa, Onogawa, and Kuma rivers. Recently, marine/estuarine fishes worldwide have expanded their distribution northward (Nicolas et al. 2011). In Japan, similar cases have been seen in some tropical/subtropical fishes including incidental dispersion or abortive migration, possibly due to ocean warming (e.g., Masuda 2008; Onikura et al. 2013). Therefore, eDNA metabarcoding may help to monitor fish responses to climate change. Our study as well as previous studies (Perry et al. 2005; Yamamoto et al. 2020) suggest that the recent increase in

Table 9.1 The numbers of all fish species, including species red-listed by the Ministry of Environment and alien species, at each river estuary

ID	River	All	Red-listed[a]	Alien	ID	River	All	Red-listed[a]	Alien
1	Mabechi	37	8	0	14	Miyagawa	37	8	1
2	Yoneshiro	40	11	2	15	Yamato	29	3	4
3	Akagawa	46	10	2	16	Kinokawa	43	3	1
4	Arakawa	28	7	0	17	Kakogawa	25	3	1
5	Naruse	34	3	1	18	Asahi	31	7	0
6	Naka	43	3	1	19	Ota	47	7	0
7	Sagami	54	3	2	20	Nakagawa	46	3	0
8	Fuji	27	5	1	21	Niyodo	47	9	5
9	Kuzuryu	42	7	2	22	Hijikawa	60	7	4
10	Yura	36	4	1	23	Onogawa	34	3	0
11	Hino	43	11	2	24	Oyodo	41	3	0
12	Takatsu	38	10	1	25	Kuma	35	6	1
13	Yahagi	40	8	4	26	Sendai	46	3	1

This table is modified from Kume et al. (2021)

[a]Red-listed included CR, EN, NT, VU, LP, and DD categories by the Ministry of Environment (2017, 2019)

water temperature due to climate change may also affect fish distributions and communities, especially in marine/estuarine fishes. Thus, long-term eDNA surveys are required to monitor their migration to non-native areas.

In addition, seven native invasive species were detected far from their original distribution area (Nakabo 2013; Hosoya 2019). These were *Gnathopogon caerulescens* from the Hino River, *Sarcocheilichthys variegatus microoculus* from the Mabechi, Yahagi, and Miyagawa rivers, *Barbatula oreas* from the Kuzuryu River, *Pseudorasbora parva* from the Mabechi, Yoneshiro, Akagawa, and Arakawa rivers,

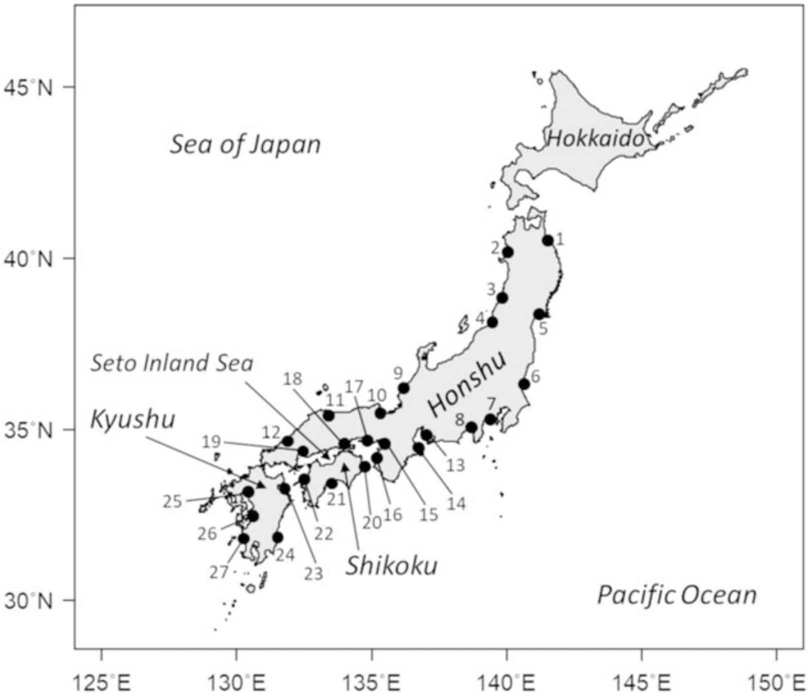

Fig. 9.1 The 26 sampling sites in the Honshu, Shikoku, and Kyushu islands of Japan. *Closed circles* indicate the study sites. *Numbers* indicate sampling river IDs as shown in Table 9.1. *Arrows* indicate warm (*solid*) and cold (*dashed*) currents. This figure is modified from Kume et al. (2021)

Table 9.2 Top 10 frequently occurring fish species detected using eDNA metabarcoding

(a) All fish			(b) Red-listed fish[a]			(c)Alien fish		
Order	Scientific name	N	Order	Scientific name	N	Order	Scientific name	N
1	*Mugil cephalus*	26	1	*Lateolabrax japonicus*	26	1	*Channa argus*	7
1	*Lateolabrax japonicus*	26	2	*Anguilla japonica*	20	2	*Rhodeus ocellatus ocellatus*	6
1	*Tridentiger* spp.	26	3	*Misgurnus anguillicaudatus*	12	3	*Lateolabrax maculatus*	4
4	*Cyprinus* spp.	25	4	*Gymnogobius petschiliensis*	9	4	*Micropterus salmoides salmoides*	3
5	*Carassius* spp.	24	5	*Squalidus* spp.	8	5	*Oncorhynchus mykiss*	2
5	*Rhinogobius* sp.	24	6	*Oncorhynchus masou masou*	7	5	*Lepomis macrochirus*	2
5	*Takifugu* spp.	24	6	*Cottus kazika*	7	7	*Micropterus dolomieu dolomieu*	1
5	*Acanthopagrus schlegelii*	23	8	*Taenioides snyderi*	6			
9	*Acanthogobius flavimanus*	23	8	*Cottus pollux*	6			
10	*Konosirus punctatus*	21	10	*Cottus reinii*	5			

(a) All fish, (b) Red-listed fish by the Ministry of Environment, and (c) Alien species, in 26 river estuaries. This table is modified from Kume et al. (2021)

N indicates the number of rivers in which the fish species were detected

[a] Red-listed included CR, EN, NT, VU, LP, and DD categories set by the Ministry of Environment (2017, 2019)

Tachysurus nudiceps from the Yahagi River, *Stichaeopsis nana* from the Hijikawa River, and *Omobranchus fasciolatoceps* from the Onogawa, Kuma, and Sendai rivers. However, it could not be determined if 15 fish species (*Anguilla japonica*, *Acheilognathus cyanostigma*, *Tanakia lanceolata*, *Tanakia limbata*, *Biwia zezera*, *Carassius* spp., *Cyprinus* spp., *Gnathopogon elongatus elongatus*, *Opsariichthys platypus*, *Oryzias sakaizumii*, *Misgurnus anguillicaudatus*, *Plecoglossus altivelis altivelis*, *Salvelinus* spp., *Oncorhynchus masou masou*, and *Oncorhynchus gorbuscha*) were either native or native invasive. Nevertheless, there are records of these species being released into rivers or fishing/aquaculture ponds in the past, as well as molecular evidence of their presence in previous studies. For example, *Plecoglossus altivelis altivelis* is widely distributed in Japan; however, their stocks from Lake Biwa, which had accidentally mixed with other fishes (e.g., *Gnathopogon caerulescens* and *Opsariichthys platypus*), were released into numerous rivers for recreational fishing and inland-water fisheries (Watanabe 2012). These types of fishes can cause genetic disruption (e.g., reduction of local genetic diversity or extinction of local genetic populations) via gene flow among the individuals of both native and invasive species (Rhymer and Simberloff 1996; Frankham et al. 2002). Recently, eDNA methodologies have been developed with improved detection accuracy to evaluate intraspecific genetic diversity (Uchii et al. 2016; Tsuji et al. 2020). Thus, such methods might be useful for assessing native invasive fishes and their effects on native fishes.

9.4 Anthropogenic Impacts on the Estuarine Fish Community

Figure 9.2 shows non-metric multidimensional scaling (NMDS) biplots used to elucidate the relationship between estuarine fish community structure and geographical/environmental factors—latitude, bank artificialization rate (BAR), tetrapod formation rate (TFR), population density, water temperature (WT), total nitrogen (TN), and dissolved oxygen of water surface ($DO_{surface}$) and water bottom (DO_{bottom}). In

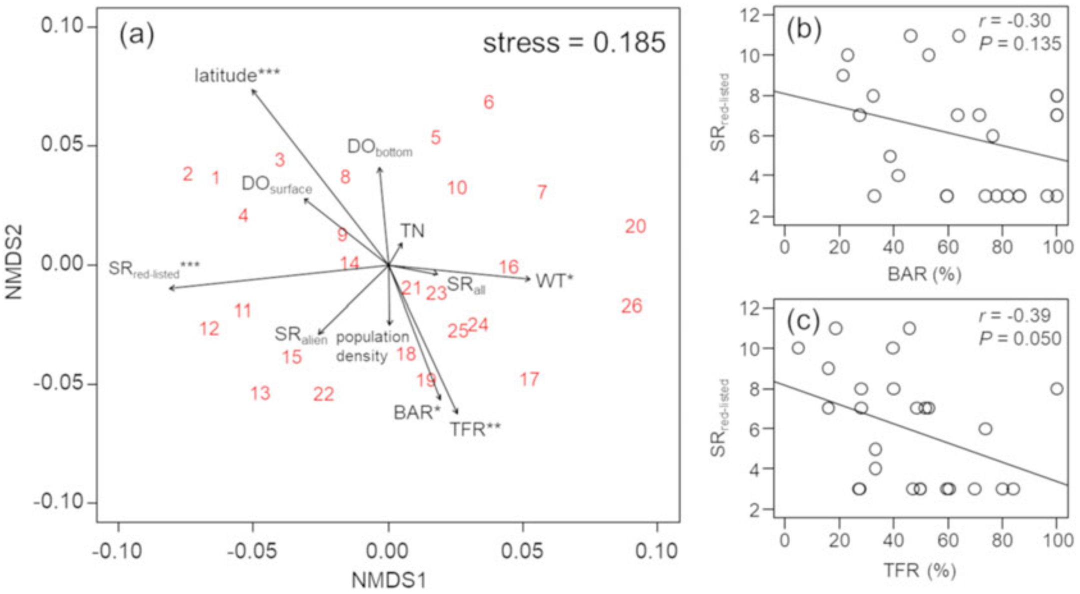

Fig. 9.2 (**a**) Non-metric multidimensional scaling (NMDS) plots with predictor fitting (*$p < 0.05$, **$p < 0.01$, and *** $p < 0.001$) fish communities around Japan. The NMDS plots fitting geographical and environmental factors, and species richness. The NMDS was performed using the dissimilarity matrix that was calculated using the Raup-Crick dissimilarity index (Chase et al. 2011) derived from presence–absence species data. *Numbers* indicate the sampling river IDs as shown in Table 9.1. Abbreviations are shown in the text. This figure is modified from Kume et al. (2021). Pearson's correlation between SR$_{\text{red-listed}}$, and (**b**) BAR and (**c**) TFR

addition to this, the species richness of all species (SR$_{\text{all}}$), species that are categorized in the Japanese Red List of the Ministry of Environment (2017, 2019) (SR$_{\text{red-listed}}$), and alien species (SR$_{\text{alien}}$) can be seen in this figure. The results of NMDS plots and vector fitting revealed that geographic location (i.e., latitude and WT) was the main factor in determining estuarine fish community structure. In addition, our results revealed that these structures might be affected by ocean currents. These can be explained by the fish-distribution patterns. In general, northern Japanese regions are characterized by the distribution of cold-water fishes, whereas the southern regions are characterized by that of warm-water fishes. In addition, there were weak, but non-significant, relationships between each community structure and the ocean currents. Thus, historical dispersal, vicariant events, and ocean currents affect fish distribution around Japan (Fukuta et al. 2017; Watanabe et al. 2017).

Freshwater fishes in Japan previously have formed faunal structures that have recently been disturbed by bank artificialization (Watanabe 2012). This suggests that estuarine fish communities are influenced by latitudinal and anthropogenic factors. The results of NMDS plots fitting anthropogenic factors revealed that BAR and TFR significantly affected fish community structure at river mouth, indicating that river-bank and shore reinforcements have a negative effect on the presence of fish inhabiting the estuary (Abdel-Fattah and Hasnain 2017). This may be explained by the relationship between the number of red-listed species, a significant effect of SR$_{\text{red-listed}}$ on estuarine fish communities, and the BAR including tetrapods. Indeed, natural banks along rivers and coasts create complex habitats that function as refugia against predators. They also function as feeding, spawning, or nursery grounds, depending on the species. However, concrete bank constructions, built for protection, simplify habitat structures, and result in a decrease in SR and abundance (Kawaguchi et al. 2006; Potter et al. 2015). Although a previous eDNA study revealed that man-made barriers, such as dams and weirs, affect the distribution of fishes because of the limitation of their upstream migration (Yamanaka and Minamoto 2016), the effects of other artificial constructions (i.e., estuary weirs) on estuarine fish community structure remain unclear in this study.

Nevertheless, we have found some support for the role of environmental factors. The NMDS results suggest that water quality has a weak effect on estuarine fish community structure. For example, river inputs can cause chemical changes in estuaries, which can modify the habitat quality, the community structure, and species composition of aquatic organisms (Pagès et al. 2020). Between the 1950s and the 1970s, river pollution due to wastewater from human activities was a serious problem in Japan (Yoshimura et al. 2005). As a countermeasure, the Japanese government established regulations concerning water quality standards for wastewater, leading to improved water quality (e.g., TN level) in previously polluted rivers (Ye and Kameyama 2020). As a result, differences in water quality among rivers have decreased over the last decades. This may explain the weak effect of water quality on estuarine fish community structure in this study.

9.5 Conclusion

The effectiveness of eDNA in assessing fish distribution and diversity in estuarine habitats has been confirmed, especially for red-listed fish species. Our most recent study revealed the effect of watershed land use on $\mathrm{SR}_{\text{red-listed}}$, especially postive relationship between forest cover and $\mathrm{SR}_{\text{red-listed}}$ in estuaries (Lavergne et al. 2021). In addition, the eDNA metabarcoding results revealed that both geographical and anthropogenic factors affected estuarine fish community structure along the Japanese Archipelago. Among the anthropogenic factors, estuarine fish community structure was significantly influenced by bank artificializations, but the structure was found to be weakly influenced by water quality. In Japan, river and coastal bank protections are essential for protecting human life and property, and the use of these measures has been increasing rapidly. This is because catastrophic natural disturbances, such as tsunamis and heavy rains, have occurred in recent years and caused serious damage to human living spaces around waterbodies, as well as to the communities of aquatic organisms (e.g., Ohtsuki and Nihei 2017; Kume et al. 2018). In light of this, the eDNA metabarcoding method has the potential to assess effects of aquatic organisms and ecosystems on a variety of natural disturbance events and subsequent applications for recovery programs. Consequently, these studies enhance the conservation and sustainable use of estuarine ecosystems.

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Appendix

List of fishes from 26 estuaries in Japan using environmental DNA metabarcoding (presence = 1/absence = 0). The river IDs are shown in Table 9.1. R* indicates red-list categories (CR, EN, NT, VU, LP, and DD) set by the Ministry of Environment (2017, 2019) and “AL” represents alien species

Scientific name	R*	River IDs																									
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Lethenteron sp. S	VU	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hemitrygon akajei		0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Aetobatus narutobiei		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0
Anguilla japonica	EN	1	0	0	0	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1
Ophisurus macrorhynchos		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Coilia nasus	EN	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Engraulis japonicus		0	0	1	0	1	1	1	1	1	1	0	0	0	0	0	1	0	0	1	1	1	0	1	0	0	1
Clupea pallasii	LP	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Etrumeus micropus		0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0
Ilisha elongata		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Konosirus punctatus		1	1	1	0	1	1	1	1	1	1	1	0	0	1	0	1	1	1	1	1	0	1	1	1	1	1
Sardinella zunasi		0	0	0	0	1	1	0	0	1	1	0	0	0	0	0	1	1	0	1	0	1	0	1	0	1	0
Sardinops melanostictus		1	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Spratelloides gracilis		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Cyprinus spp.		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1
Acheilognathus cyanostigma	CR	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Acheilognathus melanogaster	EN	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acheilognathus tabira jordani	CR	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Biwia zezera	VU	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Carassius spp.		1	1	1	1	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Ctenopharyngodon idella	AL	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0
Gnathopogon caerulescens	CR	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gnathopogon elongatus elongatus		0	1	1	0	0	1	0	0	1	0	1	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0
Hemibarbus spp.		1	1	1	1	1	1	1	0	1	1	0	0	1	1	1	1	0	1	1	1	1	1	0	1	1	0
Nipponocypris temminckii		0	0	0	0	0	0	0	0	1	0	1	1	1	1	0	0	0	0	1	0	1	1	0	1	0	1
Rhynchocypris lagowskii steindachneri		1	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhynchocypris oxycephala		0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudogobio esocinus		0	0	0	0	0	0	0	0	1	0	1	1	1	1	1	0	0	0	1	0	1	1	1	1	1	0
Pseudogobio agathonectris		0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0
Pseudogobio polystictus		1	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudorasbora parva		1	1	1	1	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0

Pungtungia herzi		0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	1	0	1	0	0	0	0	0
Rhodeus ocellatus ocellatus	AL	0	0	1	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0
Sarcocheilichthys variegatus microoculus		1	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Squalidus gracilis gracilis		0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Squalius spp.	VU	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	1	1	1	0	1	1	0	0	0	0
Tanakia lanceolata	NT	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0
Tanakia limbata	NT	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0
Pseudaspius brandtii maruta		0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudaspius brandtii brandtii	LP	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudaspius hakonensis		1	1	1	1	0	0	1	1	1	1	1	1	1	1	0	0	0	0	1	1	1	1	1	1	1	0
Pseudaspius sachalinensis	LP	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Opsariichthys platypus		0	1	1	1	0	0	1	0	0	0	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1
Cobitis minamorii saninensis	EN	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cobitis sp. BIWAE typeA		0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cobitis sp. BIWAE typeB		0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cobitis sp. BIWAE typeC		0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cobitis minamorii tokaiensis		0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Cobitis striata striata	VU	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Cobitis takatsuensis	EN	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Misgurnus anguillicaudatus	NT	1	1	1	1	1	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0
Misgurnus sp. Clade A	DD	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paramisgurnus dabryanus		0	1	0	0	1	0	0	0	0	1	1	0	1	0	1	1	0	0	0	0	0	1	0	0	0	0
Niwaella delicata	VU	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Barbatula oreas		1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lefua echigonia	EN	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Liobagrus reinii	VU	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Silurus asotus		1	0	1	1	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Plotosus japonicus		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Tachysurus nudiceps		0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hypomesus olidus	NT	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plecoglossus altivelis altivelis		1	0	0	1	0	0	1	1	1	0	1	1	1	1	1	0	0	1	1	0	1	1	1	1	1	0
Salangichthys ishikawae		0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Salanx ariakensis	CR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

(continued)

		River IDs																									
Scientific name	R*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Oncorhynchus gorbuscha		1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oncorhynchus masou masou	NT	1	1	1	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oncorhynchus mykiss	AL	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Salvelinus spp.		0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Saurida elongata		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Diaphus chrysorhynchus		0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gadus macrocephalus		0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chelon affinis		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1
Chelon haematocheila		1	1	1	1	1	0	0	0	1	1	1	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0
Chelon macrolepis		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Mugil cephalus		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Hypoatherina tsurugae		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Hypoatherina valenciennei		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	1	0	0
Oryzias sakaizumii	VU	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cypselurus spp.		0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Hyporhamphus intermedius	NT	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hyporhamphus sajori		0	0	0	1	1	1	0	0	1	1	1	0	0	1	0	1	1	0	0	0	1	0	1	0	0	0
Ablennes hians		0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Strongylura anastomella		0	0	1	1	1	1	0	1	1	1	0	0	0	1	0	1	0	0	1	0	0	0	1	0	1	1
Tylosurus crocodilus crocodilus		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	1
Pungitius spp.	LP	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cololabis saira		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Inimicus japonicus		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Hypodytes rubripinnis		0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Sebastes spp.		0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0
Sebastiscus marmoratus		0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chelidonichthys spinosus		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Platycephalus sp. 1		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Platycephalus sp. 2		0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0
Hexagrammos spp.		0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0
Rheopresbe kazika	VU	0	0	1	1	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0
Cottus pollux	NT	0	1	1	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0

Cottus reinii	EN	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Lateolabrax japonicus	LP	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Lateolabrax latus		0	0	0	0	1	1	1	1	1	0	1	0	0	1	0	1	0	0	0	0	1	1	1	1	1	1
Lateolabrax maculatus	AL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1
Coreoperca kawamebari	EN	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Acropoma japonicum		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Epinephelus areolatus		0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Epinephelus awoara		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Epinephelus merra		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Lepomis macrochirus	AL	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0
Micropterus dolomieu dolomieu	AL	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Micropterus salmoides salmoides	AL	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0
Apogon unicolor		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Sillago japonica		0	0	1	0	0	1	1	1	0	1	0	1	0	0	0	1	0	0	0	1	1	1	0	0	0	1
Seriola dumerili		0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1
Seriola lalandi		0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Seriola quinqueradiata		0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0
Trachinotus baillonii		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Trachurus japonicus		0	0	1	0	0	1	1	0	1	1	1	0	0	0	1	1	0	0	0	1	1	1	1	1	0	1
Equulites rivulatus		0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuchequula nuchalis		1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	1	1	0	0	0	1	1	0
Pterocaesio tile		0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Hapalogenys nigripinnis		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Parapristipoma trilineatum		0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	1	0	0	0	0
Plectorhinchus cinctus		0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1
Acanthopagrus latus		0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	1	0	1	1	1	1	1	1	1	1
Acanthopagrus schlegelii		0	1	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1
Evynnis tumifrons		0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
Pagrus major		1	0	1	0	0	0	0	0	0	0	1	0	1	0	1	1	0	0	1	0	0	1	0	0	0	1
Rhabdosargus sarba		0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Nibea albiflora	EN	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nibea mitsukurii		0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pennahia argentata		0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Girella punctata		0	0	1	0	1	1	1	0	0	1	0	0	0	1	0	1	0	0	0	1	0	1	0	0	0	1

(continued)

Scientific name	R*	River IDs																									
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Microcanthus strigatus		0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhynchopelates oxyrhynchus		0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	1	0	1	0	1	1	1	0	1	0	1
Terapon jarbua		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Oplegnathus fasciatus		0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0
Acanthocepola krusensternii		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Ditrema temminckii subspp.		0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0
Halichoeres tenuispinis		0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudolabrus sieboldi		0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Semicossyphus reticulatus		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Stethojulis interrupta terina		0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Dictyosoma burgeri Form a		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Dictyosoma burgeri Form b		0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Dictyosoma rubrimaculatum		0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stichaeopsis nana		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Pholis spp.		0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholis nebulosa		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Entomacrodus stellifer stellifer		0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Omobranchus fasciolatoceps		0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	1
Omobranchus punctatus		0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	1	0	0	1	1	1	1
Parablennius yatabei		0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Repomucenus valenciennei		1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Odontobutis hikimius	VU	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Odontobutis obscura		0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	1	1	0	1	1	1	1	0	0
Eleotris oxycephala		0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acanthogobius flavimanus		1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	0	1	1	1	0
Acanthogobius hasta	VU	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acentrogobius spp.		0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Amblychaeturichthys sciistius	NT	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Boleophthalmus pectinirostris	EN	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Callogobius tanegasimae		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0
Chaenogobius annularis		0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Eutaeniichthys gilli	NT	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0

Favonigobius gymnauchen		0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Acanthogobius lactipes		1	1	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	1	0
Glossogobius olivaceus		0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	1
Gymnogobius breunigii		1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	1	0	1	0
Gymnogobius castaneus		0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gymnogobius opperiens		1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gymnogobius petschiliensis	LP	0	0	1	1	0	0	0	1	0	1	1	1	0	0	0	0	0	0	1	0	1	1	0	0	0	0
Gymnogobius scrobiculatus	EN	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	0
Gymnogobius urotaenia		1	1	1	1	0	0	1	0	0	0	1	1	1	0	1	0	0	1	0	0	0	1	1	0	0	0
Leucopsarion petersii	VU	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Luciogobius guttatus		0	0	1	0	1	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0
Luciogobius pallidus	NT	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Luciogobius spp.		0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	1	0	0	0	0	0
Mugilogobius abei		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	1	0
Myersina filifer		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Odontamblyopus lacepedii	VU	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Periophthalmus modestus	NT	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Pseudogobius masago	VU	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Rhinogobius flumineus		0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	1	0	0	0	0
Rhinogobius similis		0	0	0	0	0	0	1	1	1	0	1	1	1	1	1	0	0	1	0	1	1	1	1	1	1	1
Rhinogobius sp.		1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1
Sicyopterus japonicus		0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0
Taenioides snyderi	EN	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	1	1	1
Tridentiger barbatus	NT	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tridentiger trigonocephalus		0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1
Tridentiger spp.		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Parioglossus dotui		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Scatophagus argus		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Siganus fuscescens		0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0
Prionurus scalprum		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Sphyraena japonica		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Sphyraena pinguis		0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Auxis spp.		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Sarda orientalis		0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

(continued)

Scientific name	R*	River IDs																									
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Scomber spp.		1	0	0	0	1	1	1	0	1	0	1	0	1	0	1	1	0	0	0	0	1	1	0	0	0	0
Scomberomorus niphonius		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Channa argus	AL	0	1	0	0	0	0	0	0	1	0	1	0	1	0	1	0	0	0	0	0	1	1	0	0	0	0
Paralichthys olivaceus		0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Eopsetta grigorjewi		0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Platichthys stellatus		1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Platichthys bicoloratus		0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	1	0	0	0	0
Thamnaconus modestus		0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Canthigaster rivulata		0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Takifugu spp.		1	1	1	1	1	1	1	1	1	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1

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Part III

Diversity Within Species: Phylogeographic Perspective on Japanese Fishes

Deep-Sea Fishes

10

Kay Sakuma

Abstract

The deep-sea environment has historically been regarded as representative of oceanic connectivity and homogeneity, and the Japanese seas provide an ideal model system for testing the assumptions of deep-sea connectivity. The Pacific Ocean and the three marginal seas (Sea of Okhotsk, Sea of Japan, and East China Sea) surrounding the Japanese Archipelago are connected in places with each other by shallow and narrow straits which may have played an important role as choke points between ocean basins in the divergence of local deep-sea populations. I first summarize the classical ideas of deep-sea panmictic populations with some instances around the world, then I introduce phylogeography of the deep-demersal (fully benthic), benthopelagic, and mesopelagic fishes in the seas around Japan. I also provide information of the geological history and its environmental consequences in Japanese seas, which may be useful in understanding the phylogeography of deep-sea fishes around Japan.

Keywords

Phylogeography · Deep-demersal · Mesopelagic · Benthopelagic · Vicariance · Population genetics · Sea of Japan · Climatic oscillation

10.1 Introduction

The deep-sea environment has historically been regarded as representative of oceanic connectivity and homogeneity. For freshwater and shallow-water species, the factors that have shaped present-day patterns of intraspecific diversity have always been discussed in relation to apparent geographical barriers to migration of individuals, and thus gene flow, between local populations. For deep-sea species, however, such barriers are not always assumable, as the oceanic environment is basically continuous and relatively homogeneous. Nevertheless, some populations of deep-sea fishes have attracted considerable attention, as it is possible that they can provide examples counter to the paradigm of panmictic, continuous, and homogeneous populations in the oceanic environment.

The Japanese islands provide an ideal model system for testing the assumptions of deep-sea connectivity. The Pacific Ocean and the three marginal seas (Sea of Okhotsk, Sea of Japan, and East China Sea) surrounding the Japanese Archipelago are connected in places with each

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other by shallow and narrow straits. These seaways may have played an important role as choke points between ocean basins in the divergence of local deep-sea populations. Moreover, these straits may have dried up and become land bridges during past climatic events—especially the glacial climatic oscillations in the late Pleistocene—that have brought drastic sea-level changes worldwide. Such geographic changes could have provided opportunities for population divergence, not only between the seas but also between local habitats within the seas: population-range booms and busts driven by changes in habitat area could have led to intermittent connections between local populations.

In this chapter, I first introduce the old paradigm of marine connectivity, with some examples from around the world. Then I move to intraspecific diversity of deep-sea species in the seas around Japan, with a brief introduction to the geological history and its environmental consequences. As intraspecific diversity of deep-sea fishes has been studied mainly in the fields of phylogeography and population genetics, I focus on the results of such molecular analyses. I note, however, that there have been considerable efforts to elucidate the intraspecific diversity of Japanese deep-sea species by using morphological variations (e.g., Okiyama 1970), as their contributions in biogeography and fisheries management cannot be omitted.

10.2 Intraspecific Diversity of Deep-Sea Fishes

Outlining the shapes of genetically uniform groups of individuals—populations—in geological settings is the first step when one wishes to understand the patterns of diversity on a geological scale. We recognize the possibility of genetic structuring when a break between populations is represented by a geographic boundary within a species' distribution range. The geographic locations of the edges of populations are sometimes key to understanding the factors that have prevented genetic admixture of populations.

There is considerable difference in the edge shapes of populations between freshwater and marine fish species. Freshwater fish populations are sometimes expressed as continuous lines (Fig. 10.1a). For instance, river systems have tree-like structures, and most freshwater fishes do not migrate across the land areas between them. Breaks between populations can be found as separations of these structures, such as discontinuities between river systems. Freshwater fishes are also characterized by relatively small populations and low fecundity, making the fixation of genetic characters more frequent (Avise 2000). Freshwater fish populations are therefore clearly defined by geographic boundaries in many cases; in this way, they are the ideal targets of phylogeographic studies that have helped us to understand the drivers that shaped today's patterns of diversity. For example, intensive phylogeographic studies of freshwater fishes of the family Galaxiidae have shown that past river capture events have played an important role in the diversification of lineages (Waters et al. 2020).

Conversely, marine populations had long been regarded as displaying genetic homogeneity. Oceanic habitats can be expressed as expansive areas or three-dimensional water bodies; therefore, breaks between populations are expressed as lines or surface-like structures that are sometimes not as clear as they are in freshwater fish populations (Fig. 10.1b). Large effective population sizes of marine fish species always result in an extensive single panmictic population in oceanic environment or even at the global scale, especially as determined by using conventional mitochondrial sequence analyses (Bazin et al. 2006). For these reasons, early population genetic studies failed to find structures among oceanic populations of pelagic fish species (e.g., tuna species, Ward et al. 1994; Ely et al. 2005). This is also the case for oceanic deep-sea fish species such as Blue Hake *Antimora rostrata* (see White et al. 2011); Blue Grenadier *Macruronus novaezelandiae*, Patagonian grenadier *Macruronus magellanicus*, and Southern Blue Whiting *Micromesistius australis* (see Takeshima et al. 2011); Orange Roughy *Hoplostethus*

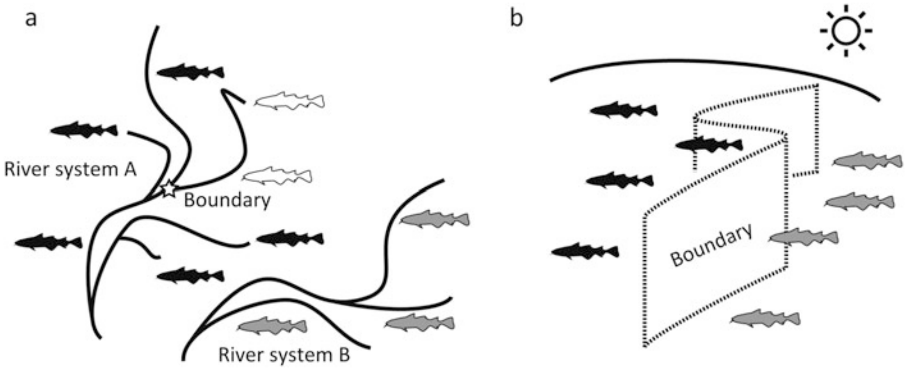

Fig. 10.1 Schematic illustration of (**a**) freshwater and (**b**) oceanic fish populations. (**a**) Freshwater fish populations in different river systems (black vs. gray fishes) are always geographically separated and migration across land areas is rarely assumable. Genetic differentiation within the river system (black vs. white fishes) is attributable to environmental or geographic drivers that co-occur with a sudden genetic boundary (marked by the star). (**b**) In oceanic environments, genetic differentiation between putative populations (black vs. gray fishes) is sometimes observed without any geographic barriers such as surface-like structures, but it is usually difficult to determine the drivers of lineage split

atlanticus (see Varela et al. 2012); and Alfonsino *Beryx decadactylus* (see Friess and Sedberry 2011).

Life history traits are among the most important factors that can explain the apparently panmictic nature of populations of deep-sea fishes. Hereafter, I further subcategorize deep-sea fishes into deep-demersal (fully benthic), benthopelagic, and mesopelagic. Deep-demersal fishes are sedentary and are basically characterized by low migratory activity of adults. Benthopelagic fishes are also near-bottom dwellers but are characterized by mobility of adult individuals. Mesopelagic fishes are free-swimmers in the twilight zone between 200 m depth and just above the seafloor (while the lower limit is sometimes defined as the depth where there is no light); for example, most species in the Myctophiformes and Stomiiformes are mesopelagic. When we consider the migratory activity of adults, deep-demersal fishes have more opportunities for population divergence, whereas mesopelagic fishes can easily be assumed to have panmictic populations. There are also two different types of early life history of these three groups of deep-sea fishes, namely more mobile planktonic larvae and almost sedentary direct hatching. The life history characteristics of these fishes influence the patterns of population structure: larval dispersal on strong oceanic currents in the sea-surface layer during the planktonic stage enables expansion of the species' range and maintains connectivity among distant habitats. Conversely, the dispersal ability of fishes without planktonic larvae can be limited: for instance, direct-hatching species start their sedentary lives just after hatching (Ferry-Graham et al. 2007). Combinations of these factors can greatly explain the degree of phylogeographic structuring across a species' distribution range. For example, all of the species in the abovementioned studies of deep-sea panmictic populations are benthopelagic with some migratory activity and have planktonic larvae. We can therefore surmise that genetic connectivity among local populations can be maintained by both larval dispersal by oceanic currents and adult migration over long distances.

In contrast, one factor supporting the heterogeneity of deep-sea fish populations is local adaptation, which can cause a decrease in fitness of immigrants and facilitate differentiation by genetic drift. There is still little evidence of local adaptation in deep-sea fishes, as such studies utilize statistics on hundreds of thousands of independent loci; suitable data can be obtained only by using modern sequencing analyses (next-generation sequencing). Milano et al. (2014) studied 381 single nucleotide polymorphisms among European Hake *Merluccius merluccius* and found some outlier loci that could express genetic heterogeneity between local populations in the Mediterranean Sea and the Atlantic coast of Europe. The significant correlations of allele frequencies at these outlier loci with seawater surface temperature and salinity might be due to local adaptation to the environmental conditions in each habitat. As next-generation sequencing has recently come to be used in population genetics and phylogeography, more results on deep-sea local adaptation should come in.

10.3 Phylogeographic Assumptions in Japanese Seas

The Japanese Archipelago and its surrounding seas were formed gradually over the past 20 million years. The long history of the seas around Japan is, however, less important than the more recent geological and climatic events (in the last one million years) if we wish to understand the intraspecific diversity of the deep-sea fishes in these seas. Speciation seems to have become increasingly frequent in the last million years (Norris and Hull 2012). Japanese seas are characterized by the variations in oceanic environment during the last million years, in particular during the Pleistocene glacial-interglacial cycles and, I would introduce the deep-sea phylogeography of the Japanese seas from this perspective.

10.3.1 Geography and its History in the Japanese Seas

The geography and oceanography of the Japanese seas are described in Chap. 2, but here I briefly restate the characteristics that seem important to our understanding of the drivers of the intraspecific diversity of deep-sea fishes and the history of these drivers. The Japanese Archipelago is surrounded by four seas: Sea of Okhotsk, Sea of Japan, western North Pacific Ocean, and East China Sea (Fig. 10.2). The seas are connected to each other by narrow and shallow seaways between the Japanese islands and the Asian continent in most cases, whereas the northernmost Tartar Strait is located between Sakhalin and the Asian continent. As a detailed tectonic history of the archipelago and the surrounding seas is beyond the scope of this section, I introduce instead a simple timeline of geological events by Taira (1990) (Fig. 10.3). Although the review and synthesis by Hall (2002) focuses mainly on Southeast Asia, it is useful for further detail of the tectonic history of the Asian continent. Also, oceanographic and geographic changes in the Sea of Japan between 3.5 million years ago (Mya) and now have been reviewed by Itaki (2016). Back-arc spreading and continental collision started in the early Miocene (Jolivet et al. 1994), and thereafter the paleo-Sea of Japan continued expanding. Itaki (2016) found that Pacific-type deep-water radiolarians disappeared around 2.75 Mya; this was probably related to the closure or shallowing of straits between the Sea of Japan and the Pacific Ocean and the intermittent occurrence of deep-sea anoxic events (see the following section). The present shape of the Japanese Archipelago and the Sea of Japan has developed since the formation of the modern Tsushima Strait about 1.7 Mya (Fig. 10.3) (Kitamura et al. 2001, but also see Itaki 2016).

10.3.2 Glacial-Induced Climate Changes and Their Impacts on Japanese Seas

In regard to the intraspecific diversity of deep-sea species around the Japanese Archipelago, one of the most important historical events was a series of climatic oscillations during the Pleistocene glacial and interglacial periods (hereafter, glacial cycles), which potentially drove the separation of deep-sea habitats, and thus putative populations, between and within the seas. The climatic oscillations are partly explained by periodic changes in the Earth's eccentricity—the shape of its orbit around the Sun—that affect the allocation of incident solar energy (Zachos et al. 2001) and its relationship to radiative forcing due to CO_2

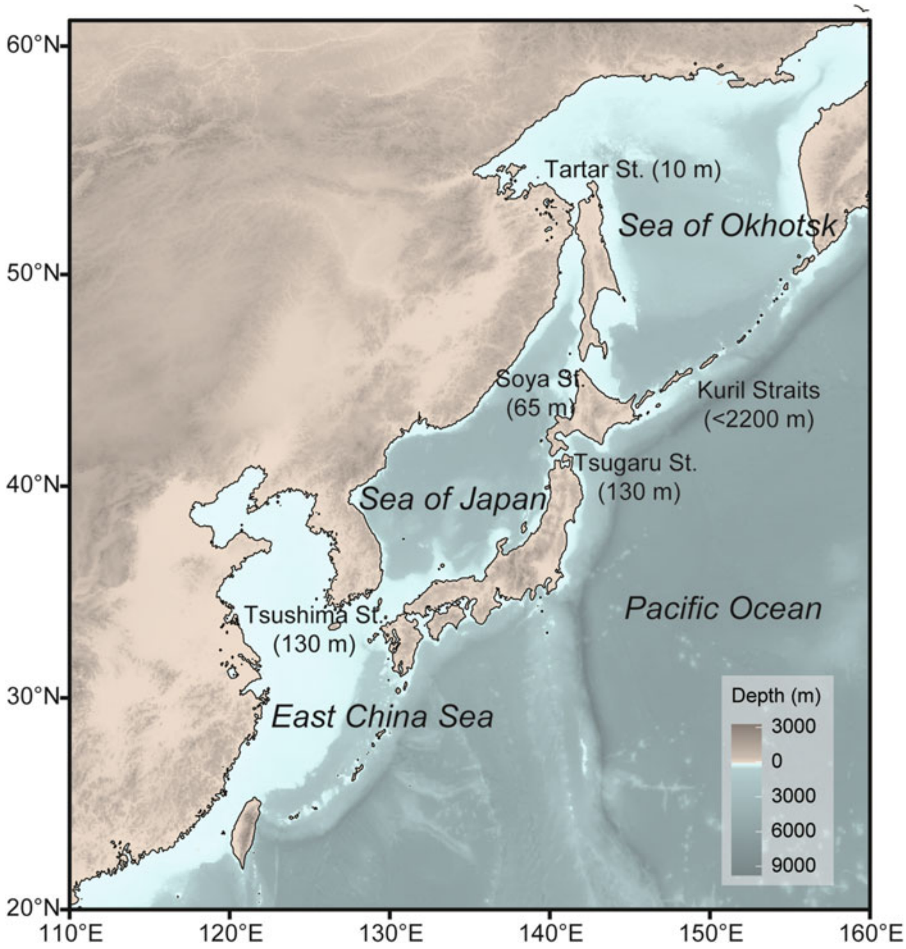

Fig. 10.2 Map of Japanese seas. Names of straits are shown, along with sill depths. The map is based on bathymetric data from the General Bathymetric Chart of the Oceans (GEBCO) and illustrated by the "*marmap*" package (Pante and Simon-Bouhet 2013) in R v. 4.03 software (R Core Team 2020)

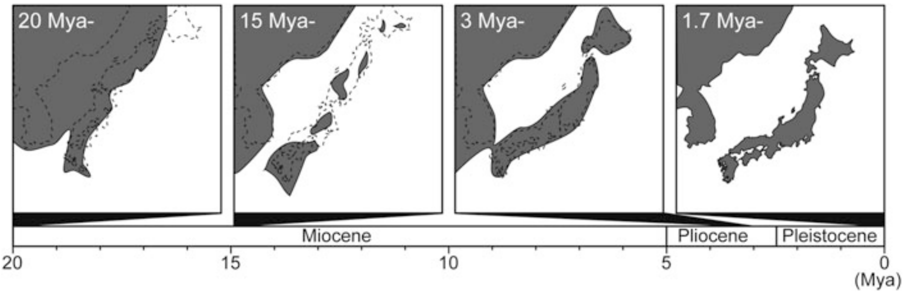

Fig. 10.3 Illustration of Japanese islands in the past 20 million years, following Taira (1990)

and CH_4 (Jouzel et al. 2007). From the early Pleistocene to the present, changes in the climate and oceanic environment have affected marine populations (Avise 2000; Provan and Bennett 2008). Rapid changes in water volume in the ocean are caused mainly by growth and decay of the continental ice sheets, which sometimes lead to rapid changes in sea level (Fig. 10.4a, summarized by Miller et al. 2005).

Because of these rapid sea-level changes, the shape of deep-sea habitats, especially on the continental shelf and slopes of the seas around Japan, may have drastically altered during the last million years, even after the shape of each sea had become almost fixed. The sea level dropped during the glacial periods, and it reached 130 m below the present shoreline during the Last Glacial Maximum (LGM, Yokoyama et al. 2018). I show the bathymetric characteristics of the seas around Japan assuming the present topography (Fig. 10.4), as well as the sea levels −130 m (0.02 Mya, LGM, Marine Isotope Stage [MIS] 2, "Würm" glacial period, Fig. 10.4b), −100 m (0.16 Mya, MIS 6, "Riss" glacial period, Fig. 10.4c), and +20 m (0.12 Mya, MIS 5d, "Riss–Würm" interglacial period, Fig. 10.4d). Notably, the East China Sea and Seto Inland Sea became land during the glacial periods because of shallowing. Shallow areas in the northern Sea of Okhotsk and shelves in the western Sea of Japan were exposed during low-sea-level stands in the glacial periods.

One of the important environmental changes due to past sea-level fluctuations was the change in connectivity among the seas around the Japanese Archipelago—especially the water flow between the Sea of Japan and the other seas. The sill depth of the straits between the seas around Japan is mostly no more than 130 m, and on this assumption, the Sea of Japan almost

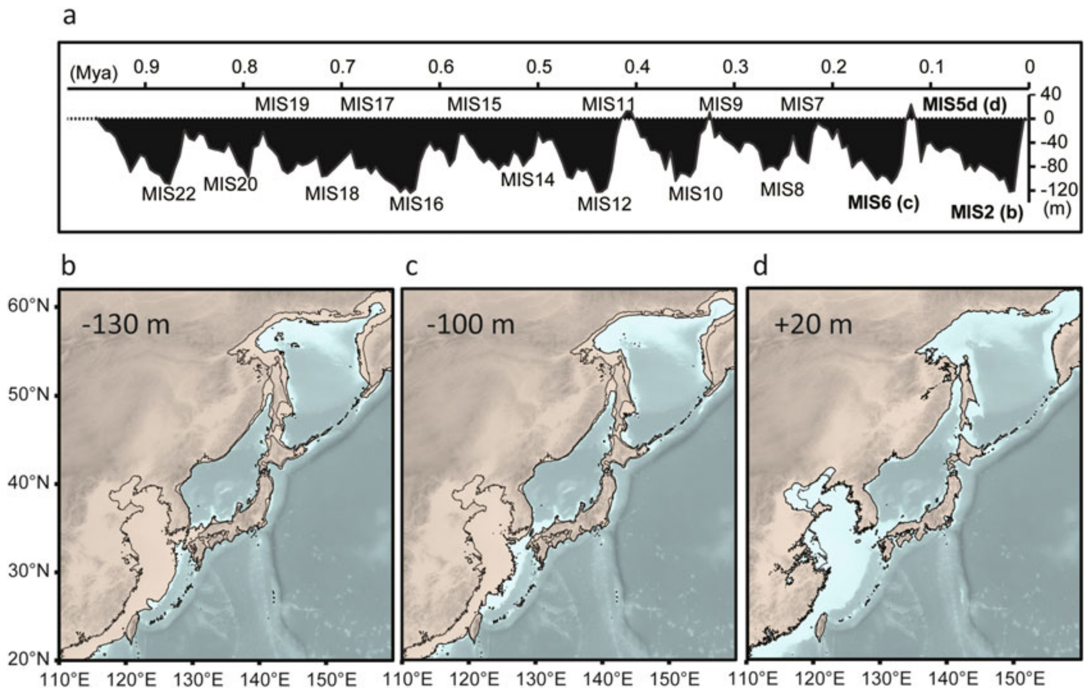

Fig. 10.4 (**a**) Glacial sea-level changes during the past one million years and (**b**–**d**) maps assuming topographies of (**b**) −130 m, (**c**) −100 m, and (**d**) +20 m. Present sea level is indicated as a dashed line, and marine isotope stages (MISs) are shown. *Bold text* in (**a**) corresponds to the maps below the diagram. In the maps, *fine dotted lines* indicate the present shorelines. The maps are based on bathymetric data from the General Bathymetric Chart of the Oceans (GEBCO) and illustrated by the "*marmap*" package in R v. 4.03 software

became isolated from the other seas during the LGM. It may be true that the connections between deep-sea areas in the Sea of Japan and adjacent seas were almost lost during past glacial periods.

The deep-sea environment may also have changed during the glacial periods as a result of lost connections between the seas. The severely anoxic conditions in the deep-sea layer of the Sea of Japan during the LGM are among the most prominent examples of glacial environmental changes around the Japanese Archipelago (Itaki et al. 2004; Fig. 10.5). Oba et al. (1991) inspected the microfossil assemblages in deep-sea sediment cores and showed that deep-sea species were absent in the layers corresponding to the LGM. They then hypothesized that strong density-dependent stratification of the water column caused by the development of low-salinity

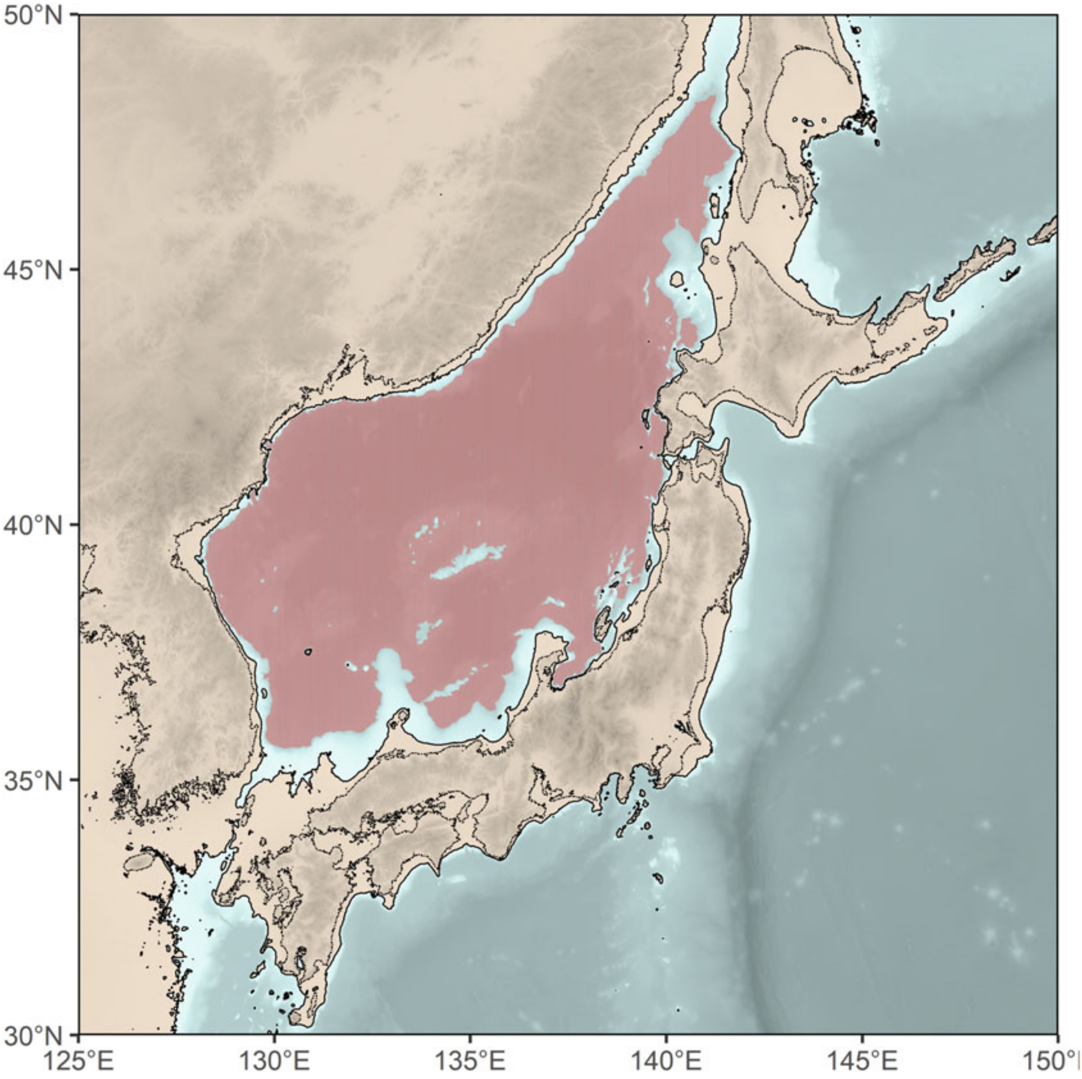

Fig. 10.5 Map of the Sea of Japan, showing potential anoxic areas in the deep sea during the last glacial maximum. Topography is based on the present bathymetry of the seafloor and topographical changes of −130 m, assuming the last glacial low-sea-level stand. Areas with a seafloor below 500 m depth are colored pink as potential areas of anoxic conditions (Itaki et al. 2004). *Dashed lines* indicate present shorelines. The maps are based on bathymetric data from the General Bathymetric Chart of the Oceans (GEBCO) and illustrated by the "*marmap*" package in R v. 4.03 software

surface water coincided with decreasing inflow of water currents into the Sea of Japan from the Tsushima and Tsugaru straits from 30,000 years ago (kya), resulting in anoxic conditions in the deep-sea layer and the extinction of deep-sea organisms in the Sea of Japan. Itaki et al. (2004), furthermore, found an intermediate well-oxygenated layer between the deep-sea anoxic water and the low-salinity surface water. This severe environment may have severely influenced deep-sea connectivity, even between local habitats within the Sea of Japan.

Today, the deep layer below 200 m depth in the Sea of Japan is filled with a highly oxygenated and extraordinarily cold deep-water mass known as the Japan Sea Proper Water (JSPW; Sudo 1986). As summarized in Chap. 7, the existence of this cold deep-water mass enables subpolar cold-adapted deep-bottom fishes to live on the continental slope areas [e.g., zoarcids *Bothrocara hollandi* and *Lycodes tanakae*; liparids *Careproctus trachysoma* and *Liparis ochotensis* (as *Liparis ingens*) (see Okiyama 2004; Shinohara et al. 2011)]. The mesopelagic fishes in the Sea of Japan is, conversely, limited to a single sternoptychid, *Maurolicus japonicus*, distributed just above the JSPW (in about the 200-m depth layer), because the deep sea is too cold for oceanic deep-sea fishes. The types of benthopelagic fishes in the deep-sea sub-bottom layer are also limited, to gadid fishes (Pacific Cod *Gadus macrocephalus* and Walleye Pollack *Gadus chelcogramma*), with a lack of deep oceanic fishes such as macrourids, probably for the same reason. There are oceanic mesopelagic or benthopelagic fishes in both the Sea of Okhotsk and the Pacific Ocean as bottom environment is much warmer; the above situation applies only to the Sea of Japan.

Glacial and interglacial environmental changes have also been suggested in the Pacific Ocean and the Sea of Okhotsk. The glacial trend of global cooling has been observed in these seas. Harada et al. (2012) analyzed bio-carbon in deep-sea core samples and suggested that extended winters in the LGM may have led to the presence of seasonal sea-ice cover in the western North Pacific areas. From ice-raft debris recorded in core samples, Sakamoto et al. (2005) determined that the Sea of Okhotsk was covered with sea ice during winter; the duration and degree of coverage depended on the period. The sea-ice coverage further influenced marine productivity during the LGM (Okazaki et al. 2005). There is, however, no evidence of anoxic conditions in these seas during past glacial periods. As the deep Kuril Straits are present between the Sea of Okhotsk and the Pacific Ocean, water exchange between the seas could have been maintained even during the past glacial periods.

10.4 Deep-Sea Intraspecific Diversity Around Japan

The complex geographic and environmental histories of the seas around Japan are reflected in the species diversity in each sea, as reviewed in the previous chapters, and this is also the case for deep-sea intraspecific diversity. There are deep-sea fishes with deeply diverged lineages in the seas around Japan, although, as shown below, evidence for deep-sea intraspecific diversity exists mainly for deep-demersal species.

10.4.1 Mesopelagic Fishes

At present, no mesopelagic species with a clear genetic structure has been found around Japan, probably owing to their prominent dispersal ability related to the migratory activity of adults and the passive transport of eggs or larvae. Okazaki et al. (2020) analyzed the mitochondrial cytochrome *b* sequence variation of the smooth lumpfish *Aptocyclus ventricosus*, and found two deeply diverged phylogroups in the Japanese seas and in the eastern North Pacific Ocean (Bering Sea and Gulf of Alaska). An important finding is that there was a putative migrant, or its descendant, in the western North Pacific off Japan, probably from the eastern North Pacific seas. As the species' breeding behavior includes parental care of large demersal eggs until hatching (Mecklenburg and Sheiko 2003), and the species lacks planktonic dispersal ability (Davenport

1985), the genetic homogeneity among the Japanese seas is therefore attributable to the adult's migration across the straits between the Sea of Japan, Sea of Okhotsk and the Pacific Ocean. As another instance, Terada et al. (2018) analyzed sequence variations among the mitochondrial COI (cytochrome *c* oxidase subunit I) and 16S ribosomal RNA coding regions of *Maurolicus japonicus* from the Sea of Japan, Sea of Okhotsk, and Pacific Ocean and found no evidence of phylogeographic structure among the populations there. They also found that the sequences of *M. australis*, in the south Pacific Ocean and *M. walvisensis*, around the Cape of Good Hope were included in the most dominant COI and 16S haplotypes of *M. japonicus*, suggesting that there was extraordinarily low genetic diversity of mitochondrial sequences at the generic level. Such low variability and high homogeneity of mitochondrial sequences is always observed in cosmopolitan species with large effective population sizes (Avise 2000). However, the genetic variability among mitochondrial genes sometimes does not correspond to what is observed in genomic datasets (e.g., yellowfin tuna *Thunnus albacares*; Ward et al. 1994; Ely et al. 2005; Grewe et al. 2015). Allopatric divergence between local *M. japonicus* populations among the seas is therefore still possible, given that there were multiple glacial isolation events in the Japanese seas, even after consideration of the passive transport of larvae in the near-sea-surface layer (<30 m depth) (Paraboles et al. 2019). Further inspection of nuclear genetic variations may resolve the question of mesopelagic intraspecific variations among the seas around Japan.

10.4.2 Deep-Demersal Fishes I: Zoarcidae

The growing body of knowledge regarding deep-sea intraspecific diversity around Japan concerns deep-demersal fishes. The limited larval- or egg-dispersal ability of some deep-demersal fishes can trigger lineage split between local habitats, whereas very few mesopelagic or benthopelagic species lack a planktonic dispersal phase (e.g., *Melanostigma atlanticum* (see Silverberg et al. 1987). The limited migratory activities of adults of deep-demersal fishes sometimes prevent the genetic admixture of local populations. Some of the apparently sedentary fishes, however, show unexpectedly high dispersal ability, causing admixture over their distribution ranges. For example, not a few species show seasonal migration along the continental slopes (e.g., *Reinhardtius hippoglossoides*, see Boje et al. 2014; *L. tanakae*, see Saveliev et al. 2011). As it is sometimes challenging to strictly define "true deep-demersal fishes," and they may be discriminated from benthopelagic fishes only by their taxonomic groupings and life history traits, patterns of species intraspecific diversity should be carefully investigated for each species. Here and in the next section, I introduce a series of works focusing on deep-demersal fishes around Japan in the families Zoarcidae and Liparidae, both of which putatively lack planktonic larvae.

Zoarcids are generally characterized by low migratory activity and a lack of planktonic dispersal phases (Anderson 1994). They are therefore potentially excellent subjects for phylogeographic study. From laboratory observation of the mesopelagic zoarcids *Lycodapus* spp., Ferry-Graham et al. (2007) suggested that burrowing is fundamental to zoarcid reproduction, probably because of its evolutionary constraints over the family. The pioneering work on zoarcid phylogeography was done by Kojima et al. (2001), who focused on the intraspecific sequence diversity of the mitochondrial control region in the zoarcid *B. hollandi*: they reported two distinct lineages, groups A (in the western part of the Sea of Japan, depth <1100 m) and B (at all sites) within the Sea of Japan (Fig. 10.6a). The present distribution of *B. hollandi* in the Sea of Japan ranges from 200 to 2000 m depth (Okiyama 2004). It is therefore possible that the populations within the Sea of Japan were fragmented by the glacial-induced anoxic conditions (Fig. 10.5; also see the previous section), although it is also possible that intermittent connection of the seas had driven secondary contacts of allopatrically diverged lineages in the seas. Kodama et al. (2008), who further expanded sampling to include the Sea of Okhotsk, found a phylogeographic structure of this species between the Sea of Okhotsk and the Sea of Japan, in addition to intra-oceanic divergence of the populations. Recently, Kido et al. (2020) reported two divergent nuclear ITS1 (internal transcribed spacer 1) lineages from *B. hollandi*, also in the Sea of Japan, although they did not completely correspond to the groups A and B found in the previous study. This series of studies implies the genetic divergence of local populations even within the Sea of Japan, probably in relation to glacial-induced inter- and intra-oceanic habitat fragmentation. The drivers of this divergence are still elusive, as it is always difficult to attribute divergence to a certain event owing to a lack of fossil records, as well as the uncertainty of genetic age estimation.

One of the keys to understanding the intraspecific diversity of deep-demersal species is the contrasting environmental conditions among the Japanese seas. As I mentioned in the previous section, glacial environmental changes hit these seas, but with different intensities. Comparison of four zoarcid phylogeographies provides insight into the environmental conditions in the continental shelf areas around the Japanese seas. I summarize the results for *Lycodes matsubarai* (see Sakuma et al. 2014), the closely related *Lycodes japonicus* and *Lycodes ocellatus* (see Sakuma et al. 2015), and *Petroschmidtia teraoi* (see Sakuma et al. 2020) in Fig. 10.6. The demographic histories of the four species are concordant in terms of their sudden expansion in the Sea of Japan, most likely after the last glacial anoxic event. Although pre-LGM demographic signals are always lost in mitochondrial datasets (Grant et al. 2012), and it is therefore not possible to determine what these species' population histories were like during the past glacial periods, the lower nucleotide diversity in the Sea of Japan (see Fig. 10.6) implies that there was a genetic bottleneck from the preglacial larger population owing to the severe environmental conditions in the Sea of Japan. In contrast, the effective populations in the Sea of Okhotsk (*L. matsubarai*) and Pacific Ocean (*L. ocellatus*) seemed to have been stable, even during the last glacial period. As these zoarcids are cold adapted (Anderson 1994), glacial cooling of the climate

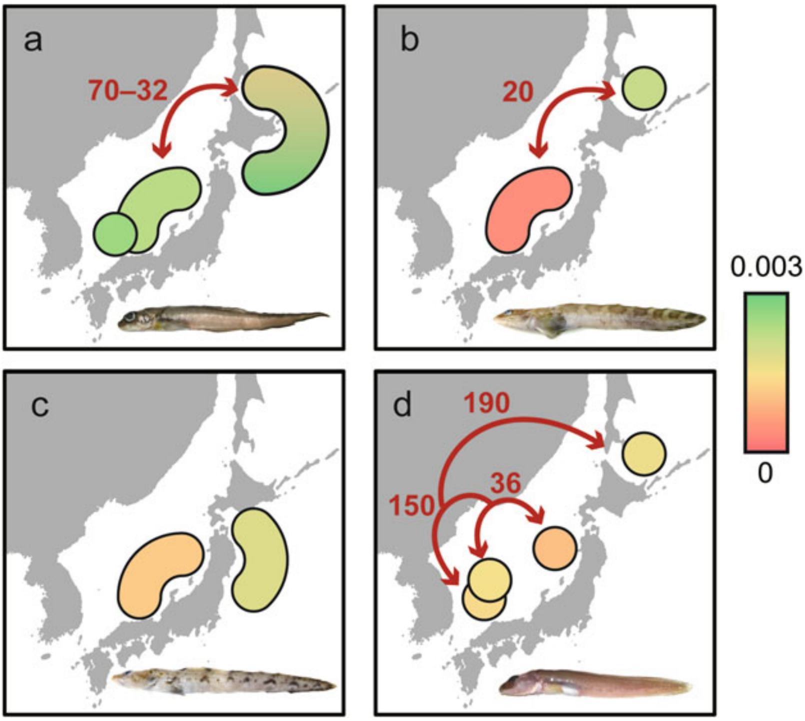

Fig. 10.6 Illustration showing the distribution of the deep-sea zoarcid populations around Japan. (**a**) *Bothrocara hollandi*, (**b**) *Lycodes matsubarai*, (**c**) *L. japonicus* and *L. ocellatus*, (**d**) *Petroschmidtia teraoi*. Nucleotide diversity of each population is color coded, showing generally lower values for the populations in the Sea of Japan. *Numerals* beside red arrows show divergence time estimates in thousand years. Nucleotide diversity and divergence time estimates are from (**a**) Kodama et al. (2008), (**b**) Sakuma et al. (2014), (**c**) Sakuma, unpublished data and (**d**) Sakuma et al. (2020)

may not have influenced the effective population size without the presence of more severe anoxia.

From another perspective, the genetic divergence between the Sea of Japan and the Sea of Okhotsk (*L. matsubarai*, *P. teraoi*) is indicative of glacial-induced habitat fragmentation. The emergence of the narrow and shallow Soya Strait land-bridge may have triggered divergence of *L. matsubarai* between the Sea of Okhotsk and the Sea of Japan during the LGM and of *P. teraoi* in a past glacial period (most likely MIS 6, the "Riss" glacial period, see Fig. 10.4). Furthermore, multiple divergences between intra-oceanic lineages of *P. teraoi* may have been driven by changes in habitat distribution. The upper continental slope habitat around the Noto Peninsula at the midpoint of the Japanese mainland changed drastically following the glacial sea-level changes (see Fig. 10.4), and intermittent connection of the slope habitat in the northern and western Sea of Japan may have driven the divergence of mitochondrial lineages. Such a mechanism of population divergence induced by habitat discontinuity may explain the multiple lineages of deep-demersal fishes within a sea.

10.4.3 Deep-Demersal Fishes II: Liparidae

Deep-sea liparid species are also notable for their diversity in the northern Pacific Ocean. Above all, fishes of the genera *Careproctus* and *Crystallichthys* have been studied in Japanese seas from both phylogeographic and taxonomic perspectives. The adult fishes in this group are sedentary and therefore potentially good targets of phylogeographic studies. Although the reproductive strategies of many member species are unclear, it is notable that some members are characterized by bizarre reproductive parasitism of adult king crabs (Lithodidae, Gardner et al. 2016), which provides long-term protection to the eggs and larvae. As low dispersal ability is inferred for species with this type of protective reproductive strategy, genetic connectivity among local populations may be limited for these species. Kai et al. (2011) found nine mitochondrial lineages among the five nominal species included in Salmon Snailfish *Careproctus rastrinus* species complex from the marginal seas of the Pacific Ocean (Fig. 10.7). These multiple lineages could correspond to some of the nominal species, but there are still cryptic species that cannot be distinguished by their morphological characteristics. It is also notable that there are multiple distant lineages in each sea; this implies secondary contact of divergent populations. Also, on the basis of mitochondrial sequence analysis and AFLP (amplified fragment length polymorphism) analysis, Tohkairin et al. (2016) found multiple lineages of *Crystallichthys matsushimae*, in the Sea of Japan and the Sea of Okhotsk and on the western North Pacific coast of Japan. The known yellow and red morphotypes in this species were correlated with the results of AFLP, suggesting the occurrence of genetic divergence between these morphotypes as well as local populations in each sea, although the results of the mitochondrial analyses do not fully support this view. These results in deep-sea liparids suggest that there are complex species, and population histories in the western North Pacific's marginal seas that have repeatedly isolated local populations during glacial sea-level oscillations.

10.4.4 Deep-Demersal Fishes III: Other Instances

There are also some deep-demersal fishes that do not show genetic structuring among populations in the seas around Japan, even though they putatively experienced glacial population changes and isolation of the local habitat in each of these seas. If we assume the low migratory activity of adults of deep-demersal fishes, genetic homogeneity was probably caused by extensive larval dispersal. It is also possible that conventional sequencing analyses have had insufficient detective power, as some of them have focused on genetic variability of the mitochondrial control region, which sometimes results in a substitutional ceiling due to multiple substitutions at limited numbers of variable sites (Takeshima et al. 2005). Adachi et al. (2009) found no evidence of

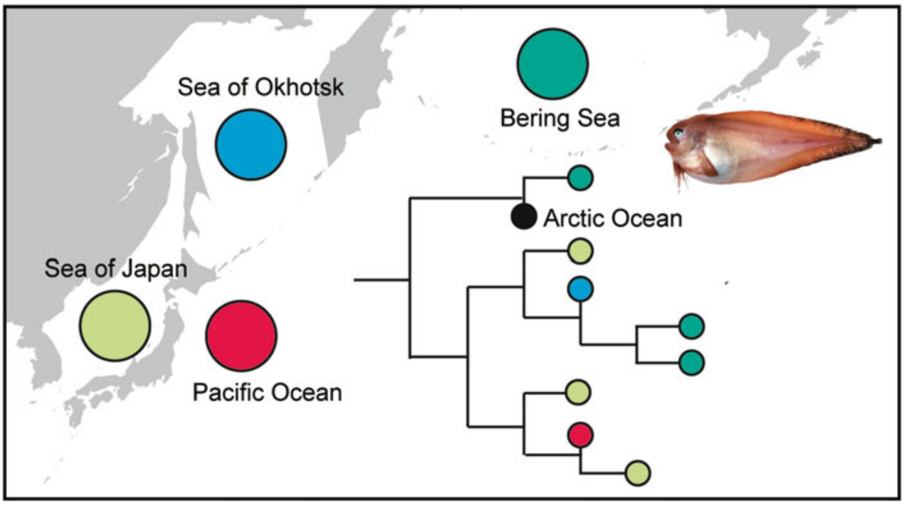

Fig. 10.7 Phylogeography of *Careproctus rastrinus* species complex inferred by Kai et al. (2011). Relationships among the phylogeographic units are shown as a dendrogram. Phylogroups within the species complex are color coded by the localities

genetic divergence between the deep-sea psychrolutid *Malacocottus gibber*, in the Sea of Japan and Darkfin Sculpin *Malacocottus zonurus*, in the Pacific Ocean. The two species are visually differentiated by presence of accessory spines on the preopercles in *M. zonurus* (see Nakabo 2002), but this differentiation was not supported by the genetic results. Populations of the deep-sea flounders *Hippoglossoides dubius* and *Cleisthenes pinetorum*, both targeted by Japanese offshore trawlers on the upper continental slopes, are genetically homogeneous over the Sea of Japan, Sea of Okhotsk, and Pacific Ocean (Kojima et al. 2014). Additional insights from the use of genomic strategies such as whole-genome resequencing may help us to understand the patterns of intraspecific diversity in these species.

10.4.5 Benthopelagic Fishes

Benthopelagic fishes have also been the subject of phylogeographic studies in the seas around Japan. As I noted in Sect. 10.2, fewer opportunities for vicariance than in deep-demersal fishes may have resulted in genetic homogeneity over distant habitats in these fishes, including in gadiform fishes. It is, however, still possible that the limited detective power of mitochondrial markers has failed to find subtle gradients of genetic composition among locally adapted populations. Careful consideration is therefore required when interpreting results that are negative for genetic structuring.

One series of studies has targeted Pacific Cod *G. macrocephalus* in the seas around Japan (Fig. 10.8). This species has attracted considerable attention in the fields of fisheries and conservation genetics for its importance to local fisheries, and it has been studied for the purpose of delineating the management unit or simply stocks, assuming that it is a demographically independent group with homogeneous biological characteristics (Kerr et al. 2016). Canino et al. (2010) inspected genetic variations among 11 microsatellite loci and mitochondrial sequences from the species' entire distribution range, from the westernmost Sea of Japan to the Georgia Basin in the eastern Pacific Ocean. They reported three putative populations, in the western North Pacific (Sea of Japan, Sea of Okhotsk), eastern North Pacific (Bering Sea, Gulf of Alaska), and Georgia Basin. Gwak and Nakayama (2011), utilizing five microsatellites, found three distinct populations, in the western, eastern, and southern seas of the Korean

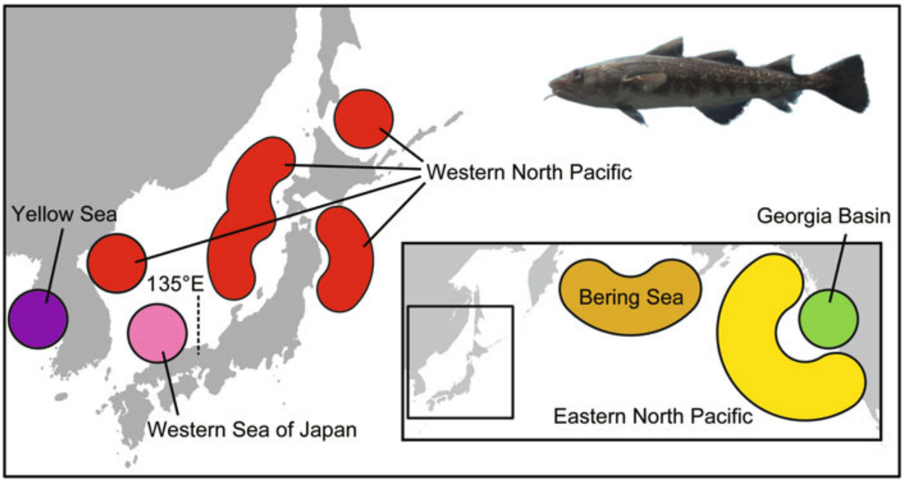

Fig. 10.8 Maps showing the distribution of the populations in Pacific cod *Gadus macrocephalus* in the north Pacific seas. Genetically distinct populations inferred from Canino et al. (2010), Gwak and Nakayama (2011), Suda et al. (2017) and Sakuma et al. (2019) are color coded. *A dashed line* indicates geographic boundary between the two populations in the Sea of Japan at 135° E

Peninsula. Suda et al. (2017) further focused on the western North Pacific population of Canino et al. (2010), using 16 microsatellites. They found two distinct populations, in the western Sea of Japan and in other regions along the Japanese coast. Sakuma et al. (2019) used a spatially explicit Bayesian clustering analysis of mitochondrial sequences and found a boundary between these two populations near 135° E along the Japanese coast of the Sea of Japan.

There arises the question of why there is such a clear genetic break along an apparently continuous coastline without any hypothetical geographic barriers. The divergence between the two populations was estimated to have occurred during the last glacial period, implying strong geographic and climatic influences on the populations. Sakuma et al. (2019) has surmised that the two Pacific cod populations are the legacy of the glacial refugia in the Sea of Japan. These two populations may currently be maintained by the thermal barrier of the Tsushima warm current running between them (Suda et al. 2017). Furthermore, local adaptation of the western population of *G. macrocephalus* to the higher temperatures in the westernmost Tsushima Strait areas is also possible (A. Suda, personal communication). Our latest project, which is based on a whole-genome-resequencing dataset, will tackle this question of invisible oceanic barriers and may help us to understand the mechanisms of genetic diversification of the highly mobile benthopelagic fish species.

10.5 Conclusion

Here, I have introduced phylogeographic assumptions and their genetic consequences in regard to deep-sea fishes in the seas around Japan. These seas have experienced great environmental changes in the past one million years of climatic oscillations. Above all, the deep-sea area in the Sea of Japan was almost separated from the neighboring seas and was hit by severely anoxic conditions. Previous phylogeographic results regarding divergent lineages concern mostly deep-demersal fishes without planktonic eggs or larvae and can be interpreted in terms of the limited dispersal ability and thus gene flow between local populations. Some of these fishes show divergence between local populations even within the sea, suggesting that there was fragmentation of local habitats in the unfavorable oceanic environment during past glacial periods. Conversely, such population histories have currently not been discovered in deep-demersal fishes with planktonic larvae or in mesopelagic fishes. Further investigations using modern sequencing techniques would be helpful for more closely comparing the genetic compositions of local populations of these fishes. In a single benthopelagic species, *G. macrocephalus*, clear genetic breaks have been found in the seas around Japan, but the factors that have driven divergence between these populations are still elusive. By using large-scale genomic datasets and a detailed comparison between the characteristics of local stocks, we will be able to determine the reasons for population divergence across invisible genetic barriers.

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Phylogeography of Coastal Fishes of Japan

11

Shoko Matsui

Abstract

This chapter introduces the phylogeographic patterns and historical demography of coastal fishes of Japan. The author examines the phylogeographic characteristics of Japan, with a particular focus on oceanographic features, such as past and present ocean currents, and paleogeographic changes, such as land bridge formation and subsequent reconnection of marginal seas during the Pleistocene glacial–interglacial cycles. The phylogeographic characteristics of the main islands of Japan are introduced, followed by discussion of the phylogeographic relationships among the biota from the Ryukyu Islands–Japanese Mainland–Ogasawara (Bonin) Islands. Phylogeographic relationships between the coastal areas of Japan and the continent are also introduced. Finally, differences in the population structure of species are examined, primarily from an ecological perspective, and future challenges are discussed.

Keywords

Population genetic structure · Population dynamics · Comparative phylogeography · Pleistocene glaciation · Sea-level oscillations · Paleogeographic changes · Ocean currents

11.1 Introduction: Characteristics and Factors Affecting the Population Structure of Coastal Fishes of Japan

Knowledge of intraspecific population dynamics can facilitate a better understanding of biodiversity (Avise 2000). Within the context of conservation, it is becoming increasingly important to clarify phylogeographic patterns and to elucidate the mechanisms that underlie the origin and maintenance of intraspecific diversity (Rocha et al. 2007). In coastal fishes, establishing a well-defined geographical population structure within species appears difficult because there are few apparent barriers to individual dispersal in coastal waters, and because many coastal fishes have a pelagic larval stage, during which time larvae can be transported long distances by ocean currents. In reality, however, individual dispersal is often restricted even in coastal fishes with planktonic larvae (Taylor and Hellberg 2003), resulting in the establishment and maintenance of marked and consistent population structures that reflect paleogeographic, oceanographic (e.g., Dawson 2001; Muss et al. 2001; White et al. 2010), and ecological factors (e.g., Rocha et al. 2002).

The population structure of coastal fishes differs markedly from those of freshwater and

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deep-sea fishes, especially in the degree of population differentiation and phylogeographic patterns. In general, population differentiation of coastal fishes is less pronounced than it is in freshwater fishes (Ward et al. 1994; Avise 2000), but stronger than it is in deep-sea fishes (cf., Stefanni and Knutsen 2007; White et al. 2011; Varela et al. 2012), although there are numerous exceptions. For example, gene flow between populations of primary freshwater fishes is typically limited to the freshwater systems in which the fish hatched, whereas barriers to gene flow are less well defined in marine fishes, resulting in higher rates of gene flow and a more homogeneous population structure (Ward et al. 1994; Avise 2000). In coastal fishes and deep-sea fishes, ecological factors such as larval dispersal ability have a major effect on the degree of population differentiation. For example, in many coastal fishes, pelagic larvae remain near their natal populations by oceanographic or behavioral mechanisms, resulting in the restriction of gene flow (Cowen and Sponaugle 2009). On the other hand, many deep-sea fishes hatch offshore and then their pelagic larvae and juveniles float in the surface to middle layer where they are transported long distances by ocean currents (Priede 2017). Additionally, physical barriers to individual dispersal often differ between coastal fishes and deep-sea fishes. For example, shallow areas such as shallow straits (e.g., Castro et al. 2007; Sakuma et al. 2014) and hydrographic boundaries that form in the deep layer (Gordeeva 2014) interrupt the continuity of suitable depth zones and often restrict the gene flow of deep-sea fishes, while the open sea can act as a barrier to gene flow in coastal fishes (e.g., Rocha et al. 2008; Kuriiwa et al. 2014). Furthermore, environmental factors such as changes in water temperature, salinity, and dissolved oxygen levels due to paleogeographic events differ between coastal and deep-sea areas. Thus, different mechanisms can affect the formation and maintenance of population structure in deep-sea, coastal, and freshwater fishes.

Paleogeography is one of the most important factors affecting the development of the population structure of coastal fishes. During the late Pleistocene glacial–interglacial cycles, changes in sea level of approximately 120–140 m occurred in 100,000-year cycles around the world (Lambeck et al. 2002). These oscillations resulted in repeated separations and reconnections of coastal areas, leading to population fragmentations, lineage divergences, and secondary contacts of coastal organisms around the world (Hewitt 2000). In particular, marginal seas have undergone repeated separations and reconnections to adjacent water bodies, continental shelves have been exposed and flooded, and coastal environments have undergone drastic changes due to cessations and resumptions of inflows of ocean currents during these glacial–interglacial cycles (Wang 1999). These fluctuations have led to significant changes in population structure and demographic characteristics of coastal organisms in marginal seas (e.g., Ni et al. 2014). The western North Pacific Ocean has numerous examples of marginal seas, and the Japanese Archipelago is surrounded by three, i.e., the Sea of Okhotsk, the Sea of Japan, and the East China Sea. The Sea of Okhotsk and the Sea of Japan are generally deeper than 200 m, while the East China Sea is generally shallow, and areas deeper than 200 m are limited to the vicinity of the Okinawa Trough (Fig. 11.1a). These marginal seas and the Pacific Ocean are interconnected by shallow straits and island arcs. For example, the Sea of Okhotsk and the Sea of Japan are connected via the Tartar Strait (<15 m) and Soya Strait (<55 m), the Sea of Japan and the East China Sea are connected via the Tsushima Strait (mostly <130 m), and the Sea of Japan and the Pacific Ocean are connected via the Tsugaru Strait (mostly <130 m). These marginal seas have been isolated at various times in the past by almost complete closure of the straits through the formation of land bridges during the Pleistocene glacial periods. The seas then reconnected with adjacent water bodies during the subsequent interglacial periods (Wang 1999). The Sea of Japan was almost entirely isolated from neighboring marginal seas after closure or narrowing of the straits connecting the seas during the glacial periods of the late Pleistocene (e.g., Oba et al. 1991; Tada et al. 1999;

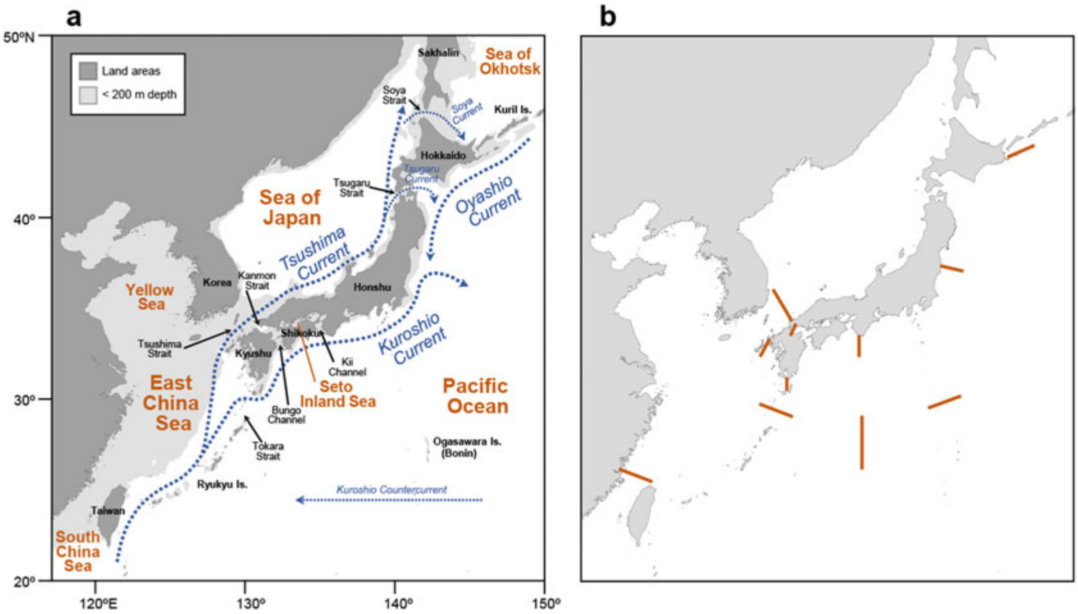

Fig. 11.1 (**a**) Approximate present routes of major ocean currents and location names around the Japanese Archipelago; (**b**) major phylogeographic boundaries of coastal fishes around the Japanese Archipelago

Gorbarenko and Southon 2000). Such isolation and reconnection of marginal seas is considered to have driven intraspecific phylogeographic splits and secondary contacts among populations of coastal fishes around the Japanese Archipelago. In addition, the coastal environment has changed considerably over geological time due to climatic fluctuations and changes in the coastline. For example, vast areas of continental shelf in the East China Sea were exposed, and the sea contained cold water as inflows of the warm Kuroshio Current were weakened during the Last Glacial Maximum (LGM: 26,500–19,000 years before present) (Ijiri et al. 2005). Similarly, shallow areas in the Sea of Japan were cold and the saline content was low during the LGM, not only because inflows of the Tsushima Current were diminished while the cold Oyashio Current passed through the Tsugaru Strait, but because large quantities of freshwater entered the sea from rivers, diluting the surface layer of the Sea of Japan (Oba et al. 1991; Gorbarenko and Southon 2000). Further, the water temperatures in areas along the Pacific coast are also considered to have been lower during the LGM than they are at present because the warm Kuroshio Current flowed further south (Chinzei et al. 1987; Oba and Murayama 2004). Such changes in the coastal environment have caused region-specific changes in the demographic characteristics of fish populations in the coastal waters around Japan.

Past and present conditions of ocean currents have also played an important role in the population structure of coastal fishes. The major contemporary currents around the Japanese Archipelago are shown in Fig. 11.1a. The warm Kuroshio Current, one of the world's major currents, flows off the Pacific coast of the Japanese Archipelago. The Kuroshio Current flows northwards past the Ryukyu Islands in the East China Sea, into the Pacific Ocean through the Tokara Strait, and then up the Pacific coast of the main islands of Japan before moving offshore (eastward) around the Boso Peninsula (located in the middle of Honshu Island). This major current has a powerful effect on the distribution and fragmentation of populations of coastal fishes, and plays a major role in the formation and maintenance of the coastal fish fauna and the intraspecific population structure of coastal fishes in the waters of the Ryukyu Islands, the Pacific coast of the main islands of Japan, and the Ogasawara (Bonin) Islands (Matsuura 2012). On the other hand, the warm Tsushima Current flows into the Sea of Japan through the Tsushima Strait, and then north-eastward along the Sea of Japan coastline before splitting at the northern end of Honshu Island; one branch, referred to as the Tsugaru Current, flows into the Pacific Ocean through the Tsugaru Strait between Honshu Island and Hokkaido Island, and a part of the Tsugaru Current flows southward together with the cold Oyashio Current along the Pacific coast of the northern part of Honshu Island; the other branch of the Tsushima Current flows northward along the west coast of Hokkaido Island. Thus, the Kuroshio Current and the Tsushima Current (and its branches) encircle the main islands of Japan, and the past and contemporary characteristics of these two warm currents has had a profound influence on the population structure of coastal fishes around Japan.

The dynamics of these paleogeographic and oceanographic factors have greatly affected the phylogeographic patterns and historical demography of coastal fishes of Japan. In some coastal fishes, significant geographic population structure has been recognized around the Japanese Archipelago, and the boundaries of genetic populations are often shared by multiple species (Fig. 11.1b), although the presence or absence and geographic locations of these boundaries often differ among species. The existence of these shared distributional characteristics suggests that common paleogeographic and oceanographic factors have had an influence on the formation and maintenance of population structures of different fishes. In addition, species-specific ecological characteristics are associated with differences in the degree of population differentiation and phylogeographic patterns among species. The first three sections (Sects. 11.2–11.4) of this chapter examine the phylogeographic factors that affect the diversity of coastal fishes in Japan, with a particular focus on ocean currents and the paleogeographic changes of these sea regions. The last section (Sect. 11.5) of this chapter examines differences in population structure among species, mainly from an ecological perspective. This chapter will focus primarily on demersal marine fishes, but aspects of pelagic fishes and diadromous fishes will also be discussed. The time scale examined will be mainly after the Pleistocene.

11.2 Population Structure of Fishes Distributed Around the Main Islands of Japan, and the Roles of the Warm Kuroshio Current and the Warm Tsushima Current in Population Dynamics

Phylogeographic patterns of coastal fishes around Japan are greatly influenced by past and contemporary oceanographic features, especially ocean currents. It is well documented that the distributional ranges of lineages of marine organisms are markedly affected by currents (e.g., Muss et al. 2001; York et al. 2008). This section will introduce the phylogeographic patterns and historical demographic characteristics of coastal fishes around the main islands of Japan (i.e., Hokkaido, Honshu, Shikoku, and mainland Kyushu), with a particular emphasis on the contribution of the currents flowing around these islands.

11.2.1 Two Major Intraspecific Groups: the Pacific Group and the Sea of Japan Group

11.2.1.1 Phylogeographic Patterns

The warm Kuroshio Current and the warm Tsushima Current have had a marked effect on the population structure of coastal fishes, resulting in the formation of two distinct lineages of fishes that correspond closely to the pathways of the two currents. These lineages are particularly apparent in several common coastal fishes, such as the gobies *Pterogobius elapoides* and *Pterogobius zonoleucus* (see Akihito et al. 2008), *Leucopsarion petersii* (see Kokita and Nohara 2011; Fig. 11.2), and *Chaenogobius*

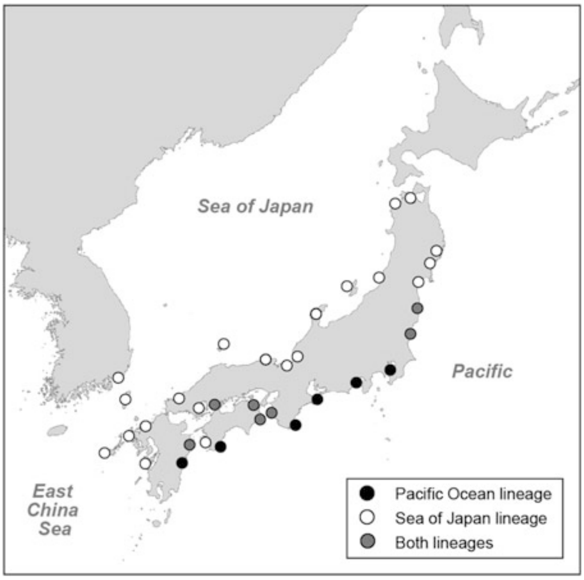

Fig. 11.2 Geographic distribution of two major lineages of *Leucopsarion petersii* around the Japanese Archipelago (based on Kokita and Nohara 2011, Fig. 1). *Closed* and *open circles* indicate populations composed of individuals of the Pacific Ocean and Sea of Japan lineages, respectively. *Gray circles* indicate populations composed of individuals of both lineages based on mitochondrial and/or nuclear DNA analyses

annularis (see Hirase et al. 2012; Hirase and Ikeda 2014b) and *Chaenogobius gulosus* (see Hirase and Ikeda 2014a). Although the distribution of the two major lineages differs somewhat among species, one lineage is distributed along the Pacific coast from mainland Kyushu to the center of Honshu Island (Pacific Ocean lineage), and the other lineage extends from Kyushu to Hokkaido Island along the Sea of Japan and then along the Pacific coast of the northeastern part of Honshu Island (Sea of Japan lineage). These two lineages are admixed in the areas where their ranges meet, i.e., along the coast of the northeastern Pacific and the Seto Inland Sea (see Sect. 11.2.2). In these contact zones, intraspecific hybridization and introgression between the two lineages has been reported in populations of *C. annularis* and *L. petersii*, and the absence of reproductive isolation between these two lineages has also been reported (Hirase and Ikeda 2015; Kokita et al. 2017). Additionally, intraspecific morphological differences (such as coloration, number of pectoral-fin rays, number of vertebrae, and body size) have been found in some species between the two lineages (Akihito et al. 2008; Kokita and Nohara 2011). Phylogeographic patterns corresponding to the pathways of the two warm currents have not only been detected in coastal fishes, but also in other coastal organisms such as gastropods (Kojima et al. 1997, 2004) and algae (Zhong et al. 2020). These observations suggest the existence of similar mechanisms among coastal fishes and other coastal organisms in which the two warm currents have played an important role, particularly in the formation and long-term maintenance of the population structure of coastal organisms in the waters around the main islands of Japan.

11.2.1.2 Mechanisms Underlying the Formation and Maintenance the Two Major Lineages

The first process underlying the development of these phylogeographic patterns is lineage divergence due to a vicariant event. As described in Sect. 11.1, during the Pleistocene, the repeated occurrence of glacial and interglacial periods caused marked oscillations in sea levels. During periods of low sea levels, the Pacific Ocean and the Sea of Japan were almost separated, and it is likely that this vicariant event restricted gene flow between populations of coastal fishes in the two seas, which in turn is considered to have promoted the divergence of the two major lineages. In many cases, estimated divergence times for the two lineages do not correspond to the last glacial period, but to the late Pliocene–middle of the Pleistocene, although the divergence time is not the same among species. For example, the estimated divergence times for *P. elapoides* is ca. 50,000–32,000 years ago, for *P. zonoleucus* it is ca. 0.6–0.4 million years ago (Ma) (Akihito et al. 2008), for *L. petersii* it is ca. 0.9–0.7 Ma (Kokita and Nohara 2011), and for *C. annularis* it is ca. 3.4 Ma (Hirase et al. 2016). These studies suggest that in many coastal fishes, the Pacific Ocean lineage and the Sea of Japan lineage had diverged long before the most recent glacial period and that they then remained distinct for one or more oscillations in sea level since lineage divergence. Similarly, for some coastal organisms, the divergence times for the East China Sea lineage from those of the adjacent marginal seas were estimated to have occurred long before the most recent glacial period (Ni et al. 2014).

After the divergence of the Pacific Ocean lineage and the Sea of Japan lineage, the two warm currents, the Kuroshio Current and the Tsushima Current, would each have played an important role in the expansion and maintenance of the distribution of the two lineages. In the Sea of Japan, the Tsushima Current flowed at almost every interglacial period from 1.7 Ma (Kitamura and Kimoto 2006; Gallagher et al. 2015), and this inflow would have contributed to spatial and demographic population expansion of coastal fishes along the Sea of Japan (for details, see Sect. 11.2.1.3). Also, since the Kuroshio Current reached its present latitude by 3 Ma, it would have flowed off the Pacific coast of the Japanese Archipelago, albeit with fluctuations in the route and intensity, during the glacial–interglacial cycles (Gallagher et al. 2015). Therefore, in general cases where phylogeographic patterns correspond to the two major currents, it is likely that the two lineages diverged before the last glacial period and that their distributions then expanded from the glacial refugia and were kept separated by ocean currents during the subsequent interglacial periods.

It is considered that no other major divergence events occurred during the glacial periods that followed the above major divergence event and that both of the lineages have been reisolated in the Pacific Ocean and the Sea of Japan, which has led to an increase in genetic differentiation between the two groups. However, minor subclades have been detected in some species of each major lineage (see Sect. 11.2.3), suggesting that vicariant events during the glacial periods that followed the major divergence contributed to the formation of these minor subclades. An exception to this phylogeographic pattern is the existence of at least four haplotype groups in the sand goby *Acentrogobius virgatulus* around the main islands of Japan (Matsui 2014; Fig. 11.3). In this case, the ancient population may have been divided into three groups (corresponding to Haplogroups 1 + 3, 2, and 4 of Fig. 11.3) during one or two glacial periods, and further divergence may have occurred in one of the three groups (Haplogroup 1 + 3) during a subsequent glacial period. This group may have been widely distributed in the East China Sea and the regions affected by the ancient Tsushima Current and its branches during an interglacial period after the first divergence. During a subsequent glacial period, this group (Haplogroup 1 + 3) may have subsequently split into at least two subgroups (Haplogroup 1 and 3), corresponding to Pacific Ocean and the Sea of Japan (to the East China Sea) populations, respectively. Nevertheless, in many coastal fishes, populations that diverged long before the last glacial period would have remained isolated with slight shifts in distribution corresponding to changes in coastlines and the location of current fronts during one or more sea-level oscillations, resulting in the extant population structure.

11.2.1.3 Historical Demography

During the late Quaternary glacial–interglacial cycles, the coastal environment changed considerably around the main islands of Japan, especially along the Sea of Japan; for example, the shallow Sea of Japan was covered by cold low-salinity water during the LGM (Oba et al. 1991; Gorbarenko and Southon 2000). Consequently, a large part of the coastal area of the Sea of Japan would have become unsuitable for temperate coastal organisms, leading to migration to glacial refugia and a decrease in population sizes in the Sea of Japan. It is likely that there

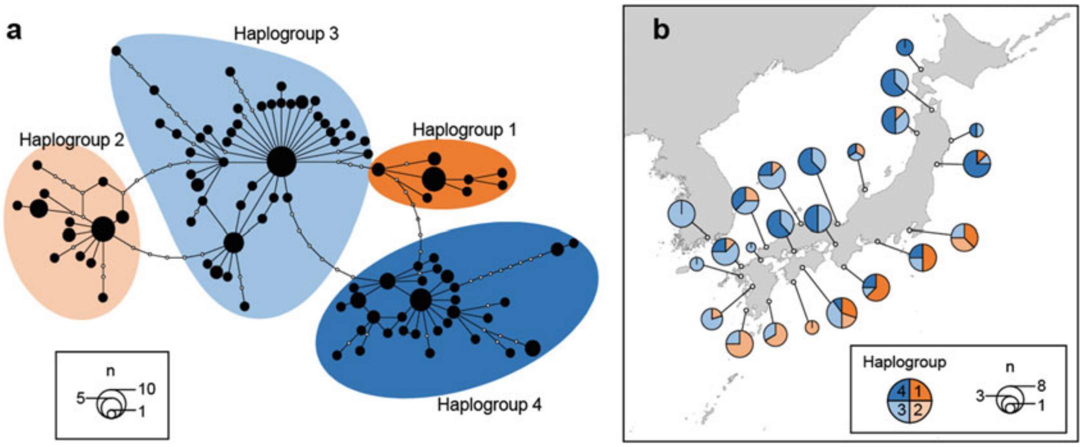

Fig. 11.3 (**a**) Parsimony network of mitochondrial cytochrome *b* gene haplotypes in *Acentrogobius virgatulus*. *Circle size* is proportional to sample size; (**b**) geographic distribution of haplogroups of *A. virgatulus*. Each color code of circle refers to haplogroups in the network (**a**). *Circle size* is proportional to sample size

were multiple refugia in the Sea of Japan for gobies, such as *L. petersii* (see Kokita and Nohara 2011) and *C. annularis* (see Hirase et al. 2016) (see Sect. 11.2.3). After the glacial period, the warm Tsushima Current resumed flowing into the Sea of Japan and suitable habitat for temperate coastal organisms would have increased, resulting in spatial and demographic population expansion of coastal organisms. Evidence of such decreases and rapid expansion of the Sea of Japan populations during the glacial–interglacial cycles has been reported in phylogeographic studies on coastal organisms such as *L. petersii* and *C. annularis* (see Kojima et al. 2004; Kokita and Nohara 2011; Hirase et al. 2016).

In general, genetic diversity tends to decrease in populations that have become smaller (Avise 2000). Especially in the central and northern areas of the Sea of Japan, low genetic diversity has been reported in coastal fishes such as *L. petersii* and *C. annularis*, suggesting that a decrease in population size may have occurred in these areas due to unsuitable coastal conditions during the last glacial period. In contrast, in the southern populations of these species in the Sea of Japan lineage, higher genetic diversity has been reported (Kokita and Nohara 2011; Hirase et al. 2016). Environmental changes along the East China Sea coast of northern Kyushu Island were relatively small during the LGM (cf., Ijiri et al. 2005). Additionally, a slight but constant flow of fresh seawater occurred into the westernmost part of the Sea of Japan through the Tsushima Strait (Gorbarenko and Southon 2000). Thus, the southern populations of at least some coastal fishes would have been relatively stable during the LGM. In many coastal fishes in the Sea of Japan lineage, the estimated time of rapid population expansion corresponds not to the postglacial period, but to the last interglacial period (Kokita and Nohara 2011; Hirase et al. 2016). In other sea regions, it has been proposed that population expansion of coastal organisms also occurred during the last interglacial period (Hoarau et al. 2007; Ni et al. 2014). However, since the coastal environment of the Sea of Japan was far from suitable for many temperate coastal fishes during the LGM, and that favorable conditions were subsequently restored, it is unlikely that populations of coastal fishes would not have experienced fluctuations. Thus, the following scenario for population expansion in the Sea of Japan is considered possible for at least some coastal fishes; large-scale population expansion from glacial refugia due to the influence of the Tsushima Current may have occurred along the Sea of Japan during the last interglacial period, these populations might have remained in multiple refugia scattered along the Sea of Japan during the last glacial period, and relatively small-scale expansion might have occurred during the post-glacial period.

Along the Pacific coast, water temperatures during the LGM are considered to have been lower than they are at present (Chinzei et al. 1987; Oba and Murayama 2004). However, in *L. petersii*, no oscillation in the population size of the Pacific Ocean lineage has been detected either during or after the LGM (Kokita and Nohara 2011), suggesting that the Pacific coast environment may have been relatively suitable for at least some temperate coastal organisms and that their population size would have been maintained during the LGM.

If a population became extinct during a glacial period without coming into secondary contact with other populations, evidence of the extinction cannot be inferred from extant populations. Therefore, in cases where only a single clade is recognized in a species with a wide distribution, it is possible that another lineage existing before the last glacial period may have become extinct during a subsequent glacial period (typically because the coastal environment in the Sea of Japan was unsuitable). Possible examples of such local extinction events include the common gobies *Acanthogobius flavimanus* (see Hirase et al. 2020b) and *Acentrogobius pflaumii* (see Matsui 2014).

11.2.2 Contact Zones Between the Two Major Lineages

In many cases where the two major lineages are detected around the main islands of Japan, they are sympatrically distributed at their boundaries, i.e., around the coast of the northeastern Pacific and the Seto Inland Sea, suggesting that the two lineages came into secondary contact after divergence in these areas. In these secondary contact zones, evidence of hybridization and introgression between the two lineages has also been reported in some species, as detailed below.

11.2.2.1 Northeastern Pacific Coast

The Kuroshio and the Oyashio currents (with the warm Tsugaru Current) converge off the Pacific coast of northeastern Honshu. In this area, which corresponds to the boundary between the Pacific Ocean lineage and the Sea of Japan lineage, two mitochondrial lineages with sympatric distributions have been reported in some coastal organisms, such as the gastropod *Batillaria cumingi* (see Kojima et al. 2004) and the gobies *L. petersii* (see Kokita and Nohara 2011; Hirase et al. 2020a) and *C. annularis* (see Hirase and Ikeda 2015). In addition, in *L. petersii* (see Hirase et al. 2020a) and *C. annularis* (see Hirase and Ikeda 2015), detailed nuclear DNA analyses showed hybridization and introgression between the two lineages in this contact zone. Introgression patterns in the contact zone were also observed to differ between the two species; in *C. annularis*, introgression patterns based on mitochondrial DNA (mtDNA) analyses and nuclear DNA analyses were concordant (Hirase and Ikeda 2015), whereas mito-nuclear discordance was observed in *L. petersii* (see Hirase et al. 2020a). Hirase et al. (2020a) noted the possibility that such differences between species may arise due to species-specific characteristics, such as mating preference or local adaptive pressure.

In *C. annularis*, most individuals in the hybrid zone appeared to be post-F_2 hybrids (Hirase and Ikeda 2015), indicating the possibility that contemporary gene flow between the two groups is negligible and that they have been isolated for a long time after hybridizing. Hirase and Ikeda (2015) proposed that hybridization may have occurred during the last interglacial period because the estimated time to the most recent common ancestor (TMRCA) of the population in the hybrid zone corresponds to the last glacial period, and also because inflow of the Tsushima Current into the Sea of Japan during the late Pleistocene interglacial periods drove spatial expansion of the Sea of Japan group.

The geographic location of the boundary area between the two lineages differs slightly among species; for example, the boundary is present (or probably present) around the southern Joban–Kashimanada coast for the gobies *P. elapoides* (see Akihito et al. 2008), *L. petersii* (see Kokita and Nohara 2011) and *C. gulosus* (see Hirase and Ikeda 2014a). On the other hand, the boundary of *C. annularis* is located around the Sanriku coast, approximately 200 km north of the Joban–Kashimanada coast (Hirase and Ikeda 2015). Hirase and Ikeda (2014a, 2015) proposed that this difference in the location of the boundary area may be related to differences in the flexibility of habitat preferences or dispersal ability among species. Kokita and Nohara (2011) noted that it is possible that the boundary area between the two lineages has shifted north and south in response to historical changes in the power balance between the Kuroshio Current and the Oyashio Current along the Pacific coast after the last glacial period; the Oyashio factor predominated between 11,000 and 8000 years before present and decreased thereafter, while the Kuroshio factor peaked approximately 6000 years before present. Therefore, during the postglacial period, the boundary area around the northeastern Pacific coast may have been translated southward by the Oyashio Current and northward by the Kuroshio Current.

11.2.2.2 The Seto Inland Sea

The Seto Inland Sea is another common contact zone between the two lineages. The Seto Inland Sea is connected to the Pacific Ocean by two channels, the Bungo Channel and Kii Channel, and to the Sea of Japan by the Kanmon Strait. Coastal organisms from both lineages are found in this area, including the gastropods *Turbo sazae* (see Kojima et al. 1997) and *B. cumingi* (see Kojima et al. 2004), and the gobies *L. petersii* (see Kokita and Nohara 2011; Hirase et al. 2020a) and *C. annularis* (see Kato et al. 2021); in *L. petersii* and *C. annularis*, evidence of introgressive hybridization has been reported in those studies.

Additionally, Kato et al. (2021) showed a lack of linkage disequilibrium between microsatellite DNA markers in a hybridized population of the two intraspecific lineages of *C. annularis* in the Seto Inland Sea, suggesting that the origin of this population is not recent hybridization, as is the case in the hybridizing population of this species in the northeastern Pacific coast. The Seto Inland Sea is a semi-enclosed shallow sea (average depth: 31 m) that was almost entirely exposed during the LGM due to low sea levels (Yashima 1994). After the LGM, seawater initially entered the Seto Inland Sea from the Pacific side, and the Seto Inland Sea became connected to the Sea of Japan after the Kanmon Strait opened approximately 7000 years ago (Yashima 1994). Therefore, it is likely that the Sea of Japan lineage colonized the Seto Inland Sea through the Kanmon Strait less than 7000 years ago, and that secondary contact and introgressive hybridization subsequently occurred.

The admixture pattern for the two groups in the Seto Inland Sea differs among species. Mitochondrial DNA haplotypes in the Seto Inland Sea are composed primarily of Pacific Ocean lineages in some rocky shore fishes (tide pools or rocky bottoms), such as the gobies *P. elapoides*, *P. zonoleucus* (see Akihito et al. 2008) and *C. annularis* (see Kato et al. 2021). However, genetic similarity to the Sea of Japan group has been observed in other species, such as *A. virgatulus*, a goby that inhabits muddy sediments (Matsui 2014; Fig. 11.3). Further, for *L. petersii*, which is an anadromous goby that inhabits shallow coastal areas, the central to western parts of the Seto Inland Sea harbor more Pacific Ocean lineage mtDNA haplotypes despite being more genetically similar, in terms of genomic DNA, to the Sea of Japan lineage (Hirase et al. 2020a). Considering that the amount of water exchange between the Seto Inland Sea and the Pacific Ocean is considerably greater than between the Seto Inland Sea and the Sea of Japan (Fujiwara 2013), it is inferred that the dispersal of contemporary taxa from the Pacific Ocean into the Seto Inland Sea would be easier than dispersal from the Sea of Japan into the Seto Inland Sea. Consequently, in cases where the Seto Inland Sea group is more genetically similar to the Sea of Japan group than the Pacific Ocean group, it seems likely that certain mechanisms are restricting gene flow from the Pacific Ocean group. Such mechanisms could include adaptive advantage, mating preference, and postglacial changes in the distribution of suitable environment. However, since mito-nuclear discordance has been observed in species such as *L. petersii* (see Hirase et al. 2020a), further detailed analyses are considered necessary.

11.2.3 Population Structure within the Two Major Groups

In some coastal fishes, subdivisions are apparent within the two major groups. In *C. annularis*, two allopatric subclades were discovered within the Sea of Japan lineage (Hirase et al. 2016): one subclade is composed of haplotypes from coastal areas in the southern part of the Sea of Japan, and the other subclade is composed of haplotypes from areas to the north. This dichotomy suggests the existence of population fragmentation in this species in multiple (at least two) glacial refugia within the Sea of Japan. Similar findings were reported in *L. petersii*, based on evidence of the widespread distribution of only one haplotype that was at the core of the parsimony network derived for the Sea of Japan lineage (Kokita and Nohara 2011).

Within the Pacific group, three distinct subgroups (northern, central, and southern) were detected by mtDNA analysis (Hirase et al. 2012), although no obvious subgroups were detected in *C. annularis* by microsatellite DNA analysis (Hirase and Ikeda 2014a). Similarly, the existence of multiple groups of other species has been suggested along the Pacific coast, including surfperch *Ditrema jordani* (see Katafuchi et al. 2011), a muddy sand goby *A. virgatulus* (see Matsui 2014; Fig. 11.3), and several other gobiid species (Matsui *unpublished data*) based on mtDNA and/or nuclear DNA analyses. These findings imply that there were also multiple populations of coastal fishes along the Pacific coast during the glacial periods.

11.2.4 Phylogeographic Characteristics of Fauna from the East China Sea Coast of Mainland Kyushu

In most coastal organisms with phylogeographic patterns that correspond to the two warm currents, representatives of either of the two major lineages were detected along most of the East China Sea coast, even though this coastal area is geographically separated from the main Kuroshio Current and the Tsushima Current. For example, haplotypes of the gobies *P. elapoides*, *P. zonoleucus* (see Akihito et al. 2008), *L. petersii* (see Kokita and Nohara 2011), and the gastropod *T. sazae* (see Kojima et al. 1997) along the East China Sea belong to the Sea of Japan lineage. In the gastropod *B. cumingi*, the Ariake Sound population is composed exclusively of the Pacific Ocean lineage, while the Goto Islands population is composed of both lineages (Kojima et al. 2004). In cases where East China Sea populations have Sea of Japan haplotypes, it is possible that the Sea of Japan lineage was distributed in the area including the East China Sea coast during the LGM. Since the coastal environment of the East China Sea off northern Kyushu Island was relatively stable during the LGM (cf., Ijiri et al. 2005), it may have been more suitable for some temperate coastal fishes than coastal areas of the Sea of Japan during that period. Further, off the East China Sea coast of mainland Kyushu, a northward branch of the Kuroshio Current tends to veer eastward (onshore) near the Goto Islands before flowing southward along mainland Kyushu, but the current structure is complicated due to seasonal fluctuations (Hishida et al. 1990). Such complex currents might be associated with shaping the distribution patterns of the two lineages along the East China Sea coast.

In another case, the East China Sea population constitutes an independent lineage that is distinct from the Pacific Ocean and the Sea of Japan lineages. In the goby *C. annularis*, the discovery by Kato et al. (2021) of a lineage that is dominant along the East China Sea coast suggests that at least one ancient geographical isolation event occurred along the East China Sea in this species. In that study, the divergence time of the East China Sea lineage was estimated to be 2.16 Ma, and it was proposed that lineage divergence may have been associated with bathymetric changes in the northern part of the Okinawa Trough starting approximately 2 Ma. This suggests that the distributional range of the East China Sea lineage of the goby has been maintained in this sea during the Quaternary, and that the habitats of coastal organisms, especially species like *C. annularis*, which inhabits intertidal rocky shores, have persisted. In addition, the East China Sea lineage showed remarkable mito-nuclear discordance (i.e., being similar to the Sea of Japan lineage based on microsatellite DNA analyses while being similar to the Pacific Ocean lineage based on mtDNA). This mito-nuclear discordance suggests that the East China Sea lineage was likely derived from a previous hybridization event. Furthermore, a hybrid zone between the East China Sea lineage and the Sea of Japan lineage exists close to the Tsushima Strait along the northeastern Kyushu coast (Kato et al. 2021). As in the other two hybrid zones (i.e., in the northeastern Pacific region and the Seto Inland Sea; see Sect. 11.2.2), the hybridization observed in this population did not occur recently (Kato et al. 2021). Furthermore, the evidence of multiple hybridization events of this area in that study suggests that population isolation and contact occurred multiple times and that these events corresponded to the opening and closing of the Tsushima Strait during the glacial–interglacial cycles.

For phylogeographic relationships with the continental coast, see Sect. 11.4.

11.2.5 Phylogeographic Characteristics of Hokkaido Island

Hokkaido Island is surrounded by three seas, i.e., the Sea of Japan, the Sea of Okhotsk, and the Pacific Ocean, and each section of coast is affected by different currents. The warm Tsushima Current, which flows up along Honshu Island, extends further up along the Sea of Japan side of Hokkaido Island, branches around the Soya Strait, which is located near the northern edge of Hokkaido Island, and then the one branch flows into the Sea of Okhotsk coast through the Soya Strait (so-called Soya Current). On the other hand, the cold Oyashio Current flows off the Pacific coast of Hokkaido Island; from the eastern part of the island the current flows westward to the central coast, and then part of the current continues beyond Cape Erimo. The southwestern area of the Pacific coast of Hokkaido is also affected by the warm Tsugaru Current, a branch of the Tsushima Current. In some temperate coastal fishes, such as *C. annularis* (see Hirase et al. 2012) and *C. gulosus* (see Hirase and Ikeda 2014a), the distribution of the Sea of Japan lineage extends all the way to the Sea of Japan coast of Hokkaido Island. However, because of the subarctic climate and effects of the cold Oyashio Current, the fish fauna of the Hokkaido coast differs considerably from that south of Honshu, and most temperate species are not found in Hokkaido, especially along the Sea of Okhotsk coast or the Pacific coast of Hokkaido Island (Nakabo 2002).

One of the phylogeographic patterns of coastal fishes around Hokkaido Island is that the distribution of genetically distinct populations corresponds to the pathways of the Tsushima Current (and its branches), and the Oyashio Current. For example, two groups with different mtDNA haplotype frequencies are recognized for the Japanese sandfish, *Arctoscopus japonicus*; one group is distributed along the Sea of Japan coast (including the Korean coast, the Honshu Island coast, and the western coast of Hokkaido Island) and the coast of Nemuro (the easternmost part of Hokkaido), and the other is found along the Pacific coast of Hokkaido Island (Yanagimoto 2004). Similarly, the distribution of distinct lineages corresponding to the pathways of the two currents has also been observed in the anadromous three-spined sticklebacks, *Gasterosteus aculeatus* (or more precisely, the species complex previously recognized as *G. aculeatus*) (Higuchi and Goto 1996); the lineages are now regarded as two different species (Higuchi et al. 2014).

Another haplotype distribution pattern is characterized by the absence of any population differentiation around the Hokkaido Island coast; for example, no genetic differentiation was observed among the three seas, i.e., the Sea of Japan, Sea of Okhotsk, and Pacific Ocean in Mottled Skate *Beringraja pulchra* (see Misawa et al. 2019). Similarly, in the gastropod *B. cumingi*, the Sea of Japan lineage is not only distributed along the Sea of Japan and Sea of Okhotsk, but also along the Pacific Ocean coast of Hokkaido Island (Kojima et al. 2004). Such incongruence in the population structure among species would likely have originated in response to differences in habitat distribution during the glacial periods when habitat fragmentation occurred between the Sea of Japan and the Pacific Ocean. At least some arctic–subarctic species, like the sandfish *A. japonicus* would have been vicariant along the Sea of Japan coast and the Pacific coast during the glacial periods, and after the glacial periods, the population that had persisted in the Sea of Japan would have expanded to the eastern coast of Hokkaido Island via the Soya Strait, while the population that had survived in the Pacific coast around Hokkaido Island was dispersed along the Pacific coast by the cold Oyashio Current. On the other hand, it is likely that the glacial distribution of temperate species like the gastropod *B. cumingi* did not exist along the Pacific coast around Hokkaido Island but in a more southern area along the Pacific coast. During the subsequent interglacial period, only the Sea of Japan lineage would have expanded clockwise to colonize the entire coast of Hokkaido Island by ocean currents (i.e., the Tsushima Current, Soya Current, and Oyashio Current).

The Sea of Okhotsk and the Sea of Japan are connected to their neighboring seas by narrow shallow channels. These seas were isolated during the Pleistocene glacial periods (Yokoyama et al. 2007), and this isolation likely drove intraspecific lineage divergence (e.g., Sakuma et al. 2014; Tohkairin et al. 2016) and speciation (Briggs and Bowen 2012) in some deep-sea fishes. In addition, the shallow Soya Strait (approximately <55 m deep), which connects the Sea of Japan and the Sea of Okhotsk, acts as a barrier to contemporary gene flow in some deep-sea species and therefore plays a role in maintaining population differentiation between the two seas. In coastal species, however, no significant genetic differentiation has been reported between the two seas (e.g., Higuchi and Goto 1996; Kojima et al. 2004; Orlova et al. 2019), although the number of phylogeographic studies on the two seas is limited. Thus, at least for some coastal species, the Soya Strait would not act as a marked barrier to contemporary gene flow between the two seas.

11.3 Population Structure of Coastal Fishes in the Ryukyu Islands–Japanese Mainland–Ogasawara Islands Region and the Effects of the Kuroshio Current

The warm Kuroshio Current, a powerful current flowing along the Ryukyu Islands and the Pacific coast of the main islands of Japan, has a marked effect on fauna and the formation and maintenance of the population structure of coastal fishes of Japan. While the Kuroshio Current plays an import role in larval transport, it also acts as a barrier to larval dispersal across the Kuroshio axis. This section describes phylogeographical relationships among the Ryukyu Islands, the main islands of Japan, and the Ogasawara (Bonin) Islands, with a focus on the roles of the Kuroshio Current in past and present gene flow among the sea regions.

11.3.1 Phylogeographic Relationships Between the Ryukyu Islands and the Main Islands of Japan

11.3.1.1 Biogeographic Characteristics of the Ryukyu Islands

The Ryukyu Islands are isolated from the main islands of Japan and the continent, and some of them remained isolated during the Pleistocene glacial-interglacial cycles by deep gaps, such as the Tokara Gap and the Kerama Gap. Such geographic isolation has driven speciation and subspecies differentiation from groups on the main islands of Japan and the Asian continent in both terrestrial animals (e.g., Ota 1998; Millien-Parra and Jaeger 1999) and freshwater fishes (including some brackish water and diadromous species) (e.g., Nishida 1990; Sakai et al. 2001; Mukai et al. 2003, 2004), and these gaps are recognized as important biogeographic borders. However, for coastal fishes, especially for species with a pelagic larval stage, deep gaps do not necessarily act as barriers to dispersal. Rather, ocean currents play a more important role in shaping the intraspecific population structure of coastal fishes (Matsuura 2012). The path of the Kuroshio Current forms a C-shape as it flows around the Ryukyu Islands; the current flows between Taiwan and Yonaguni-jima Island, goes up along the East China coast of the Ryukyu Islands, and then goes back into the Pacific Ocean through the Tokara Strait before reaching the coast of the main islands of Japan.

11.3.1.2 Transportation of Larvae by the Kuroshio Current

The population structure of some coastal fishes with ranges extending from the Ryukyu Islands to the main islands of Japan suggests that gene flow from the Ryukyu Islands to the main islands of Japan is uninhibited, likely due to transportation of eggs and larvae by the Kuroshio Current. For example, in Blacktip Grouper *Epinephelus fasciatus*, which is widely distributed in the Indo-Pacific, three largely distinct lineages were recognized in the Pacific region (Kuriiwa et al. 2014; Fig. 11.4a). The frequency distributions of the three lineages (Lineage A, B, C in Kuriiwa et al. 2014) differ significantly among the three regions, i.e., from the tropical western Pacific to the Ryukyu Islands, the main islands of Japan, and Ogasawara Islands (Fig. 11.4b), suggesting that there are three demographic groups in this species in the Pacific Ocean. Lineage B is dominant from the tropical western Pacific to the Ryukyu Islands, Lineages A and B are common along the main islands of Japan, and Lineages A, B, and C were detected at similar frequencies in the Ogasawara Islands. Focusing on the frequency distribution of Lineage B around the main islands of Japan, the closer the site is to the Ryukyu Islands, the higher the frequency of Lineage B tends to be. Furthermore, the pelagic larval duration (PLD) for this species is approximately 2 months, which allows larvae to be carried considerable distances by sea currents. Therefore, the Kuroshio Current likely acts as a vehicle for the transport of *E. fasciatus* larvae from the Ryukyu Islands to the main islands of Japan, and drives gene flow between the two sea regions. In another example, in Cocos Frill-goby *Bathygobius cocosensis*, which is widely distributed in the Indo-Pacific, no significant genetic differentiation was detected between the Ryukyu Islands and the main islands of Japan, suggesting that gene flow occurs between regions due to the transportation of larvae by the Kuroshio Current (Mukai et al. 2009).

11.3.1.3 The Kuroshio Current as a Barrier to Larval Dispersal

In contrast, restriction of gene flow from mainland Kyushu to the Ryukyu Islands is suggested in some coastal fishes, such as Neon Damselfish *Pomacentrus coelestis* (Liu et al. 2008), Blacktip Grouper *E. fasciatus* (see Kuriiwa et al. 2014), and Shadow Goby *Yongeichthys nebulosus* (see Nohara 2019); in *E. fasciatus*, introduced above, few or no Lineage A haplotypes were found at sites in the Ryukyu Islands, while haplotypes of this lineage were frequently encountered from mainland Kyushu to the Ogasawara Islands (Kuriiwa et al. 2014; Fig. 11.4b). This finding suggests that larval dispersal from mainland Kyushu to the Ryukyu Islands is highly restricted in this species. Similarly, in *P. coelestis*, pairwise genetic differentiation was detected between sites near the main islands of Japan and Taiwan, Sesoko-jima Island in the Okinawa Islands, and Nakanoshima Island in the Tokara Islands. The Kuroshio Current flows from the East China Sea to the Pacific Ocean through the Tokara Strait, separating the two regions of the Ryukyu Islands and the main islands of Japan. In many coastal fishes, pelagic larvae can be transported considerable distances by ocean currents, but their

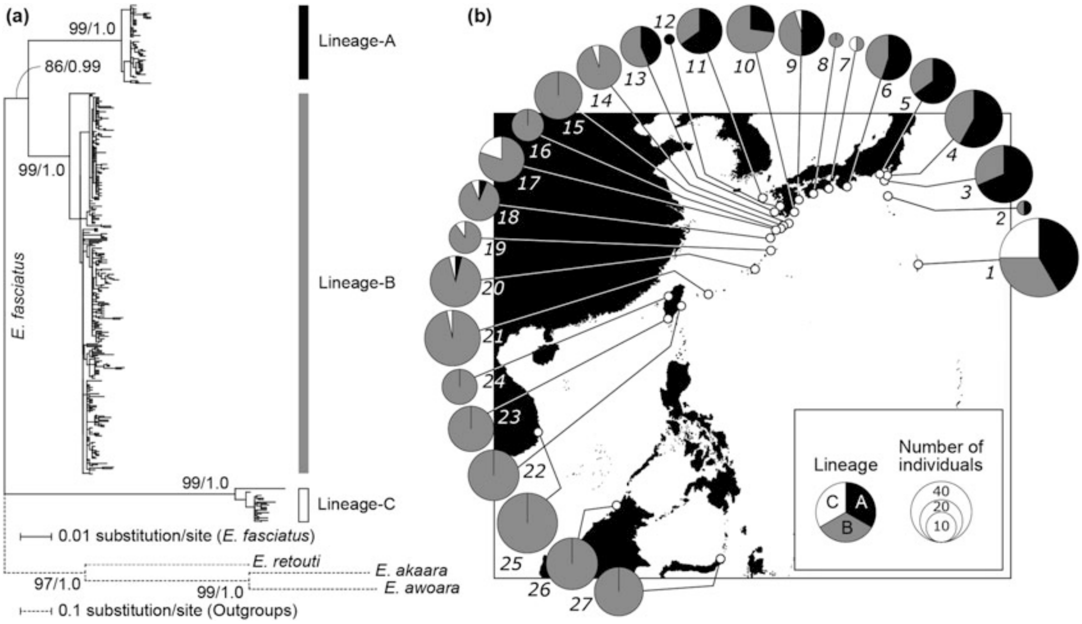

Fig. 11.4 (**a**) Maximum likelihood tree of mitochondrial cytochrome *b* gene of *Epinephelus fasciatus* and (**b**) geographic distribution of intraspecific lineages of the phylogenetic tree (**a**) (Kuriiwa et al. 2014, Fig. 3)

capacity for migration is not high after larval settlement. Thus, in these coastal fishes, the Kuroshio Current acts as a barrier to larval dispersal from mainland Kyushu to the Ryukyu Islands, leading to population differentiation between these regions.

On the other hand, in coastal fishes such as Neon Damselfish *P. coelestis* (see Liu et al. 2008) and Blacktip Grouper *E. fasciatus* (see Kuriiwa et al. 2014), no significant genetic differentiation was observed between the Ryukyu Islands and Taiwan, although the number of phylogeographic studies on regions including both the Ryukyu Islands and Taiwan is somewhat limited. This suggests that the Kuroshio Current, which flows between Taiwan and Yonaguni-jima Island, does not act as a barrier to larval dispersal in this region, at least for some coastal fishes.

The location of boundaries between groups based on genetic differentiation differs slightly among species. For example, in *P. coelestis*, the boundary is located between Nakanoshima Island in the Tokara Islands and Tanegashima Island, which lies slightly to the south of mainland Kyushu. On the other hand, in *E. fasciatus*, the boundary lies between Tanegashima Island and mainland Kyushu. It is likely that such differences among species are related to fluctuations of the Kuroshio axis, changes in the Osumi Branch Current (a branch of the Kuroshio Current) along with current fluctuations, and species-specific characteristics of larval dispersal.

In examples so far, the Kuroshio Current likely drives genetic homogeneity within the Ryukyu Islands. However, there are some cases where populations of coastal organisms are fragmented within the Ryukyu Islands, irrespective of the path of the Kuroshio Current, for example, Shuttles Hoppfish *Periophthalmus modestus* (see Mukai and Sugimoto 2006), Shadow Goby *Y. nebulosus* (see Nohara 2019), and the mud goby *Acentrogobius* sp. (see Matsui 2014). In Shuttles Hoppfish *P. modestus*, each population on Tanegashima and Okinawa-jima Island is composed entirely of endemic haplotypes, indicating the existence of genetic isolation from each other and from populations on the main islands of Japan (Mukai and Sugimoto 2006). In

Acentrogobius sp., each population on Miyako-jima Island and Okinawa-jima Island is also composed entirely of endemic haplotypes, and gene flow is considered to be strictly restricted within these islands and between each island and the main islands of Japan. In these species, it seems that the role of the Kuroshio Current as a vehicle for larval transport is not that significant. Whether or not population fragmentation of coastal fishes occurs within the Ryukyu Islands would largely depend on species-specific dispersal ability. Since all three of these species are gobies that mainly inhabit muddy tidal flats of inner bays, it is likely that their larvae tend to remain around the spawning sites and that they have little chance of being transported to other islands via the Kuroshio Current that flows off the coasts of the islands where they are found.

11.3.1.4 Lineage Divergence and Historical Migration

The genetic population structure of taxa distributed from the Ryukyu Islands to the main islands of Japan has been greatly affected by historical fluctuations in the path of the Kuroshio Current. The estimated divergence time of the two lineages of Blacktip Grouper *E. fasciatus*—Lineage A (from the main islands of Japan and the Ogasawara Islands) and Lineage B (widely distributed in the western Pacific region, including the Ryukyu Islands)—corresponds approximately to the Middle Pleistocene (Kuriiwa et al. 2014). During the Pleistocene glacial periods, the island arc of Taiwan—the Ryukyu Islands—mainland Kyushu formed a land bridge (with some deep straits), and it has been proposed that the ancient Kuroshio Current was deflected eastward at the southern end of the Ryukyu Islands (Ujiié and Ujiié 1999; Ujiié et al. 2003). Kuriiwa et al. (2014) surmised that, at the timing of such a route change of the ancient Kuroshio Current during a glacial period, Lineage A would have become differentiated around the main islands of Japan, while Lineage B would have remained south of the Ryukyu Islands until the LGM whereafter it underwent range expansion and its distribution extended to the main islands of Japan. On the other hand, in Shuttles Hoppfish *P. modestus*, although unique haplotypes are found in Tanegashima Island and Okinawa-jima Island respectively, these haplotypes do not form independent lineages and are included in the haplotype groups of the main islands of Japan (Mukai and Sugimoto 2006). These findings suggest that gene flow between the Ryukyu Islands and the main islands of Japan region has occurred in this species until relatively recently, and that population differentiation then occurred.

11.3.2 Phylogeographic Relationships Between the Ogasawara Islands and the Main Islands of Japan

11.3.2.1 Biogeographic Characteristics of the Ogasawara Islands

The Ogasawara Islands, oceanic islands located approximately 1000 km south of the main islands of Japan, are members of the Izu-Ogasawara-Mariana Arc on the eastern edge of the Philippine Sea Plate. While the biota of the Ogasawara Islands is unique, the fish fauna is more similar to the Izu Islands and the main islands of Japan than the Ryukyu Islands, which are located at almost the same latitude as the Ogasawara Islands (Senou et al. 2006; Matsuura 2012). One reason for the similarity between the Ogasawara Islands and the Izu Islands is that both are located on the same island arc and that there are numerous islands between the two regions. It is known that islands on the arc act as “stepping stones” and that they promote larval dispersal. Another reason for this similarity can be attributed to the Kuroshio meander. The Kuroshio Current flows along the coast of Honshu Island to approximately the Kii Peninsula, whereafter the course of the current fluctuates; the Kuroshio Current sometimes flows eastward close to the Izu Peninsula, and at other times, it swerves southward widely and then flows northward close to the coast of Honshu Island. Therefore, fish larvae can be transported from the mainland of Japan to the Izu Islands and the Ogasawara Islands by the southward-flowing stretch of the Kuroshio Current, and also from the Ogasawara Islands to the Izu Islands and the mainland of Japan by the northward-flowing stretch of the current.

11.3.2.2 Phylogeographic Patterns in the Region from the Ogasawara Islands to the Main Islands of Japan

Individual dispersal between the Ogasawara Islands and the main islands of Japan is also supported, at least partly, by phylogeographic studies on coastal fishes. In Blacktip Grouper *E. fasciatus*, two of the three lineages, Lineages A and B, which are distributed near the main islands of Japan and the Izu Islands, are also common in the Ogasawara Islands (Kuriiwa et al. 2014; Fig. 11.4b). This distribution implies that individual dispersal occurs from the main islands of Japan to the Ogasawara Islands within species.

In contrast, no or few haplotypes of Lineage C, which is mainly distributed in the Ogasawara Islands, were found at the sites off the main islands of Japan and the Izu Islands. This suggests that individual dispersal rarely occurs from the Ogasawara Islands to the main islands of Japan. To explain this asymmetric structure, Kuriiwa et al. (2014) proposed that the opportunities for southward and northward dispersal might differ; that is, southward dispersal may occur relatively frequently, whereas dispersal in the opposite direction may hardly occur.

On the other hand, in Cocos Frill-goby *B. cocosensis*, mtDNA haplotypes are composed of two largely distinct lineages (Mukai et al. 2009); one lineage is composed of populations from the main islands of Japan, the Ryukyu Islands, and Guam, while the other is composed of populations from the Ogasawara Islands. This distribution pattern indicates that population fragmentation has occurred between the two regions, and suggests that both northward and southward dispersal in this species is highly restricted between the main islands of Japan and the Ogasawara Islands.

Such differentiation among species in contemporary gene flow could be attributed to species-specific dispersal ability, especially PLD. It has been well established that PLD is one of the most important factors underlying the formation of the population structure (e.g., Doherty et al. 1995; Bohonak 1999). The PLD in *E. fasciatus* is approximately 2 months (Kuriiwa et al. 2014), and the larvae would be able to disperse over long distances using the islands of the Izu-Ogasawara-Mariana Arc as stepping stones. However, it is likely that the dispersal of larvae of *B. cocosensis*, which have a shorter PLD (16–31 days, Thia et al. 2018), is more limited, leading to a restriction in gene flow between the regions.

11.3.2.3 Historical Demography of Populations in the Ogasawara Islands

The Ogasawara Islands rose up during the Early Pleistocene (Government of Japan 2010). In Cocos Frill-goby *B. cocosensis*, it is assumed that the Ogasawara Islands population was isolated after island emergence and that they remained isolated from other populations in narrow areas around the Ogasawara Islands for at least 1.1–1.3 million years (Mukai et al. 2009). Additionally, evidence of low genetic diversity and population expansion has been reported in the Ogasawara population of this species, suggesting that this population has experienced bottlenecks and population expansion corresponding to the oscillations in sea levels during the glacial-interglacial cycles.

Conversely, in Blacktip Grouper *E. fasciatus*, analyses of population dynamics have shown that Lineage C, which is mainly distributed in the Ogasawara Islands, has consistently and gradually been increasing in size since approximately 0.115 Ma (TMRCA of the lineage), even during the sea-level changes before and after the LGM (Kuriiwa et al. 2014). This suggests that, at least in some coastal species, the population off the Ogasawara Islands has experienced relatively few environmental changes in the past. This stability is considered to be because the Ogasawara

Islands are typical oceanic islands. Although lack of information at this time makes it difficult to clarify the causes of these differences in the demographic histories of species, Kuriiwa et al. (2014) proposed that the Ogasawara population of *E. fasciatus* is mainly distributed outside the Ogasawara Islands based on the large estimated population size, and that this may account for the difference among species.

11.3.3 Phylogeographic Relationships Between the Ogasawara Islands and the Ryukyu Islands

Despite being at the same latitude, the fish fauna of the Ogasawara Islands and the Ryukyu Islands is markedly different, and it is accepted that this difference is mainly attributed to the vast ocean area between the two regions. Since the vastness of this ocean area is due to expansion of the Philippine Sea Plate, there are no major islands that can act as stepping stones. Additionally, there are no strong currents like the Kuroshio Current between the two regions, only a weak westerly current (Kuroshio Countercurrent). It is therefore considered that the eggs and larvae of most costal fishes cannot traverse this large ocean, and that direct dispersal of individuals is restricted (Matsuura 2012).

This restriction of dispersal between the two regions is also supported by phylogeographic studies of coastal fishes. In Cocos Frill-goby *B. cocosensis*, as described above, significant genetic differentiation was detected between a region near the main islands of Japan—the Ryukyu Islands—Guam and the Ogasawara Islands, which further suggests the existence of a strong restriction in gene flow between the Ogasawara islands and the Ryukyu Islands (Mukai et al. 2009). Also, in Blacktip Grouper *E. fasciatus*, the distribution frequencies of the three intraspecific lineages differ markedly between the two regions (Kuriiwa et al. 2014; Fig. 11.4b). In the Ogasawara Islands, the three lineages are found at nearly the same frequency, whereas Lineage B is dominant in the Ryukyu Islands. However, the other two lineages (Lineages A and C) are also found at low frequencies in the Ryukyu Islands. Lineage A is also distributed along the main islands of Japan, but it is unlikely that it is able to disperse from the main islands of Japan to the Ryukyu Islands due to the powerful barrier formed by the Kuroshio Current. Additionally, other than the Ogasawara Islands, Lineage C has not been found at high frequencies elsewhere. Thus, Kuriiwa et al. (2014) proposed that dispersal of *E. fasciatus* from the Ogasawara Islands to the Ryukyu Islands via the Kuroshio Countercurrent would occur only rarely, and that the success of long-distance dispersal would be droved by the long PLD.

11.4 Phylogeographic Relationships Between the Japanese Coast and the Continental Coast

Since numerous fishes are common to the continental coast and the Japanese coast, understanding the population structure of coastal fishes in the East China Sea, which is bound by the continent and the Japanese Archipelago, is important for understanding the phylogeographic characteristics of the costal fishes of Japan. Large areas of the East China Sea are shallower than 120 m, which means that the East China Sea was both largely exposed and smaller during the glacial periods of the Pleistocene, while larger during the interglacial periods (Wang 1999). In addition, during the glacial periods, the East China Sea was almost isolated from the three adjacent seas (Pacific Ocean, Sea of Japan, and South China Sea) by a land bridge that comprised Taiwan, the Ryukyu Islands, mainland Kyushu, and Tsushima Island. Such dramatic historical changes have resulted in a complex phylogeographic pattern and historical demography of coastal fishes around the East China Sea.

11.4.1 Population Structure around the East China Sea and the Surrounding Waters: Several Patterns of Genetic Population Structure of Coastal Fishes are Known in the East China Sea and the Surrounding Waters

11.4.1.1 Pattern 1: Geographic Population Structure Corresponding to Sea Regions

The first pattern of population differentiation corresponds to sea regions, and is apparent in coastal fishes such as So-iuy Mullet *Planiliza haematocheilus* (see Liu et al. 2007), Silver Croaker *Pennahia argentata* (see Han et al. 2008), Japanese Sardinella *Sardinella zunasi* (see Ying et al. 2011), Dotted Gizzard Shad *Konosirus punctatus* (see Gwak et al. 2015), Mottled Skate *Beringraja pulchra* (see Misawa et al. 2019), Forktongue Goby *Chaenogobius annularis* (see Kato et al. 2021), some molluscs and crustaceans (Ni et al. 2014; Wang et al. 2016), and algae (Zhong et al. 2020). For example, in So-iuy Mullet *P. haematocheilus*, three intraspecific lineages were detected, and their distribution corresponded to three sea regions (Japanese water, East China Sea, and the South China Sea) (Liu et al. 2007). This suggests that fragmentation of the three marginal seas around the East China Sea resulted in lineage divergence of this species. As in the case of the two major lineages around the main islands of Japan, the estimated divergence times among the three lineages predates the last glacial period and likely occurred during the middle to late Pleistocene, suggesting that genetic heterogeneity among sea regions has been maintained for one or more glacial and interglacial periods since lineage divergence. Although the mechanisms underlying the maintenance of such genetic heterogeneity is not well understood, oceanographic characteristics such as ocean currents along the continental coast may have facilitated the separation of populations.

As described in Sect. 11.1, during the glacial–interglacial cycles, the coastal environment of the marginal seas changed considerably, and this would have had a marked influence on the population dynamics of the fragmentated populations of coastal fishes. During the glacial periods, the size and temperature of the East China Sea both decreased (Ijiri et al. 2005). In the same way, the coastal areas in the Sea of Japan were covered by low-temperature and low-salinity water (Oba et al. 1991; Tada 1994; Gorbarenko and Southon 2000). Although such significant changes in the coastal environment likely threatened the existence of coastal fish populations, it is also likely that there were glacial refugia in all of the marginal seas that supported coastal fishes. In the East China Sea, it is estimated that there is a refugium near the Okinawa Trough for coastal species such as So-iuy Mullet *P. haematocheilus* (see Liu et al. 2007) and False Kelpfish *Sebastiscus marmoratus* (see Xu et al. 2019). In the Sea of Japan, it is estimated that there was more than one refugium, as described in Sect. 11.2. In the South China Sea, on the other hand, since vast areas are deeper than 200 m, large areas would have remained relatively suitable for supporting coastal fishes such as *P. haematocheilus* (see Liu et al. 2007) and Lesser-spotted Leatherjacket *Thamnaconus hypargyreus* (see Wang et al. 2016) during the glacial periods. After the glacial periods, suitable habitat for temperate coastal organisms would have increased, leading to spatial and demographic expansion, especially in the East China Sea (Liu et al. 2007; Ni et al. 2014) and the Sea of Japan (as described in Sect. 11.2). Conversely, no significant expansion was detected in the South China Sea populations of *P. haematocheilus* (see Liu et al. 2007) or *T. hypargyreus* (see Wang et al. 2016), suggesting that the populations of coastal fishes in this sea were stable, even during the glacial periods.

On the other hand, contemporary oceanographic conditions have resulted in fragmentated populations of some species being maintained. In Mottled Skate *B. pulchra*, population differentiation was observed between the Sea of Japan and the Yellow Sea, which is the northwestern part of the East China Sea (Misawa et al. 2019). Considering that this species prefers cool water, Misawa et al. (2019) noted that the warm water mass of the Tsushima Current between the Sea of Japan and the Yellow Sea would act as a barrier to individuals migrating between the two seas. Similar restrictions on the expansion of species ranges due to the warm Tsushima Current have also reported in members of the genus *Ammodytes* (see Han et al. 2012; Orr et al. 2015).

11.4.1.2 Pattern 2: Geographic Population Structure in the East China Sea

Although there are relatively few reports of marked geographic structure of coastal fishes in the East China Sea, population differentiation within the sea (e.g., between the continental coast and the Japanese coast) has been reported in species such as Great Blue Spotted Mudskipper *Boleophthalmus pectinirostris* (see Kanemori et al. 2006) and Roughskin Sculpin *Trachidermus fasciatus* (see Li et al. 2016). In the case of Great Blue Spotted Mudskipper *B. pectinirostris*, it is accepted that the ancient population along the continental coast expanded to the ancient Japanese coast due to a decrease in sea area during the Early to Middle Pleistocene glacial period, and that a part of the population was relict in a semi-closed area of the Japanese coast (i.e., the Ariake Sound or the Yatsushiro Sound) due to sea-level rise during the following interglacial period, resulting in population fragmentation (Kanemori et al. 2006). For phylogeographic characteristics of the Ariake Sound, see Sect. 11.4.2.

11.4.1.3 Pattern 3: Weak Genetic Differentiation Among Sampling Sites Within the East China Sea

In False Kelpfish *S. marmoratus*, although no geographic structure was detected, weak but statistically significant levels of genetic differentiation were observed among almost all sampling sites, including those off the main islands of Japan and Chinese coasts (Xu et al. 2019). Since this species is a viviparous demersal fish, dispersal ability would be low and contemporary gene flow would be restricted. Therefore, it is likely that such weak genetic differentiation is derived from relatively recent (perhaps post-LGM) recolonization from a glacial refugium accompanied by population subdivision. In addition, because the highest genetic diversity was detected at the site in the center of the Chinese coast of the East China Sea (Xu et al. 2019), an ancestral population might have persisted in a refugium that formed near the Okinawa Trough during the LGM.

11.4.1.4 Pattern 4: No Genetic Differentiation Around the East China Sea

This pattern has been reported in some coastal fishes such as Lesser-spotted Leatherjacket *T. hypargyreus* (see Wang et al. 2016), Japanese Spanish Mackerel *Scomberomorus niphonius*, Japanese Anchovy *Engraulis japonica*, Yellow Croaker *Larimichthys polyactis*, and Silver Pomfret *Pampus argenteus* (see Ni et al. 2014). In many cases, the lack of genetic differentiation in these species is likely due to species-specific factors such as life history traits (for details see Sect. 11.5), although it is possible that genetic differentiation will be detected around the East China Sea by high-resolution genetic analyses.

11.4.2 Phylogeographic Characteristics of the Ariake Sound

The Ariake Sound is a semi-closed bay located in the northwestern part of Kyushu Island, and there are many endemic species whose distribution in Japan is limited to this sea (and the adjacent Yatsushiro Sound) (Fig. 11.5). Because such species and their close relatives are also distributed along the continental coast of the East China Sea, it has been considered that their distribution range expanded to the Japanese coast during the last glacial period when the sea area was considerably smaller than it is today due to sea-level fall, and

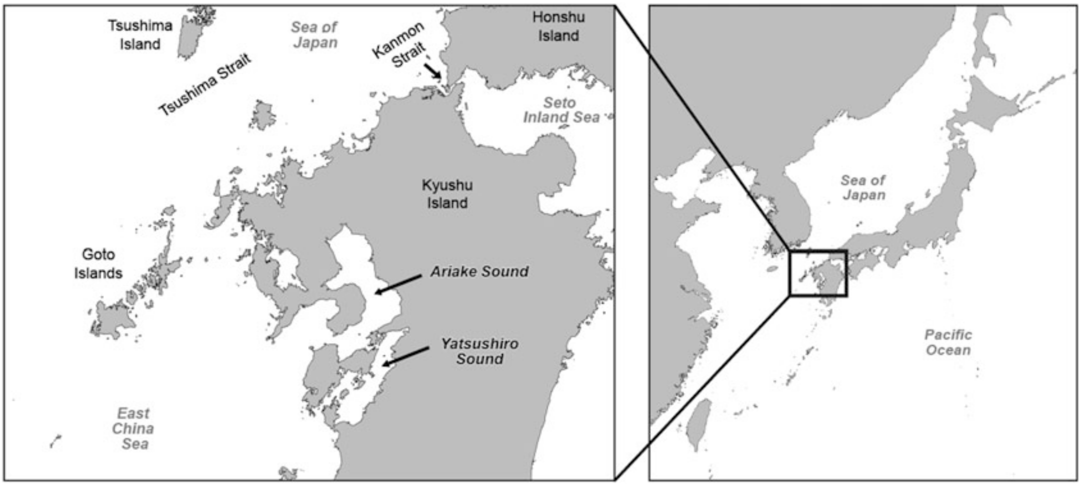

Fig. 11.5 A map around the northern Kyushu Island

that they were relict in a semi-closed area due to sea-level rise after the LGM (Shimoyama 2000).

However, phylogeographic studies on the endemic species in the last two decades have shown that the divergence time of the Ariake population from the continental population is not always equivalent to the post-LGM. For example, in the clam *Sinonovacula constricta*, a low genetic distance between the Japanese population and the Korean population was detected by allozyme analysis, suggesting relatively recent divergence between these two populations (Furukawa et al. 1996). In contrast, in Great Blue Spotted Mudskipper *B. pectinirostris*, there are three mtDNA lineages corresponding to the Japanese population (the Ariake Sound and the Yatsushiro Sound), the Korean population, and the Chinese population, and the estimated divergence time of the Japanese lineages from the ancient continental population is 0.96–2.65 Ma, which is much older than the LGM (Kanemori et al. 2006). In the Ariake Icefish *Salanx ariakensis*, although no significant geographic population structure was detected, genetic differentiation was observed among all sampling sites, including the Ariake Sound, the Korean coast, and the Chinese coast, and the estimated fragmentation times between pairwise populations are 21,000–56,000 years ago (Hua et al. 2009). These studies suggest that Ariake populations of *B. pectinirostris* and *S. ariakensis* have experienced one or more oscillations in sea level after population fragmentation, considering that the LGM occurred from 26,500 to 19,000 years ago and that global oscillations in sea levels occurred on an approximately 100,000-year cycle during the late Pleistocene. Although there is no evidence that the Ariake populations of these species were distributed around the Ariake Sound before the last glacial period, it is probable that the Ariake populations have persisted around the Ariake Sound and that they remained isolated with some migration occurring in response to changes in coastlines since fragmenting from ancient continental populations.

In some endemic species in the Ariake Sound, such as *B. pectinirostris* (see Kanemori et al. 2006) and *S. ariakensis* (see Hua et al. 2009), lower genetic diversity of the population in the Ariake Sound compared to that of the continental population has been reported. For example, in *B. pectinirostris*, haplotype diversity and nucleotide diversity of the Japanese population (including the Ariake Sound and the Yatsushiro Sound) are lower than those of the Chinese population, suggesting that the Japanese population experienced population bottlenecks during founder events. That is to say, the Japanese population of *B. pectinirostris* would have been derived from a small founder population that had fragmentated from continental populations.

11.5 Conclusion: Differences in Population Structure Among Species and Challenges for the Future

11.5.1 Differences in Population Structure Among Species

The previous sections mainly introduced cases of significant geographic population structure in coastal fishes that followed population fragmentation and lineage divergence caused by historical and barriers formed by currents. However, there are many cases where the population structure differs among species in both the extent of structuring and in the geographic patterns of fragmentation, even in the same sea region. For example, along the main islands of Japan, geographic population structures corresponding to the two warm currents have been reported in some species, as discussed in Sect. 11.1, but no significant geographic structure has been detected in others, such as in the common gobies *Acanthogobius flavimanus* (see Hirase et al. 2020b) and *Acentrogobius pflaumii* (see Matsui 2014). Instead, in *A. flavimanus*, isolation by distance (IBD) was recognized even between the Sea of Japan and the Pacific Ocean populations in association with high dispersal ability (Hirase et al. 2020b). On the other hand, habitat characteristics, such as water depth and wave exposure, would have a marked effect on differences in the population structure between *A. pflaumii* and two congeneric species (Matsui 2014); *A. pflaumii* inhabits relatively deep exposed environments in open bays, but two congeneric species (*Acentrogobius* sp. and *A. virgatulus*) inhabit shallow enclosed environments in inner bays (Matsui et al. 2012; Fig. 11.6a). Populations of the latter two species showed significant structure and high pairwise differences (pairwise Φ_{ST} values) between locations within species, whereas populations of *A. pflaumii* showed no significant structure and no or low pairwise differences (Fig. 11.6b).

Differences in population structure among species, even within the same sea region, are highly dependent upon species-specific factors. The first factor is the life history traits associated with local retention and self-recruitment. Among the life history traits, studies examining the cause of differences among marine fishes typically focus on PLD. In many demersal fishes, it is considered that dispersal ability is a function of the length of PLD (Doherty et al. 1995; Bohonak 1999; Shanks et al. 2003), because passive dispersal during the pelagic larval stage accounts for a major part of individual dispersal. However, other life history traits, such as egg characteristics (e.g., Bohonak 1999; Jones et al. 2009), larval behavior (e.g., Burton and Feldman 1982; Woodson and McManus 2007), and adult migration (e.g., Doherty et al. 1995; Bernardi 2000; André et al. 2016) are also known to affect gene flow. The second factor is related to habitat and distribution characteristics including aspects such as habitat preference (e.g., Rocha et al. 2002; Hickey et al. 2009), habitat specificity (e.g., Ayre et al. 2009), and habitat continuity (e.g., Riginos and Nachman 2001; Banks et al. 2007; Binks et al. 2019). In general, genetic differentiation in coastal fishes increases as the degree of exposure and water depth decreases, habitat specificity increases, and habitat continuity decreases. The third factor is species-specific demographic history. For example, even if the ancient population experienced events, no significant population differentiation would be observed if the contemporary populations had not experienced events, such as extirpation of a part of the ancient population during a subsequent glacial period (cf., Xu et al. 2019; Hirase et al. 2020b). The fourth factor is natural selection, such as mate selection and local selection, within species. In cases where local adaptive pressure exists, a species-specific population structure could form depending on the availability of suitable environment for each population (Conover et al. 2006). These factors often act simultaneously and drive the development of species-specific population structure.

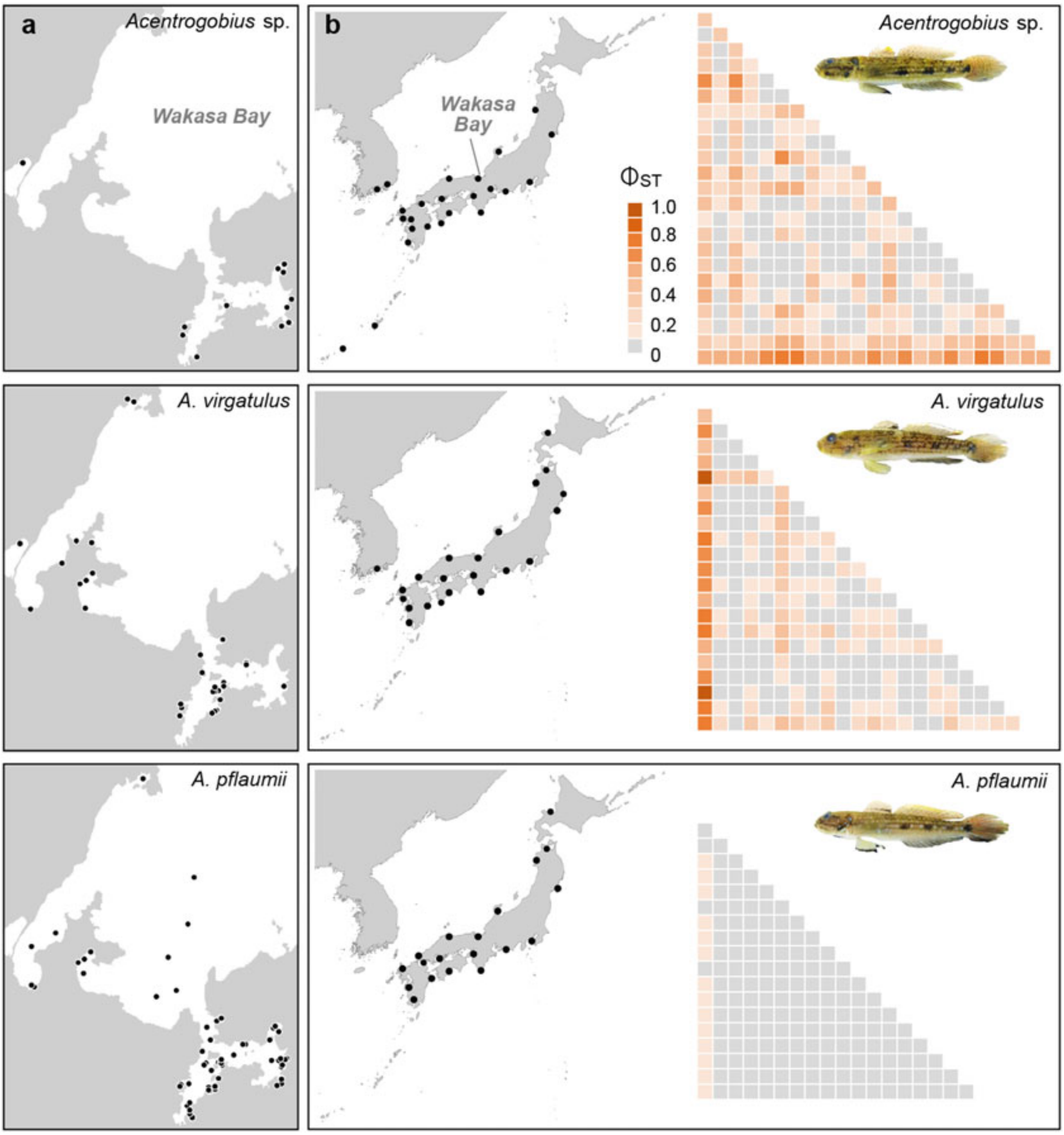

Fig. 11.6 Relationships between distribution characteristics and the degree of population differentiation of three *Acentrogobius* species (*Acentrogobius* sp., *A. virgatulus*, and *A. pflaumii*) species. (**a**) Distribution of three species in Wakasa Bay, located in the middle of the Sea of Japan coast of Honshu Island. *Closed circles* indicate points where each species was present (Matsui 2014, Figs. 3–6); (**b**) color-coded plots of pairwise Φ_{ST} values between locations within species based on mitochondrial cytochrome *b* gene of the three species. Sampling locations of each species are shown in each map of the Japanese Archipelago

11.5.2 Challenges for the Future

In response to the rapid development of techniques for molecular genetic analysis, phylogeographic research on coastal fishes around Japan has progressed considerably over the last two decades or so. These techniques have facilitated a more thorough understanding of population structure and the underlying formation mechanisms in some species, especially those found in the waters off the main islands of Japan. However, other regions have not been studied as extensively, and cross-border studies are woefully insufficient. For example, since almost no cross-border phylogeographic studies have been conducted in northern regions, including not only the Hokkaido coast, but also the continental coast of the Sea of Japan and the Sea of Okhotsk, Sakhalin, and the Kuril Islands. Consequently, the phylogeographic characteristics of cool-temperate to arctic coastal fish populations of Hokkaido Island is largely unknown. Also, only a limited number of phylogeographic studies have been conducted on fishes of the East China Sea coast, including sites within and outside Japan. As a result, a holistic understanding of the population structure of wide-ranging tropical to temperate species found around the East China Sea and species that originated from the continent has not yet been achieved. Further studies involving international cooperation and focusing on wide areas will contribute to a more comprehensive understanding of population structure of coastal fishes in the western North Pacific Ocean.

There are many challenges related to estimation accuracy. Since numerous molecular phylogeographic studies of coastal fishes from the western North Pacific Ocean have considered only a single mtDNA gene, it is unclear whether the estimated population structures accurately reflect the extant population structure or the ghosts of previous hybridization events. In addition, it is also unclear whether past and present hybridization and introgression has occurred and how this would affect population structure. Further studies including nuclear DNA analyses are therefore necessary to understand intraspecific lineages and population structures more precisely. Also, more precise estimates are required for phylogenetic relationships, the timing of population events (e.g., divergence time, TMRCA, and population expansion time), the past distribution and location of glacial refugia, past migration routes, and the identification of paleogeographic or oceanographic factors affecting population events; all of these are universal challenges. In phylogeographic studies based on nuclear DNA, microsatellite polymorphisms have been widely used. However, this technique is being replaced by new methods, such as reduced-representation sequencing [e.g., RAD-seq (Restriction site associated DNA sequencing by Andrews et al. 2016), MIG-seq (multiplexed ISSR genotyping by sequencing by Suyama and Matsuki 2015), and GRAS-Di (genotyping by random amplicon sequencing, direct by Hosoya et al. 2019)], in which polymorphism information at the genomic level can be obtained more efficiently using next-generation sequencing (NGS). These methods allow us to simultaneously analyze target regions scattered throughout the whole genome. Further, cost effective analytical techniques using whole genome sequences have been developed, even for non-model species (e.g., Fonseca et al. 2016; Armstrong et al. 2018). Adopting such techniques will lead to more precise estimates of population structure, phylogenetic relationships, and population history.

In addition, studies on and measures for the conservation of genetic diversity in marine organisms are less advanced than they are for terrestrial and freshwater organisms. To identify populations requiring conservation action, it is necessary to be able to clarify population traits, such as local endemism, population size, and genetic diversity, and to target many species over a wide geographic range. It is also necessary to develop analytical methods for efficiently screening populations in need of conservation. For example, one of the most difficult aspects of phylogeographic studies is the collection of samples of target species from various locations. Today, however, environmental DNA methods have enabled us to not only detect a target species and monitor biodiversity at a specific location, but also to make certain inferences regarding the population structure and intraspecific genetic diversity of a target species from water samples collected at target locations (Sigsgaard et al. 2020). Future studies of intraspecific population structure using such novel methods are expected to identify populations in need of conservation remarkably efficiently.

Furthermore, species-specific factors affecting population structure, especially ecological factors such as life history traits and habitat characteristics are of great interest for understanding the universality and diversity of the mechanisms that underlie the formation of population structure. However, most previous phylogeographic studies on coastal fishes around Japan have focused on only a few taxonomic groups inhabiting extremely shallow water or species that are economically important. Comparative phylogeographic approaches or meta-analyses focusing on many species in a variety of habitats and with different life history traits will advance our understanding of the effects of species-specific factors on the population structure of coastal fishes of Japan.

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Lake Biwa and the Phylogeography of Freshwater Fishes in Japan

12

Ryoichi Tabata

Abstract

This chapter discusses the geographic classification, phylogeographic analysis, and population genetic analysis of freshwater fishes in the Japanese Archipelago. Freshwater fishes serve as an excellent target for phylogenetic geographic analysis due to inherent restrictions on migration and dispersal. In the Japanese Archipelago, many geographical barriers exist; therefore, genetic differentiations of freshwater fishes between regions are evident. First, various examples of systematic geographic analyses in Japanese freshwater fishes will be introduced. Next, the origin of endemic species and the evolutionary history of fishes inhabiting Lake Biwa, which harbors the richest freshwater fish fauna in Japan, and the influence of Lake Biwa fishes on freshwater fish fauna in western Japan will be discussed.

Keywords

Lake Biwa · Freshwater fishes · Phylogeography · Endemic species · mtDNA

12.1 Geographical Regions Based on the Distribution of Japanese Freshwater Fishes

The objective of phylogeography is to determine the processes driving the distribution of organisms based on geographical distribution, intraspecific phylogenetic relationships, and intraspecific genetic variations (Avise 2000). Genetic differences among individuals due to mutation become clear when comparing base sequences of DNA. If divergence from a common ancestor is recent, differences in the base sequence are small, but if the divergence is more ancient, these differences are large. Based on these differences in base sequences, phylogenetic tree estimation and population genetic analysis can be performed and, subsequently, evolutionary processes such as population differentiation and past population dynamics as well as the processes driving distribution can be estimated (Kakioka 2018). Phylogeographic analyses have been conducted for various taxa of plants and animals, and freshwater fishes in particular have been studied extensively in this context (Avise 2000; Watanabe and Takahashi 2010; Watanabe et al. 2017).

Freshwater fishes are defined as fish that spend at least one stage of their life history in freshwater, and more than 300 species of freshwater fishes are native to Japan (Watanabe and Takahashi 2010). Of these, about 150 are primary freshwater fishes that live only in rivers and lakes

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(Myers 1938) and/or are very dependent on freshwater environments. Such strongly freshwater-dependent fishes have served as optimal study organisms in phylogeography because of their limited migration and their propensity to be greatly affected by geographical barriers (Avise 2000; Watanabe and Takahashi 2010; Watanabe et al. 2017).

Because the Japanese Archipelago stretches a great distance from north to south, a variety of freshwater fishes from cold to subtropical waters inhabit the country (Tabata and Watanabe 2018). In addition, numerous mountain ranges limit the migration of freshwater fishes in Japan. Therefore, different fish taxa occur in each region, and genetic differentiation within species is often observed in each area (Fig. 12.1). On a large scale, the freshwater fish fauna of the Japanese Archipelago is first divided into northeast and southwest regions along the boundary line of the Ishikari lowlands in Hokkaido. In the southwestern area, fish fauna can be further divided into east and west regions, via the western portion of the Fossa Magna region in central Honshu (i.e., the Itoigawa-Shizuoka Tectonic Line).

In western Japan, fish species richness is extremely high, particularly in the Lake Biwa-Yodo River system and northern Kyushu. Lake Biwa is an ancient lake within East Asia, over 4 million years old, and its long history and diverse environments, such as rocky reefs and vast offshore areas, have produced more than a dozen endemic fish species (e.g., *Gnathopogon caerulescens*, *Sarcocheilichthys biwaensis*, *Silurus lithophilus*, and *Gymnogobius isaza*). Both the number of species and the genetic diversity of each fish species are high and, as a whole, these fishes have strongly affected the general species composition of fishes in western Japan, mainly in the area around the Seto Inland Sea. Details of Lake Biwa will be introduced later, with a focus on the research results of Tabata et al. (2016). In northern Kyushu, multiple species are endemic, including *Aphyocypris chinensis*, *Tachysurus aurantiacus*, and multiple *Cobitis* species (e.g., *Cobitis kaibarai* and *Cobitis striata hakataensis*). Not only do many species inhabit this area but species exhibiting genetic differentiations from Honshu populations also occur, such as *Hemigrammocypris neglecta*, *Biwia zezera*, and *Abbottina rivularis*. Therefore, the freshwater fish fauna of northern Kyushu also contributes to the diversity within species. On the other hand, phylogeographic analyses that include foreign samples have revealed (mitochondrial DNA) mtDNA haplotypes of alien species and clades in northern Kyushu populations of species such as *A. rivularis* and *A. chinensis* (see Jang-Liaw et al. 2019; Watanabe et al. 2020). Some populations appear to have hybridized with alien populations (Fig. 12.2). In particular, pure Japanese populations of *A. chinensis* are very likely to be extinct both in the wild and in captivity (Watanabe et al. 2020).

The freshwater fish fauna of western Japan in areas other than Lake Biwa and northern Kyushu are also composed of various temperate species. In western Japan, many families of fishes occur that are not naturally distributed in eastern Japan; examples include species such as “Moroko” (willow gudgeon; Cyprinidae); various striped loach species (Cobitidae); catfish, which are large native carnivorous fish; and *Coreoperca kawamebari*, the only pure freshwater Percoidei native to Japan. In addition, when considering systematic geographic analysis, several key areas exist in western Japan, such as the Sanyo region, which harbors various fish species such as the Natural Monument *Parabotia curtus*; and the region around Ise Bay inhabited by the Natural Monument *Tachysurus ichikawai* and the recently described species *Silurus tomodai* (see Hibino and Tabata 2018). Many freshwater fishes in western Japan have closely related species in the eastern part of the Eurasian continent, such as in the Korean Peninsula and China. Therefore, genetic exchanges with the eastern part of the Eurasian continent are thought to be deeply involved in the formation of the fish fauna in western Japan. Phylogeographic analyses that include all of these areas also include research on the Japanese dace *Pseudaspius hakonensis* in addition to the above-mentioned research on *A. chinensis* and *A. rivularis* (Watanabe et al. 2018, 2020; Jang-Liaw et al. 2019). However, few analyses cover each region or use a large

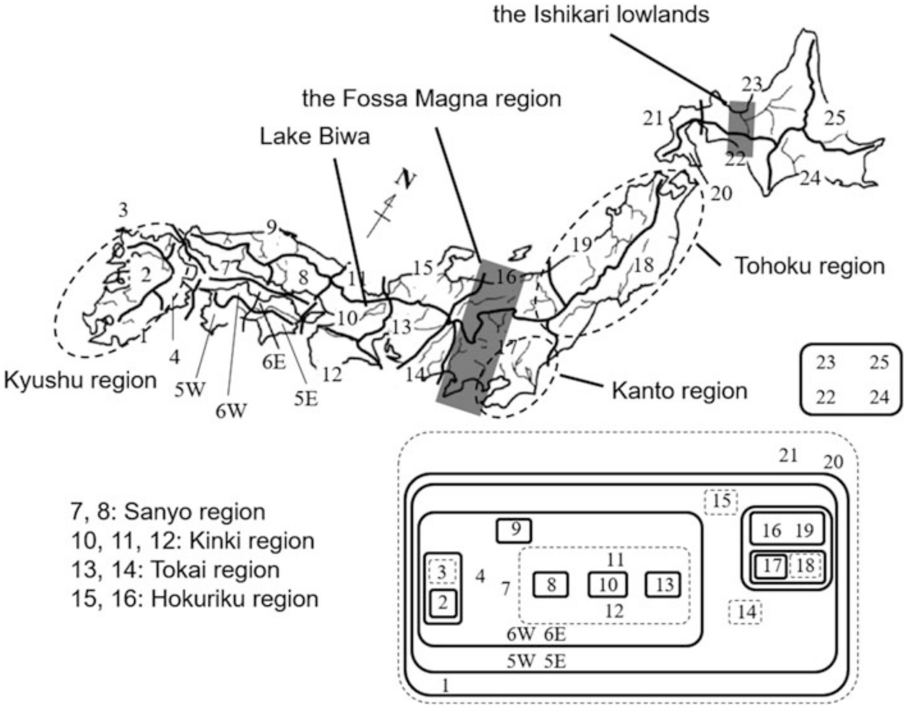

Fig. 12.1 Regional bifurcation diagram of freshwater fish fauna obtained by re-conservation analysis of geographical division and regional peculiarity of the Japanese Archipelago. The Venn diagram at the bottom is organized by region with similar uniqueness (after Watanabe 2012, partly modified). The *numbers* represent each region

number of samples in each region, and cooperation between ichthyological researchers in other countries is expected in the future.

The freshwater fish fauna east of the Fossa Magna region is poorer than that of western Japan. This low species richness has possibly been caused by the severe effects of global cooling and geological instability. However, the fish fauna of eastern Japan is also composed of various elements. The eastern part of the Ishikari lowlands in Hokkaido contains a very different fish fauna from the western area, as many cold-water freshwater fishes inhabit the former. For example, the Ishikari lowlands form the southern distribution limit of the stone loach *Barbatula barbatula*, and representative cold-water freshwater fish groups such as Cottidae, Gasterosteiformes, and Salmonidae, comprise a major portion of the freshwater fauna of this region. Several species, such as five subspecies of *Oncorhynchus masou* and the sculpin *Cottus* sp. (*Cottus pullux* middle egg type), are distributed not only in Hokkaido but also in Honshu and Shikoku. In addition, phylogeographic analyses covering the nationwide distribution area have been conducted (Tsukagoshi et al. 2011; Yamamoto et al. 2020). Due to the wide distribution range, genetic differentiation can be observed within species depending on the distance between populations, but the degree of differentiation is often slightly gradual compared to the large degree of genetic differentiation within the narrow distribution of primary freshwater fishes. Freshwater fishes inhabiting eastern Japan include those that inhabit western Japan beyond the Fossa Magna and those that are endemic to eastern Japan. The former includes *Tanakia lanceolata*, which has served as a good target for systematic geographic analysis as a widespread species (Tominaga et al. 2016). On the other hand, for some species such as catfish *Silurus asotus*, their distribution east of Fossa

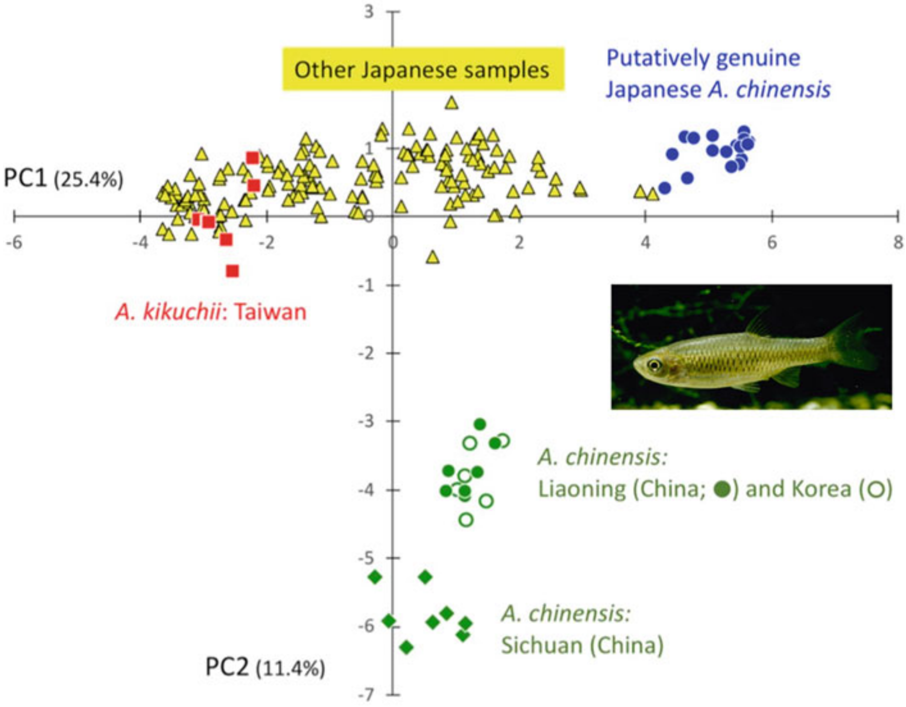

Fig. 12.2 Scatter plot of the first and second principal components for 240 SNPs from the MIG-seq analysis of *Aphyocypris chinensis*. The percent of variation explained by each axis is shown in parentheses. (After Watanabe 2020, partly modified. The photo provided by Lake Biwa Museum)

Magna may be the result of artificial transplantation. Such population colonization by artificial transplantation has been demonstrated via phylogeographic analysis in some populations of *T. lanceolata* and *Liobagrus reinii* (see Nakagawa et al. 2016; Tominaga et al. 2020). Fish species that are only found in eastern Japan include *Tachysurus tokiensis*, *Pseudorhodeus tanago*, and *Pseudogobio polystictus*, which will be described later. In the eastern area of Honshu, the number of freshwater fish species tends to decrease from Kanto to Tohoku (Fig. 12.1). The degree of genetic divergence is also lower than in western Japan. Multiple species in eastern Japan exhibit a genetic population structure in which the genetic diversity and distribution have rapidly expanded from a historical state of low genetic diversity and restricted distribution due to events such as glaciation (Watanabe and Nishida 2003; Tominaga et al. 2016; Watanabe and Takahashi 2010).

For several species whose distribution ranges are wide, phylogeographic studies have also demonstrated that western and eastern populations differ genetically at the species level. For example, in the genus *Pseudogobio* in Japan, the species “*Pseudogobio esocinus*” is distributed from Tohoku to Kyushu, but phylogenetic geographic analysis has indicated that it can be divided into three clades: clade A, which inhabits a wide range from Kyushu to central Honshu; clade B, which inhabits the middle and upper reaches of rivers in the Tokai, Kinki and Sanyo regions; and clade C, which inhabits eastern Japan (Tominaga et al. 2016; Fig. 12.3). Subsequent taxonomic study of Tominaga and Kawase (2019) has described clade A as *P. esocinus* and clades B and C as their new species, *Pseudogobio agathonectris* and *Pseudogobio polystictus*, respectively. Several phylogenetic geographic analyses have revealed multiple clades within fish species, including

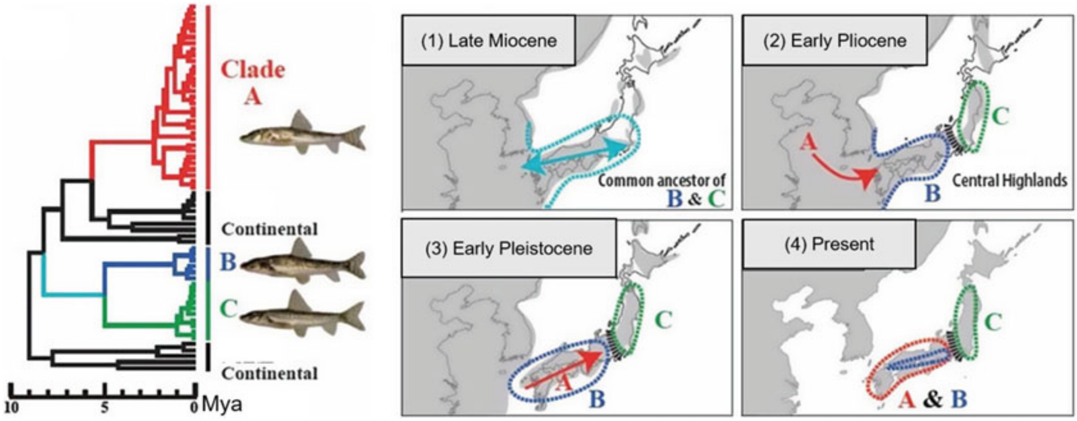

Fig. 12.3 The phylogeny of Japanese *Pseudogobio* fishes and the history of distribution formation estimated based on it. (After Tominaga et al. 2016, partly modified)

those that appear to be cryptic species, such as *L. reinii* (see Nakagawa et al. 2016), *S. asotus* (see Tabata et al. 2016), and *B. zezera* (see Watanabe et al. 2010). In the latter two species, the cryptic clades have been described as *S. tomodai* and *Biwia yodoensis*, respectively. Because additional fish species with cryptic clades are very likely to exist and have the potential to be recognized as undescribed species, further analyses are ongoing (Watanabe et al. 2017).

12.2 The Origin of Endemic Fishes in Lake Biwa

As introduced in the previous section, Lake Biwa is located in western Japan and is the largest lake in the country. Lake Biwa is a 4-million-year-old ancient lake (Fig. 12.4). The lake harbors approximately 60 species of native freshwater fishes that inhabit various environments, such as rocky shores and pelagic areas. Lake Biwa contains 15 endemic species; *Biwia yodoensis* inhabits the Yodo River basin, downstream of Lake Biwa, but the main habitats of other endemic species include the pelagic area or rocky shores in the northern basin of the lake (Table 12.1; Fig. 12.5).

Gnathopogon caerulescens (Cyprinidae) has an upward-turned mouth that is suitable for feeding on suspended food such as plankton and has an elongated body that is more suitable for swimming than its closely related species, *Gnathopogon elongatus*. *Gymnogobius isaza* (Gobiidae) inhabits the relatively deep area (greater than 30 m) of the northern basin and exhibits a unique lifestyle involving diurnal vertical migration. In contrast, the closely related *Gymnogobius urotaenia* inhabits the shallow coastal area of Lake Biwa and the inflowing river. *Silurus lithophilus* (Siluridae) lives mainly in the rocky areas of the northern and eastern areas of the northern basin and has a brown body color and eyes protruding sideways that appear to be suitable for rocky areas.

Based on these traits, many endemic species have shapes and colors suitable for inhabiting offshore environments and rocky zones, and their life histories appear to be well adapted to the present environment of Lake Biwa. Such environments were created in Lake Biwa beginning approximately 0.4 Mya. Therefore, many of the endemic species of Lake Biwa are thought to have differentiated from closely related species by adapting to the unique environment of the lake (e.g., rocky shore and large pelagic area) that existed 0.4 Mya (Tomoda 1978). On the other hand, some endemic species may represent relic species, as they are more closely related to species found only on the continent (Kawanabe

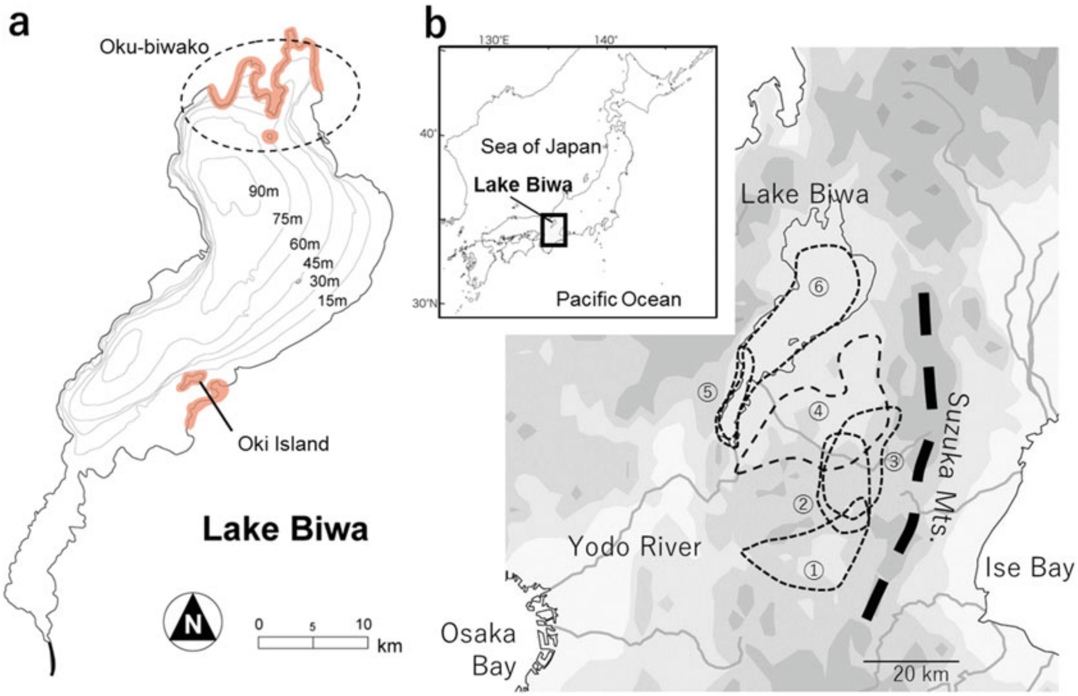

Fig. 12.4 (**a**) "Present" Lake Biwa (after Komiya et al. 2011, partly modified). Northern and eastern rocky zones are shaded in orange. A rocky or pebbly environment according to quantitative data on substratum constitutions reported by Nishino (1991). (**b**) Changes in the position of Paleo-Lake Biwa (after Watanabe 2013, partially modified). *1* Lake Ohyamada (>3.2 Mya), *2* Lake Ayama (3.0–2.7 Mya), *3* Lake Koka (2.7–2.5 Mya), *4* Lake Gamo (2.5–1.8 Mya), *5* Lake Katata (1.0–0.4 Mya), *6* "present" Lake Biwa (<0.4 Mya). (Drawn mainly based on Kawabe 1994)

1978; Tomoda 1978). In fact, the endemic species of Lake Biwa have traditionally been grouped as "endemic species in situ" and "relic endemic species" (Table 12.1; Kawanabe 1978, 1996).

However, results of mtDNA genetic analyses conducted in the 2000s indicated that many of the endemic species of Lake Biwa exhibit evolutionary histories that differ from the above-mentioned traditional grouping (e.g., Harada et al. 2002; Kakioka et al. 2013; Tabata et al. 2016). Eight of the 12 species analyzed to date did not diverge from related species during the era of present Lake Biwa (beginning 0.4 Mya) but, instead, reflect divergence between about 1 and about 10 Mya (Fig. 12.6). Therefore, divergence occurred at various times throughout the history of Lake Biwa and includes typical Lake Biwa endemic species that have adapted to the environment of Lake Biwa, such as *G. isaza* and *G. caerulescens*. On the other hand, three species are estimated to have diverged beginning 0.4 Mya: *Sarcocheilichthys biwaensis*, *Sarcocheilichthys variegatus microoculus*, and *Squalidus biwae biwae*. These species have minimal genetic differentiation in mtDNA from closely related species, and the age of divergence is estimated to have occurred in the last tens of thousands of years. In addition, Biwa Salmon *Oncorhynchus* sp. was estimated to have diverged from other cherry salmon species groups (*Oncorhynchus masou masou*, *Oncorhynchus masou ishikawae* and *Oncorhynchus masou formosanus*), 0.52 Mya. Because the 95% highest posterior density (HPD) of divergence age for Biwa Salmon is estimated to be 0.29–0.75 Mya, its divergence was likely to have been strongly influenced by the establishment of present conditions in Lake Biwa. Overall, it is clear that

Table 12.1 Fish species endemic to Lake Biwa

Scientific name	Category[a]	Note
Salmonidae		
Oncorhynchus sp. (Biwa salmon)	S	Undescribed
Cyprinidae		
Opsariichthys uncirostris	R	Semi-endemic
Ischikauia steenackeri	R	
Gnathopogon caerulescens	S	
Sarcocheilichthys biwaensis	S	
Sarcocheilichthys variegatus microoculus	S	
Squalidus biwae biwae	R	
Biwia yodoensis	–	
Carassius buergeri grandoculis	S	
Carassius cuvieri	S	
Cobitidae		
Cobitis minamorii oumiensis	–	
Cobitis magnostriata	–	
Siluridae		
Silurus lithophilus	S	
Silurus biwaensis	S	
Gobiidae		
Rhinogobius biwaensis	S	
Gymnogobius isaza	S	
Cottidae		
Cottus reinii	S	Endemic ecotype

S in situ, *R* relic
– not described at that time
[a]Category of endemic species based on distribution and ecology in Kawanabe (1978), Tomoda (1978), and Kawanabe (1996)

various ("old-endemic" and "new-endemic": Tabata et al. 2016) divergence ages exist among the endemic freshwater fish species of Lake Biwa. Such variation in the timing of divergence may have occurred via several possible mechanisms. For example, the habitats of ancestral species have undergone vicariant divisions due to global climate change and crustal movements in the Japanese Archipelago and, as a result, Lake Biwa has changed in location, depth, and size over its 4-million-year history.

Despite the variation in divergence age of endemic species in Lake Biwa, the population expansion of the majority of the approximately 40 species in and around Lake Biwa, including non-endemic species, likely began after 0.4 Mya; in other words, when present conditions in Lake Biwa were established (Fig. 12.7; Tabata et al. 2016). Such findings suggest that none of the populations of endemic species with old divergence ages have stabilized since the time of divergence, and most endemic species have experienced a bottleneck event followed by population expansion in present Lake Biwa. The general sequence of events involving the divergence of old-endemic species from closely related species is thought to have initially occurred via geographical or climatic events, followed by subsequent unstable environments in Paleo-Lake Biwa that caused bottlenecks in the endemic populations and, ultimately, culminated in population expansions during the relatively stable current period of present Lake Biwa. This process is likely to represent the primary reason for differences in the timing of divergence and the timing of population expansion. In addition, this potential sequence of events may also explain the acquisition of current traits adapted to the offshore and rocky areas of present Lake Biwa, beginning 0.4 Mya, perhaps contributing to

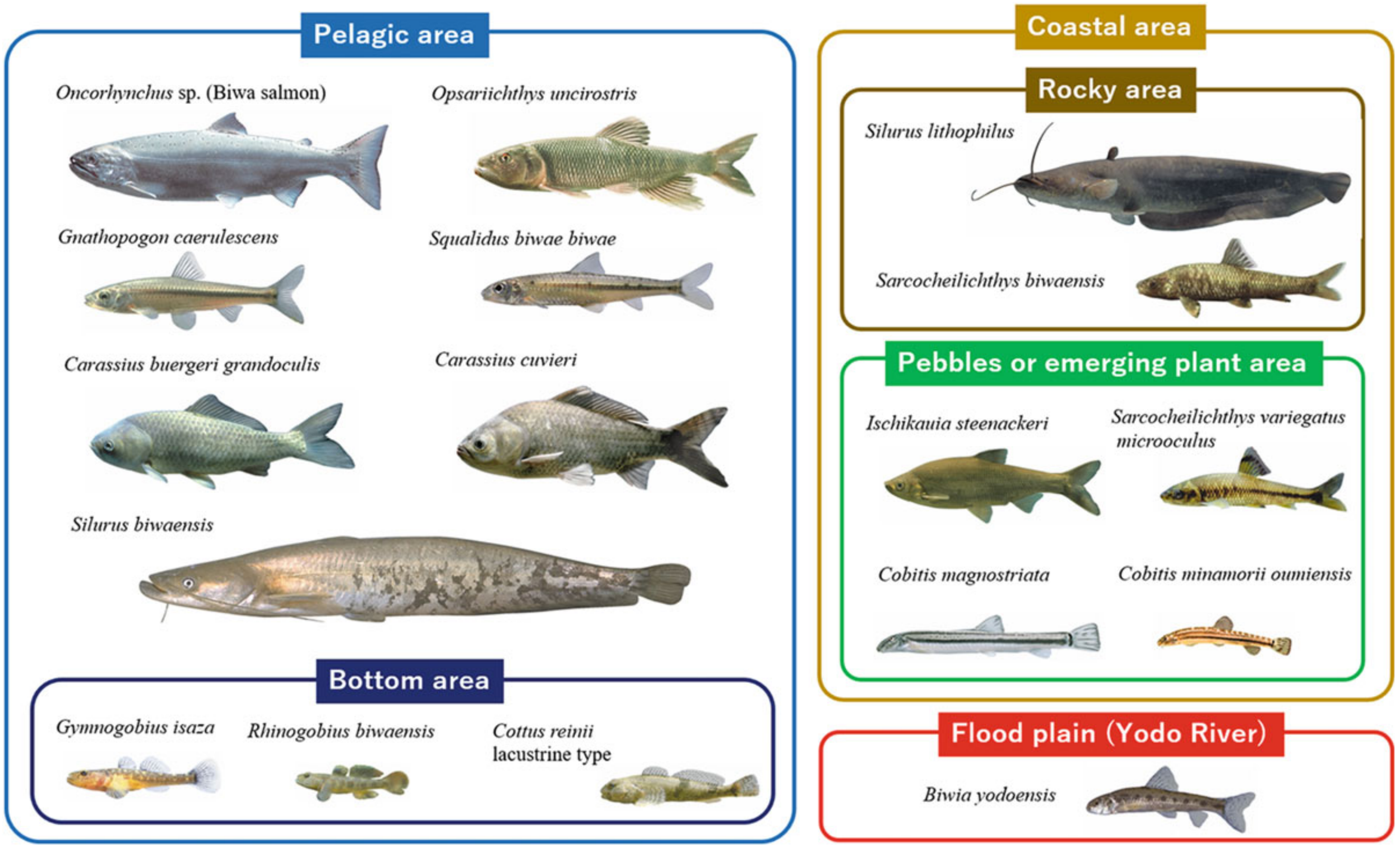

Fig. 12.5 Endemic and semi-endemic fishes in Lake Biwa and their habitat. Note that a semi-endemic species is not endemic to Lake Biwa, but its distribution is mostly restricted to Lake Biwa. (The photo provided by Lake Biwa Museum)

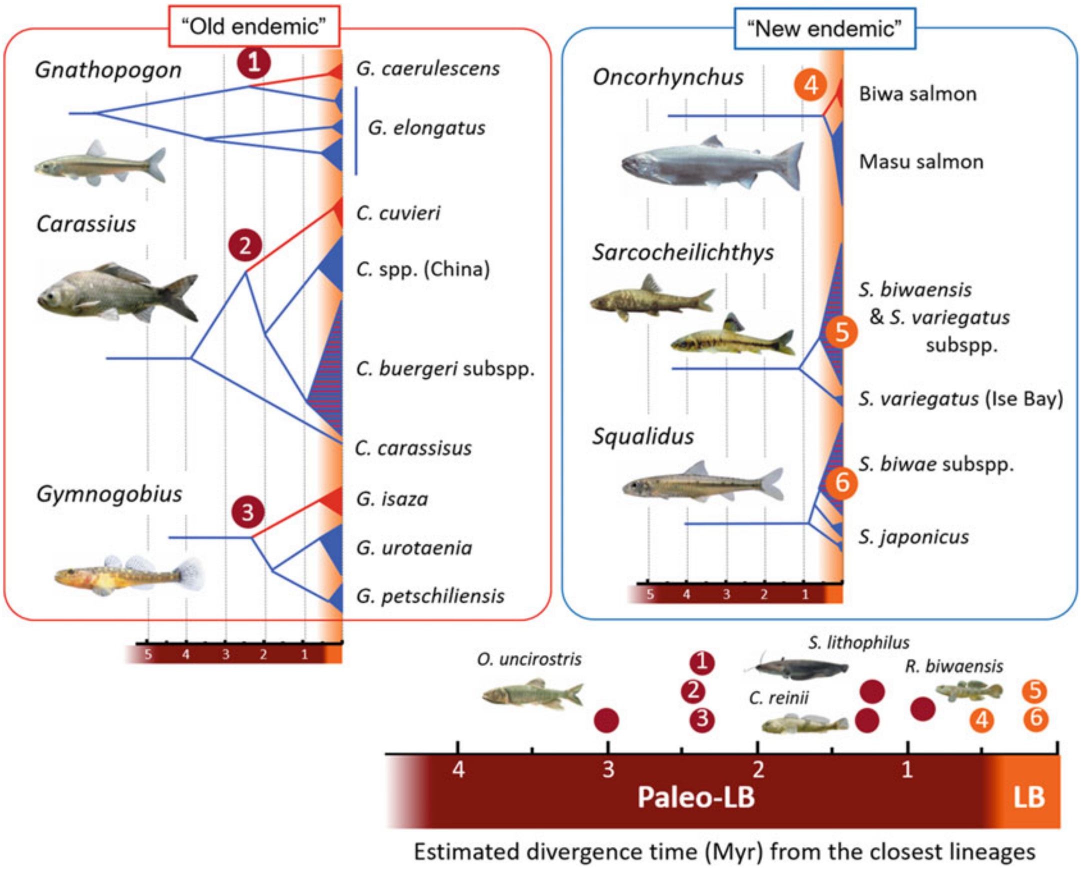

Fig. 12.6 Phylogenetic trees and divergence time of each fish group including species/subspecies endemic to Lake Biwa. (After Watanabe 2020, partly modified)

population expansion. On the other hand, endemic species with more recent divergence ages may have experienced lineage differentiation (i.e., speciation) due to the evolution of certain traits and life histories during the process of adaptation to present Lake Biwa, as put forward in the ecological speciation hypothesis.

12.3 The History of Fishes in and Around Lake Biwa Based on Population Genetic Analysis and Phylogeographic Analysis

The majority of the freshwater fish species living in Lake Biwa expanded in population size after bottleneck events. On the other hand, several species exhibit multiple mtDNA groups within their populations. Most of these are nonendemic species, but some endemic species also have multiple intraspecific groups of mtDNA. One such endemic species is *Gymnogobius isaza*, a small goby with a total length of about 5–8 cm that inhabits areas of Lake Biwa at depths of 30 m or more. This species usually inhabits the bottom waters, but it comes to close the water surface at night to feed on zooplankton. Thus, *G. isaza* appears to exhibit a specialized life history in the deep environment characteristic of present Lake Biwa, and it has not yet been found in areas other than Lake Biwa. As mentioned in the above section, because *Gymnogobius urotaenia* inhabits the shores of Lake Biwa and the inflowing rivers, *G. isaza* may have differentiated from *G. urotaniea* (or its ancestral species) via adaptive evolution to the offshore environments

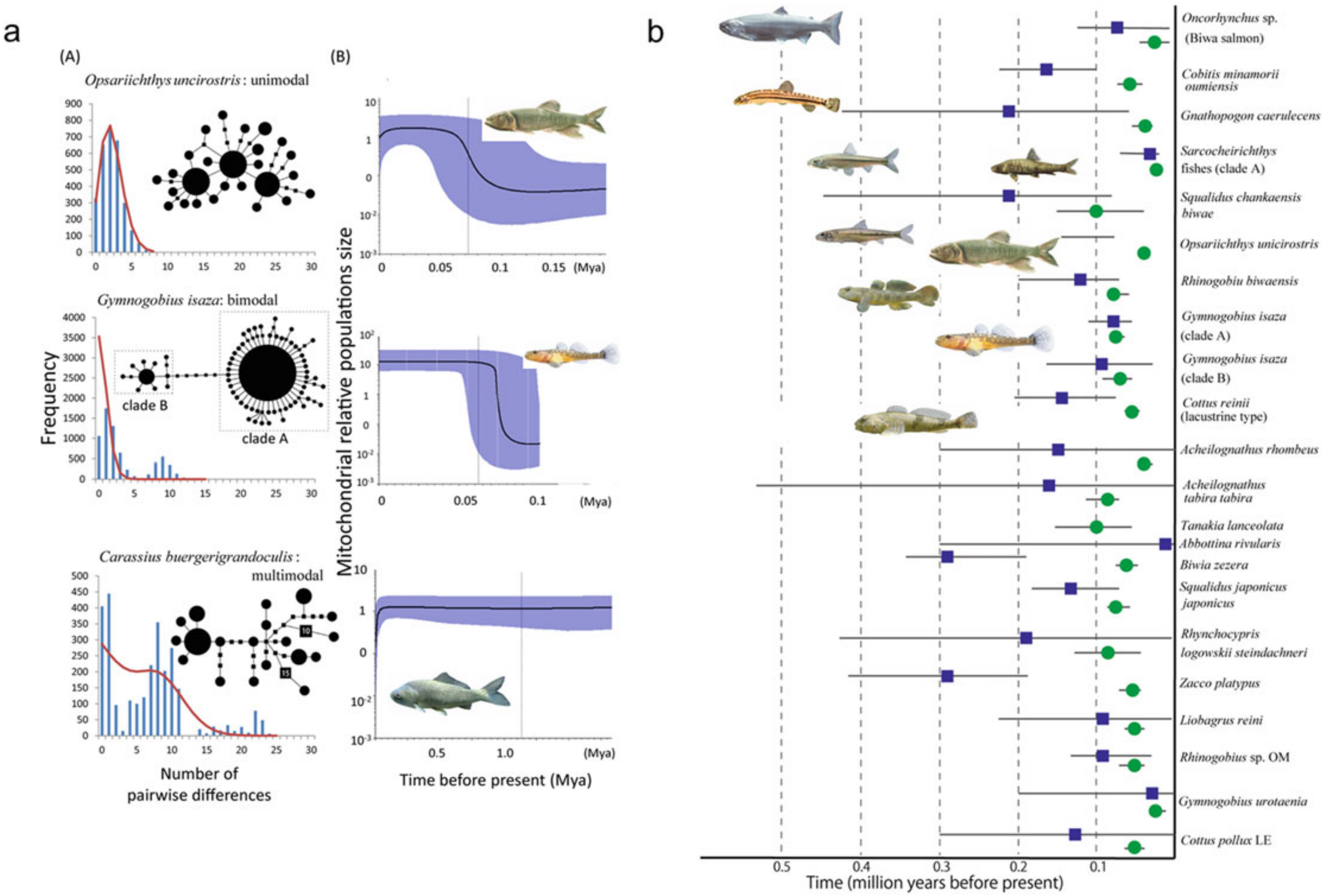

Fig. 12.7 (**a**) The typical results of mismatch distributions, statistical parsimony networks of mtDNA cytochrome *b* haplotypes and Bayesian skyline plots for representative endemic species. (**b**) Timing of population expansion in the populations of endemic and non-endemic fishes in Lake Biwa. The *squares* represent the time based on the mismatch distribution analysis. The *circles* represent the time estimated with the Bayesian skyline plot analysis. (After Tabata et al. 2016, partly modified)

that began to appear 0.4 Mya (Takahashi 1989). However, molecular phylogenetic analysis using partial base sequences of mtDNA has estimated that *G. isaza* diverged from the common ancestor of *G. urotaenia* and *Gymnogobius petschiliensis* about 2.3 Mya (Harada et al. 2002). At that point in time, the Paleo-Lake Biwa was called Lake Koka, which is thought to have been similar to the deep, wide lake of present Lake Biwa (Kawabe 1994; Satoguchi 2018). However, Paleo-Lake Biwa experienced an era of shallow lakes after the era of Lake Koka, followed by an era of swamps without large lakes, and then an era of riverine environments. Therefore, several eras included conditions that were unsuitable for *G. isaza*. To determine a more detailed history of *G. isaza*, a population genetic analysis using a partial base sequence of mtDNA was performed (Tabata and Watanabe 2013). As a result, two mtDNA clades with a 1.6% difference at the uncorrected *p*-distance for cytochrome *b* were found in *G. isaza*. The divergence time of these two clades was about 0.7 Mya (95% HPD: 0.4–0.9 Mya). Both clades expanded their populations beginning 0.1 Mya and, in the samples collected from several locations within the lake, both clades exhibit the same ratio at each location (clade A:clade B ≈ 10:1). Subsequently, a nuclear genome analysis (Tabata et al. unpublished data) revealed that the two clades represent one population. Based on these findings, these clades currently appear to be completely mixed within the population. Given these results, combined with the lack of geographical barriers within the lake that would have created mass divergence since the present conditions of Lake Biwa evolved, the most likely sequence of events is that *G. isaza* diverged 2.5 Mya, expanded to several areas of western Japan, and two of these populations subsequently colonized Lake Biwa (Fig. 12.8).

Multiple intraspecific clades have been found in several other fish species, such as *Sarcocheilichthys biwaensis* and *Sarcocheilichthys variegatus microoculus* (see Komiya et al. 2011, 2014; Tabata et al. 2016). Because mtDNA and microsatellite markers cannot distinguish between *S. biwaensis* and *S. v. microoculus*, they are also herein referred to as *Sarcocheilichthys* spp. *S. v. microoculus* is a cyprinid with a total length of about 15–20 cm and inhabits the coast of Lake Biwa and its inflow rivers and the outflow Seta River. This species has a closely related subspecies *Sarcocheilichthys variegatus variegatus*, which inhabits the Tokai, Kinki, Sanyo, and northern Kyushu regions. Compared to *S. v. microoculus*, *S. biwaensis* has a darker black and tan color, even on the abdomen, its eyes protrude sideways, and its head is long. *S. biwaensis* only inhabits the rocky area around Oki Island (a small island in the northern part of Lake Biwa) and the northernmost part of Lake Biwa (Oku-biwako), thus, its physical features likely arose as a result of adaptive evolution to rocky areas. Because *S. biwaensis* and *S. v. microoculus* cannot be differentiated via mtDNA and microsatellite markers and they exhibit little genetic differentiation from closely related species (i.e., *S. v. variegatus* populations, with the exception of the population around Ise Bay), these two species are likely to represent one endemic species that speciated while adapting to present Lake Biwa. However, the intraspecific lineage shows that the history of *Sarcocheilichthys* in Lake Biwa is complicated in that three mtDNA clades (A, B, and C) existing in the population (Komiya et al. 2011, 2014). Of these, the majority are individuals of clade A. Haplotypes of the A, B, and C strains have been found in the Sanyo region (clades A and B) and northern Kyushu (clade C). These results suggest that the *Sarcocheilichthys* of Lake Biwa colonized the lake multiple times from other areas, and gene flow with these areas continued for some time (Fig. 12.9a).

Species with multiple genetic lineages within Lake Biwa, such as *Sarcocheilichthys*, can provide evidence of past genetic exchanges with other regions. Twelve species, including *Pseudogobio esocinus* and *Rhynchocypris oxycephala jouyi*, among the 40 species in Lake Biwa, have been the subject of population genetic analyses. For example, in *P. esocinus*, two mtDNA groups have been found in Lake Biwa and its inflowing rivers, but only one of these was found in the Lake Biwa and Yodogawa river

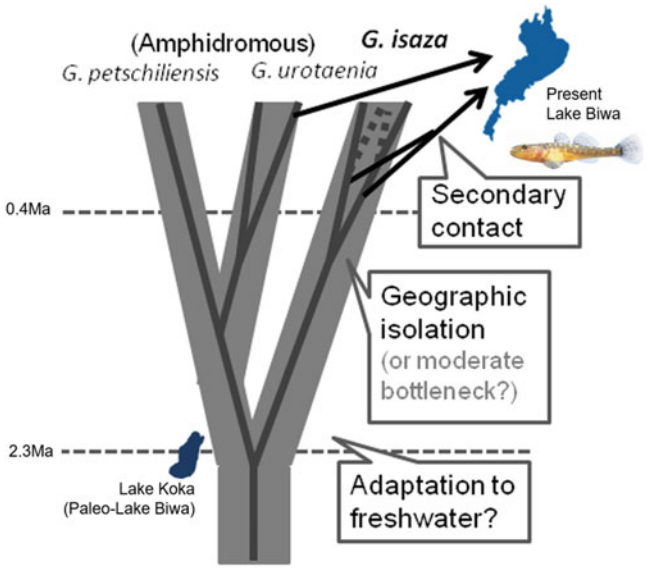

Fig. 12.8 History of *Gymnogobius isaza* inferred from phylogenetic and population genetic analysis. (After Tabata and Watanabe 2013, partly modified)

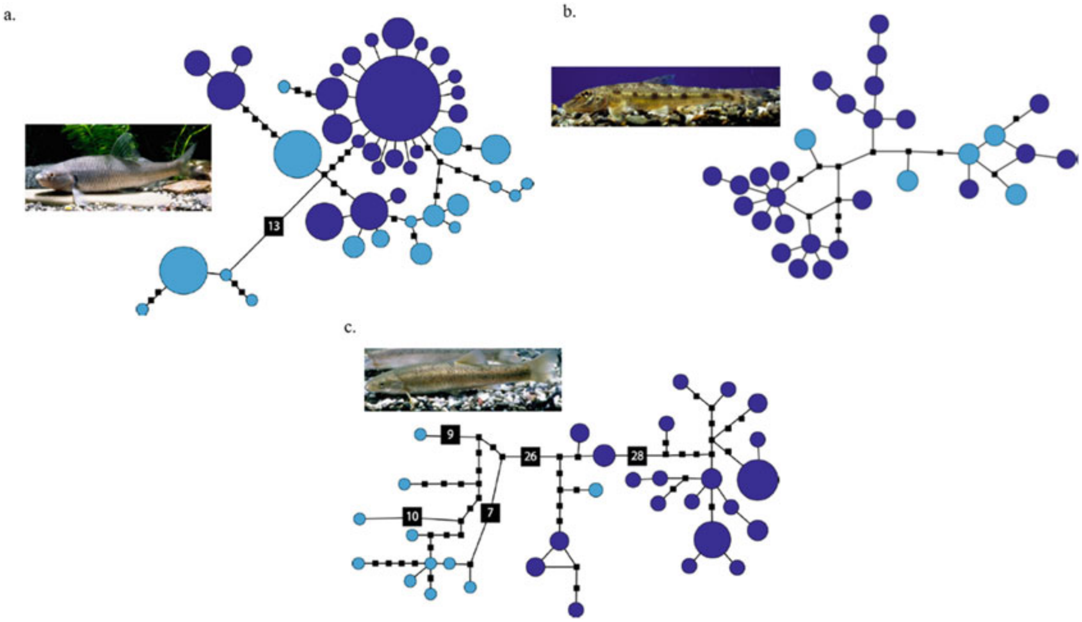

Fig. 12.9 Statistical parsimony networks of mtDNA cytochrome *b* haplotypes of representative fishes including Lake Biwa and other local populations. The *dark circles* represent haplotypes found in Lake Biwa and rivers connected to the lake. The *pale circles* represent haplotypes detected from the areas outside Lake Biwa (after Tabata et al. 2016, partly modified). (**a**) *Sarcocheilichthys* species, (**b**) *Pseudogobio esocinus* species, (**c**) *Rhynchocypris oxycephala* species

systems, and the other is a group widely found in western Japan (Fig. 12.9b; Tabata et al. 2016; Tominaga et al. 2016). *Rhynchocypris oxycephala jouyi* inhabits the upper reaches of inflowing rivers around Lake Biwa, and is largely genetically differentiated within the western and eastern regions of the lake. In inflowing rivers to the western area of Lake Biwa, several cases exist in which multiple, greatly differentiated clades are found at the same time. Phylogeographic analyses of *R. o. jouyi* in other regions have indicated that this species has haplotypes close to the populations of neighboring regions such as Hokuriku and Kinki, and that they may have crossed the mountains and entered Shiga Prefecture (Fig. 12.9c; Tabata et al. 2016).

Lake Biwa has not only served as an evolutionary site for the creation of endemic species and adaptive traits but it also represents a genetic reservoir for the rich freshwater fish fauna of western Japan by retaining genetic groups in each region. In this chapter, we describe primarily the results of mtDNA analyses, but the authors are currently conducting nuclear genome analyses, such as MIG-seq (Multiplexed ISSR Genotyping by sequencing; Suyama and Matsuki 2015), RAD-seq (Restriction Site Associated DNA Sequence; Baird et al. 2008) and resequencing analysis. We expect that such nuclear genome analyses will reveal the detailed history of the populations of freshwater fish in Lake Biwa. For example, we hope to determine which multiple strains harbor traces of past genetic exchanges and which bottleneck events of the past could not be detected by mtDNA. A new phylogenetic map of Japanese freshwater fish may be created by adding or redrawing the phylogeographic structure using mtDNA in the nuclear genome.

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Part IV

Morphological and Ecological Diversifications

Migration of Fishes in Japan

13

Shun Watanabe

Abstract

The Japanese Archipelago is unique in that it extends from the near-arctic island of Hokkaido to the subtropical southern Ryukyu Islands that are situated along the Kuroshio Current, and this latitudinal range supports a remarkable diversity of migratory fishes. These fishes include diadromous species that are anadromous and use the sea for a feeding and growth biome and freshwater for a reproductive biome (salmons and lampreys), catadromous species that use freshwater for their feeding and growth biome and the sea for a reproductive biome (freshwater eels and sculpins), freshwater amphidromous species that use both the sea and freshwater for feeding and growth biomes and freshwater for the reproductive biome (Ayu *Plecoglossus altivelis*, sculpins and gobies), potamodromous fishes that make relatively short migrations in freshwater, such as in Lake Biwa (cyprinids), and oceanodromous species that make migrations between their marine spawning and feeding areas (tunas, yellowtails, etc.). The geomorphology of the Japanese Archipelago and the northward flowing Kuroshio and Tsushima warm currents have likely shaped this diverse fauna of migratory fishes in both the marine waters and freshwater rivers where a relatively high percentage of species are diadromous. The diadromous species are particularly vulnerable to anthropogenic impacts of habitat loss or blockages to connectivity between the ocean and freshwater habitats and require careful considerations for conservation.

Keywords

Fish migration · Oceanodromy · Potamodromy · Diadromy · Anadromy · Catadromy · Amphidromy

13.1 Fish Migration

The marine and freshwater fishes of Japan consist of a wide diversity of species living in many different types of habitats (Nakabo 2002), but only a relatively small subset of these species include true migrations in their life histories. In Japan however, the types of fishes that make true migrations are taxonomically and morphologically very diverse (Fig. 13.1). Most fishes make at least some movements among different habitats according to their developmental stages and seasonal changes in their life histories. When these movements between habitats occur regularly in response to a particular season or a stage of life history and they are conducted by the majority of the members of the species or population, the

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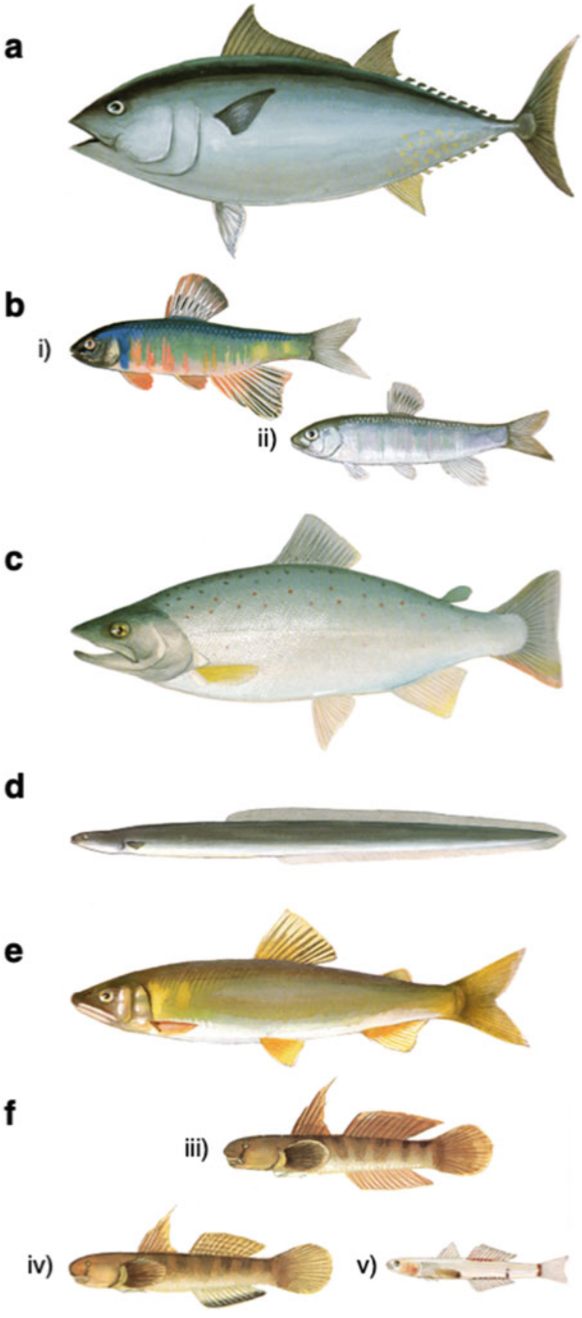

Fig. 13.1 The body forms of different types of migratory fishes showing (**a**) oceanodromous Pacific Bluefin Tuna (*Thunnus orientalis*), (**b**) (i) male and (ii) female of potamodromous Pale Chub (*Opsariichthys platypus*), (**c**) anadromous Satsuki-Masu Salmon (*Oncorhynchus masou ishikawae*), (**d**) catadromous Japanese Eel (*Anguilla japonica*), (**e**) amphidromous Ayu (*Plecoglossus altivelis*), (**f**) (iii) male, (iv) female and (v) larva of amphidromous Monk Goby (*Sicyopterus japonicus*) that were illustrated by Shojiro Fukui (Fukui 1999)

movements can be considered as true migrations. Therefore, migrations and life history cannot be considered separately, and migration and life history are the basis of many important aspects of the fish ecology of each species.

The most important events in the life history of fishes are growth and reproduction, and the habitats in which these events occur are the defining features of their life history and migrations. When spawning and growth take place in different respective areas, the fish must migrate between these two habitats. Therefore, many migrations can be defined as movements between spawning and growth habitats (Fig. 13.2). In

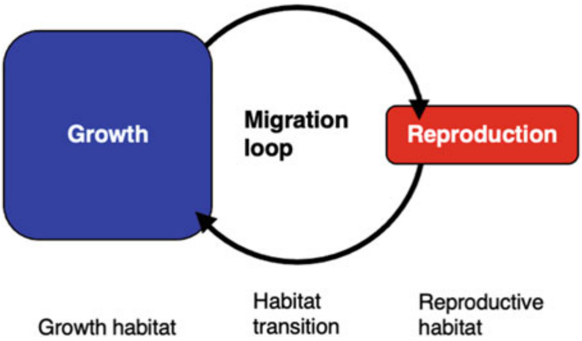

Fig. 13.2 A simple diagrammatical representation of migration and the concept of a migration loop. (Modified from Tsukamoto et al. 2009)

general, the spawning areas are small to increase the rate of encounters with breeding partners, and growth areas are large to reduce competition for food (Fig. 13.2).

Fish migration has remained an important subject for fish ecology and conservation not only in Japan, but around the world (Moralis and Daverdat 2016; Lennox et al. 2019). Japan has an interesting ecological diversity of migratory fishes that have migration loops (Tsukamoto et al. 2009) ranging from thousands of kilometers in the case of anadromous salmons, catadromous eels, or cross-Pacific basin round-trips of tunas, to much shorter landlocked migrations in freshwater or between freshwater and estuaries or coastal waters. These migratory species are highly morphologically diverse in size, shapes, and niches they occupy, and some groups such as gobies of *Rhinogobius* and Japanese amphidromous sculpins have diversified into multiple species or subspecies with slightly different life history characteristics. This chapter focuses on typical examples of the migrations of fishes in and around Japan, with an emphasis on species that have large-scale migrations or have their growth and spawning habitats separated between freshwater and the sea.

13.2 Types of Fish Migration

Myers (1949) is frequently cited for establishing the terms that define the types of fish migration as they are now most frequently used in the ichthyological literature. These descriptive terms for classifying migratory fishes of Myers (1949) have been discussed by McDowall (1988, 1997, 2009a), and as outlined below they are based on the types of directional movement in relation to freshwater and the sea, and the purpose of these migrations as outlined in the following sections. Japan has at least some examples of fishes with all of these types of migration, which mostly consist of taxonomic groups of migratory fishes that are present in other parts of the world.

13.2.1 Oceanodromy

These are migratory fishes that live and migrate only among different oceanic habitats, but determining which types of even large-scale movements for feeding are considered migrations or not is somewhat complicated unless they are considered as essential for the completion of the life history and then they can be considered examples of oceanodromous migrations (Couto et al. 2016). Examples in Japanese waters are Pacific Bluefin Tuna (*Thunnus orientalis*), Skipjack Tuna (*Katsuwonus pelamis*) and Pacific Saury (*Cololabis saira*). However, many of the Japanese fisheries species have different spawning and post-larval feeding areas with migrations being made between the different ocean areas as overviewed by Yatsu (2019).

13.2.2 Potamodromy

These are migratory fishes in which all species live and migrate only within freshwater habitats. These fishes may migrate between lakes or streams, between different river areas that are usually used for either feeding or spawning, but can also include refuge habitats (Lucas and Baras 2001; Brönmark et al. 2013; Thurow 2016). The river drainages in Japan are generally quite short compared to continental river systems and lakes, so the scale of distances moved by this migratory type may be shorter in Japanese freshwaters. The large inland water body of Lake Biwa has a fish fauna that has diversified into a variety of migratory types (Hosoya 2020). However landlocked species of diadromous taxa occur, which have also been considered to be potamodromous fishes (Thurow 2016). In Japan, these partially include several species or populations of salmonids, Ayu, and freshwater sculpins, and the fishes in these groups can have fluvial and lacustrine life histories (Goto et al. 2015).

13.2.3 Diadromy

These are migratory fishes that travel between the sea and freshwater, and the categories of diadromous were expanded and refined by McDowall (1988, 1997, 2009a) (Fig. 13.3). Diadromy is best known in fishes, among which there are probably around 250 diadromous species (McDowall 1988), but they are a very small minority (<1%) of the approximately 34,600 fish species known worldwide (Froese and Pauly 2021). Diadromous fishes have strong osmoregulatory abilities, because of the salinity differences between freshwater and the sea. It is probably the ability of osmoregulation that limits the diversity of diadromy species, although many euryhaline species are not diadromous (McDowall 2009a). Within the groups of diadromous fishes however, life history variations occur in the degree to which there is separation between which biome (the sea or freshwater) is used for feeding, such as in landlocked or non-migrant anadromous species, or for some catadromous eels that do not enter or spend significant time in freshwater.

13.2.3.1 Anadromy

Anadromous fishes feed and grow mainly in the sea before they migrate back into freshwater habitats as fully grown adults to reproduce. After leaving the sea (feeding and growing biome), they either do not feed after entering freshwater (reproductive biome), or if they feed to some extent, they do not grow any more (Fig. 13.3a). There are 17 orders of fishes that have anadromous fishes, but many members of the Salmoniformes, Clupeiformes, Osmeriformes, Acipenseriformes, and Petromyzontiformes comprise 82% of all anadromous species (Acolas and Lambert 2016). Pacific salmon and trout of *Oncorhynchus* are the classic examples of anadromous fishes, which also have a wide range of life history variations (Quinn and Myers 2004). Examples of anadromous fishes in Japan are Japanese Chum Salmon (*Oncorhynchus keta*), Arctic Lamprey (*Lethenteron camtschaticum*), Maruta Dace (*Pseudaspius brandti maruta*), Shishamo Smelt (*Spirinchus lanceolatus*), Japanese Smelt (*Hypomesus nipponensis*), Sakhalin Taimen (*Parahucho perryi*) and Ice Goby (*Leucopsarion petersii*).

13.2.3.2 Catadromy

Catadromous fishes feed and grow in freshwater before they mature, and adult fishes migrate to marine or estuarine waters to reproduce. Therefore, the principal feeding and growing biome is freshwater, and the reproductive biome is the sea or estuaries (Fig. 13.3b). Some species make relatively short migrations from freshwater to estuarine or coastal areas, but only the catadromous eels make long migrations offshore to spawn in the open ocean (Tsukamoto et al. 2002; Aoyama 2009; Miller 2016). Examples in Japan are Japanese Eel (*Anguilla japonica*), Fourspine Sculpin (*Rheopresbe kazika*) and Roughskin Sculpin (*Trachidermus fasciatus*).

13.2.3.3 Amphidromy

Larvae of amphidromous fishes are born in freshwater and they then migrate (or drift) to the sea soon after hatching for early feeding and growth, before the small postlarval and juvenile fishes migrate from the sea back into freshwater. There is then prolonged feeding in freshwater where the fishes grow from juvenile to adult stages until they mature and reproduce offspring. Therefore,

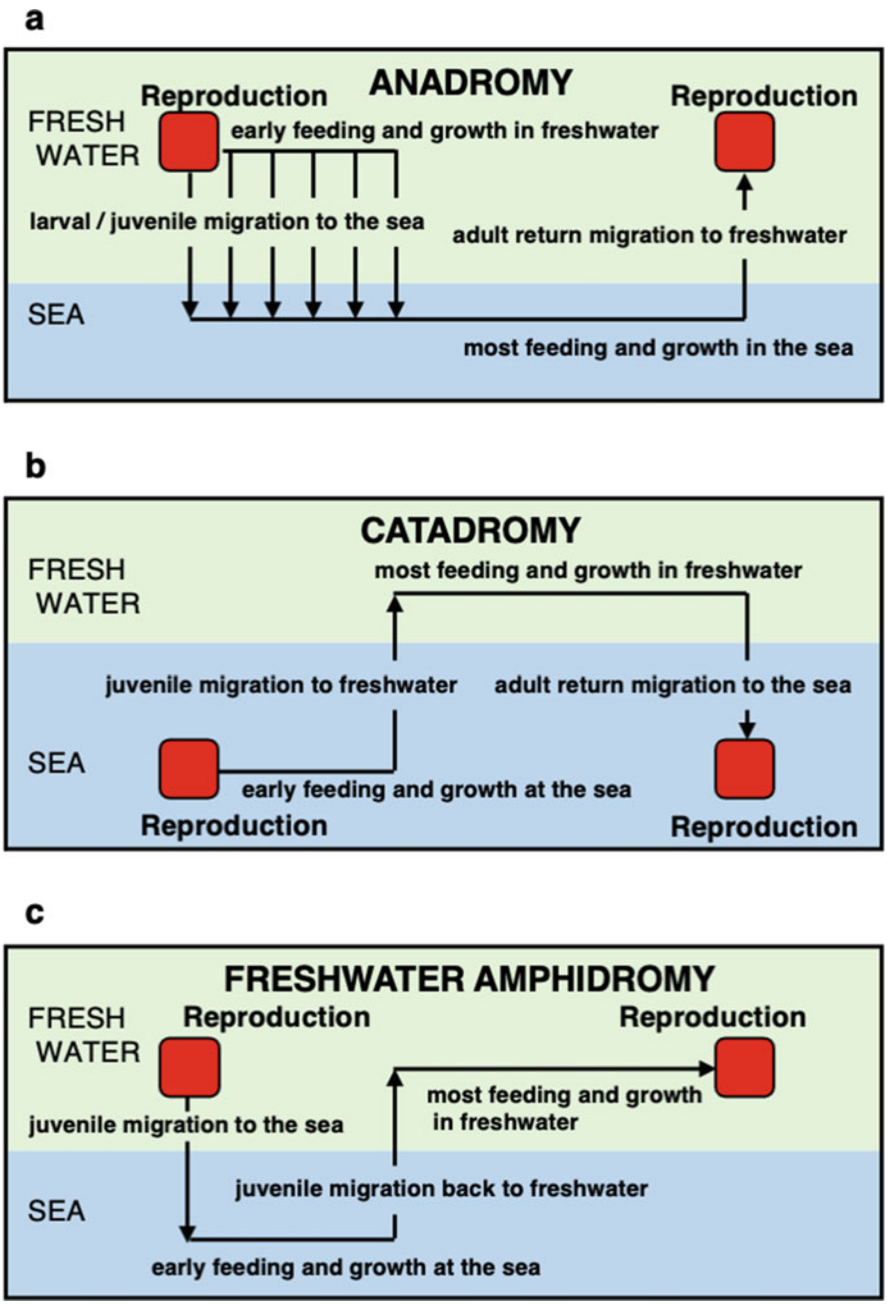

Fig. 13.3 The three different types of diadromous migrations: (**a**) anadromy, (**b**) catadromy, and (**c**) freshwater amphidromy. (Redrawn from McDowall 1997, 2009a)

the principal feeding and reproductive biome is the same, but the larvae use primarily coastal marine waters for early growth (Fig. 13.3c). These types of fishes live in many oceanic tropical areas and some temperate regions (Keith 2003; McDowall 2007; Closs and Warburton 2016). Examples in Japan are Ayu (*Plecoglossus altivelis*), Hangiong Sculpin (*Cottus* *hangiongensis*), Spined Sleeper (*Eleotris oxycephala*), Paradise Goby (*Rhinogobius similis*) and Monk Goby (*Sicyopterus japonicus*). Both freshwater and marine amphidromy exist, as first noted by McDowall (1988). However, little attention has been given to marine amphidromy, which consists of Flathead Gray Mullet (*Mugil cephalus*).

13.3 Migration Diversity of Fishes in Japan

13.3.1 Oceanodromy

Pacific Bluefin Tuna (Fig. 13.1a) is representative of oceanodromous fishes in the western North Pacific including Japan. Their primary spawning area is in the northwest region of the Philippine Sea, between eastern Taiwan and the Ryukyu Islands in the southern part of Japan (Bayliff 1994; Chen et al. 2006; Tanaka et al. 2006; Kitagawa et al. 2010; Shiao et al. 2010) and their spawning season is from late April to July when the sea surface temperatures are about 26 ± 2 °C, which has been confirmed in rearing experiments (Kimura et al. 2010). In addition, considerably large-scale spawning occurs from July to August in the Sea of Japan (Bayliff 1994; Chen et al. 2006; Tanaka et al. 2007). After being transported by ocean currents such as the Kuroshio Current and the Tsushima Current to Japanese coastal areas at 60–90 days after hatching (Kitagawa et al. 2010), juveniles (<1 year, fork length of 15–60 cm) remain in coastal waters around Japan (Bayliff 1994; Kitagawa et al. 2000). Fujioka et al. (2018) suggest that the seasonal habitat use and movement behavior of juveniles are influenced by the distance of the Kuroshio axis from the coast, and the ultimate drivers are likely variations in oceanographic conditions and prey availability along the southern coast of Japan. Many juveniles swim east in their first or second year, a distance of approximately 8000 km, and reside in the eastern Pacific for several years (Boustany et al. 2010; Madigan et al. 2018). From the ages 3–7, many individuals of Pacific Bluefin Tuna return to the west and by age 7 or older, most individuals have recently migrated from the eastern Pacific (Tawa et al. 2017). These data suggest that most juveniles migrate eastward while feeding and then they eventually return to the west to spawn. This species also migrates to the northern tip of Hokkaido in the west or Vancouver Island in the east, where there are low water temperatures. They have a body adapted to high-speed swimming and a mechanism to keep high body temperature (Graham and Dickson 2001) to migrate in the North Pacific. It is interesting that the spawning area is small compared to large area for growth habitat.

As mentioned previously, several important fisheries species in Japan spawn in southern areas of Japan and then migrate northward for feeding and growth (Yatsu 2019). However, the distances and patterns of migration of these species such as Pacific Saury (Suyama et al. 2012; Fuji et al. 2021) and Chub Mackerel (*Scomber japonicus*) (Kanamori et al. 2019) are much shorter and likely more variable than those of Pacific Bluefin Tuna and other large pelagic fishes. Yellowtail (*Seriola quinqueradiata*) spawn in a wide area from about Okinawa to northern Kyushu, and the juveniles spread out north all the way to Hokkaido, before migrating back south for spawning (Tan et al. 2012).

13.3.2 Potamodromy

Japan is an island country, so, most rivers in Japan are shorter and steeper than rivers on the Eurasian, African and North and South American continents. There are few rivers in Japan that become wide and flow slowly in lower reaches like large rivers on continents, but the maximum widths of the landmasses of Japan are only a few hundred kilometers and no river drainages in Japan exceed 400 km, which is quite short compared to the world's longest rivers exceeding 1400 km (Yoshimura et al. 2005). As a result of this, there are no dynamic potamodromous fishes that make large-scale migrations within freshwater, although there are smaller-scale migrations made by some native fishes as described below.

For example, Pale Chub (*Opsariichthys platypus*) (Fig. 13.1b) have a small-scale migration, that may be included within potamodromous fishes. Their hatched larvae drift downstream with the river flow and then tend to swim upstream when they reach the immature stage. Silver Carp (*Hypophthalmichthys molitrix*) are an invasive alien species that is an example of a potamodromous fish living in Japan. This species mainly inhabits Lake Kasumigaura and Kitaura in Ibaraki Prefecture. Adults swim upstream more than 100 km in the Tone-gawa River from May to July during the spawning season and they gather at a river area near Kuki City for spawning. It is possible that their timing of spawning is related to seasonal heavy rain and strong river flow.

Lake Biwa, the largest lake in the Japanese Archipelago, has a geological history of at least 4 million years. This long time-scale has enabled fishes to adapt to this unique lacustrine environment with some small rivers flowing into the lake. Hosoya (2020) overviews the migratory fishes and the unique characteristics of Lake Biwa, which includes 117 in-flowing rivers, channels leading from the lake to rice paddies, and a connection to the Pacific Ocean through an outlet river, the Yodo-gawa River. Hosoya's analysis found that the migratory patterns of the fish species of the lake could be separated into eight migration types (A–H) in Lake Biwa and adjacent waters. Fishes classified as Type A are the most specialized as nonmigrants by remaining in the main lake, although some cyprinids or loaches migrate for reproduction from Lake Biwa to its much smaller associated lakes, scattered along the coasts of the main lake. Type B is composed of pelagic fishes in the lake: cyprinids endemic to the lake, Gengorou Crucian Carp (*Carassius cuvieri*) and Biwa Moroko Gudgeon (*Gnathopogon caerulescens*). Type C is represented by two shoreline or benthic carp species: Carp (*Cyprinus carpio*) and Nigoro Crucian Carp (*Carassius buergeri grandoculis*). Type D is composed of fishes migrating into paddy fields through channels: Swamp Moroko Gudgeon (*Gnathopogon elongatus elongatus*) and Kissing Loach (*Parabotia curtus*). Type E is composed of fishes migrating from the lake into inlet rivers: Biwa Salmon (*Oncorhynchus* sp.), Piscivorous Chub (*Opsariichthys uncirostris uncirostris*) and Japanese Amphidromous Sculpin (*Cottus reinii*). Type F represents a diadromous migration and includes the sole catadromous migrant (Japanese Eel) and the anadromous Satsuki-masu Salmon (*Oncorhynchus masou ishikawae*) (Fig. 13.1c). Type G fishes are general residents in the smaller associated lakes while Type H fishes are those localized in the Yasu-gawa River that always remain or perform potamodromous migrations seasonally within the riverine areas.

In addition to these species, Lake Biwa has a landlocked population of Ayu. As described below, Ayu is a type of amphidromous fish, but in Lake Biwa they are a landlocked form, so their migrations are performed only in freshwater. Tsukamoto et al. (1987) studied the life history details of the Lake Biwa ayu that migrate from the lake to spawn in inlet rivers.

13.3.3 Anadromy

There are several diadromous species of salmons found in Japanese waters, with Masu Salmon (*Oncorhynchus masou*), Japanese Chum Salmon (*Oncorhynchus keta*) and Pink Salmon (*Oncorhynchus gorbuscha*) also being produced in hatcheries for stock enhancement (Morita et al. 2006; Morita 2014). Pink Salmon mostly spawn in the rivers along the northern coast of Hokkaido (Saito et al. 2016) with a short freshwater period before their oceanic feeding migrations, but Masu Salmon have more varieties in their life history types, with the presence of both migratory and non-migratory forms (Munakata 2012).

Japanese Chum Salmon is a representative of the anadromous fishes in Japan. They shift their marine distribution depending on the life stage and season (Seeb et al. 2004; Urawa 2015). Their juveniles go to the sea during the spring snowmelting. After that, they form schools and live in the coastal area near the estuary from 1 to 3 months. During this time, their ability to swim and catch food increases. They migrate to the

Okhotsk Sea in the early summer and stay in the Okhotsk Sea. With the decrease of ocean surface temperatures in November, they move to the western part of the North Pacific Ocean where they are distributed in a narrow area during the first winter. In the next spring, the young individuals (ocean age 1) migrate to the Bering Sea, which is the most suitable place for growth. In the late fall, they migrate southeast from the Bering Sea to the Gulf of Alaska, where they overwinter. After that, they go back and forth between the Bering Sea in the spring and the Gulf of Alaska in the winter. They become mature on average at age 4 in the Bering Sea. It has also been recently found that the Bering Sea shelf appears to play an important role for the growth of the later stage Japanese Chum Salmon (Matsubayashi et al. 2020). During their last summer in the Bering Sea, mature individuals begin to migrate south along the Kuril Islands from the Bering Sea. From September to December, they are known to return to their natal rivers on the coast of Japan to spawn. They enter freshwater during an advanced stage of sexual development and spawning occurs almost immediately. Males and females die after spawning.

Each anadromous species in Japan likely has slightly different life history migration patterns, but a lesser-known at least partial anadromous life history has been found to occur in Sakhalin Taimen, which is present in northern Hokkaido. This fish has been caught at sea or in freshwater, and may include both freshwater and migratory contingents based on otolith Sr:Ca studies (Arai et al. 2004; Suzuki et al. 2011; Zimmerman et al. 2011). Another anadromous species in Hokkaido is Arctic Lamprey, that is a circumpolar species in which the juveniles go out to sea and then migrate back to rivers to reproduce (Clemens et al. 2020), such as in the Shubuto-gawa River in southwest Hokkaido (Miyazaki et al. 2013). There are also at least two species of anadromous sturgeon that may have historically entered freshwater in northern Japan for spawning. The extinct Sakhalin Sturgeon (*Acipenser mikadoi*) historically migrated into freshwater in Japan including the Ishikari River in central Hokkaido and the Teshio-gawa River in northwestern Hokkaido (Shmigirilov et al. 2007). That species and the two other species in the region, Amur Sturgeon (*Acipenser schrenckii*) and Kaluga (*Huso dauricus*) have been collected in the seas off Hokkaido, but native spawning populations of sturgeon in Japan may be extinct (Omoto et al. 2004).

Japanese Dace (*Pseudaspius hakonensis*), exhibit intraspecific variation in life history, including fluvial, lacustrine, and anadoromy types. This species occurs in rivers, lakes, and river mouths to coastal areas throughout the range of the genus, and possesses high osmoregulatory capability (Sakai 1995). *Pseudaspius brandtii* has an anadromous lifestyle, and includes two subspecies: Jusan Dace (*Pseudaspius brandtii brandtii*) and Maruta Dace (*Pseudaspius brandtii maruta*) (Sakai and Amano 2014). The genus *Pseudaspius* (including hitherto *Tribolodon*) was re-described as valid on the basis of molecular phylogenies and morphological characters (Sakai et al. 2020).

13.3.4 Catadromy

The Japanese Eel (Fig. 13.1d) is a representative of catadromous fishes in Japan, although the Indo-Pacific Eel (*Anguilla marmorata*) is found in freshwaters of the southern parts of Japan (e.g., Itakura and Wakiya 2020) and migrates to a similar offshore area as the Japanese Eel to reproduce. The spawning area of the Japanese Eel was discovered to be in the North Equatorial Current (NEC) of the western North Pacific (Tsukamoto 1992) and spawning was found to occur at the latitudes of the southern part of the West Mariana Ridge by collecting the newly hatched larvae called preleptocephali (Tsukamoto 2006), spawning-condition adults (Chow et al. 2009; Kurogi et al. 2011) and fertilized eggs (Tsukamoto et al. 2011; Aoyama et al. 2014; Takeuchi et al. 2021). The leptocephali are first carried westward toward the Philippines by the NEC. They are then transferred into the Kuroshio

Current traveling northwards to the east of the Philippines, eventually reaching Taiwan, China, South Korea and Japan in East Asia. As they approach the continental shelf, the leptocephali turn into transparent glass eels. Then, when they reach river estuaries, the glass eels start to swim upstream or stop their migration. They can settle in estuaries, rivers and lakes, where they stay for several years to several decades. During their yellow eel growth phase, the Japanese Eel in Japan and other temperate anguillid eels have been found to move back and forth between the estuaries and freshwater (Tsukamoto and Arai 2001; Daverat et al. 2006; Yokouchi et al. 2012), but these are movements, not migrations.

Once grown to a sufficient size, yellow eels turn into silver eels that develop enlarged eyes and their bodies turn dark brown with a metallic sheen, which are adaptations for their oceanic migrations (Tsukamoto 2009). They migrate downstream to estuaries during fall mostly during rainy or high water-flow periods, and the timing of migration out of coastal waters may also be related to environmental conditions (Sudo et al. 2017). From there, they migrate into the open sea and have been found to perform diel vertical migration behaviors during their spawning migration (Manabe et al. 2011; Chow et al. 2015; Higuchi et al. 2018, 2021). When the maturing eels come back to their spawning areas, they spawn in the darkness of the night in new moon (Higuchi et al. 2020), bringing their lives to an end after migrating thousands of kilometers as both adults and larvae.

In contrast, there are two species of sculpins present in southern Japan and nearby regions that are considered to be catadromous, which are Fourspine Sculpin and Roughskin Sculpin (Takeshita et al. 2004); but their spawning migrations are of a much smaller scale because they only migrate downstream in rivers to spawn in benthic nests in the lower reaches of estuaries (Takeshita et al. 1999; Onikura et al. 2002). The larvae of both species appear to remain near the river mouths before migrating upstream into freshwater for juvenile growth (Harada et al. 1999; Kinoshita et al. 1999; Onikura et al. 1999; Islam et al. 2007).

13.3.5 Amphidromy

Amphidromous fishes are probably the least widely recognized subcategory of diadromy, but they have been increasingly realized to represent a clearly distinct pattern of migration. They move between marine and freshwater at certain phases of their lives, but the final migration occurs long before maturation and spawning occur (Fig. 13.3c). The main distinction between freshwater amphidromy and anadromy is that the migration into freshwater usually occurs in the juvenile stage in freshwater amphidromy and in the adult stage in anadoromy (McDowall 2007).

Ayu (Fig. 13.1e) are the most well-known representative of amphidromous fishes in Japan because it is an important food fish. This species is an annual fish, with a 1-year lifespan. Spawning occurs during fall to early winter, and the adults spawn along river shorelines above pebbles at night. Eggs are around 1 mm in size and adhere to the sand or pebbles for 14–20 days before hatching. After hatching, the larvae are 6 mm in length and they drift with the water current out to sea. They remain at sea, especially in the surf zone during winter for about 4–6 months where they feed on plankton (Murase et al. 2019). Murase et al. (2020) suggested that juvenile Ayu select coastal habitats as they develop swimming ability and that riverine estuary/exposed beach, embayed beach, and lagoon estuary habitats function as a corridor, primary nursery, and possible foraging areas, respectively. In springtime, juveniles swim in schools back into rivers. After the young move upstream to the middle reaches of rivers, they feed on algae until they become reproductively mature. Those that are ready to spawn (about 20 cm in total length) move downstream to the lower reaches of the river in fall and spawn from one to several times (Shimizu et al. 2007). They die after spawning, but some individuals spawn 2 years in succession.

The other amphidromous fishes in Japan include several species of sculpins of the genus *Cottus*. These species, including Ainu Amphidromous Sculpin (*Cottus amblystomopsis*), Hangiong Sculpin, Japanese

Amphidromous Sculpin (small egg type) (*Cottus reinii*) and Japanese Amphidromous Sculpin (medium-sized egg type) (*Cottus pollux*) (Goto 1990; Shimizu et al. 1994; Goto and Arai 2003, 2006; Yokoyama and Goto 2005; Tsukagoshi et al. 2011), produce many small eggs (Goto 2001), and they generally spawn on gravel substrates in the lower reaches of rivers. The newly hatched larvae swim to the river surface (a phototactic response) while drifting downstream to the estuary (Goto 1981, 1990), which may contribute to higher survival of the larvae (Goto 1988, 1993). The pelagic larvae spend about 2 weeks to 1 month in coastal marine areas before migrating to river mouths where they settle on the riverbed and grow until they mature as adults.

Monk Goby (*Sicyopterus japonicus*) (Fig. 13.1f) are distributed from Taiwan to Fukushima Prefecture, Japan (Akihito et al. 2000; Iguchi et al. 2005), almost exclusively in areas along the powerful Kuroshio Current. The late-stage larvae recruit in spring and quickly metamorphose into young-of-the-year/juveniles immediately after recruitment to the estuary (Dôtu and Mito 1955; Iida et al. 2008, 2013). Then they migrate upstream to the middle river reaches where they graze on algae on stones (Dôtu and Mito 1955) from summer to fall for growth, but they do not reproduce during the year of recruitment. This species can climb above the water line on any wet surface using their sucker-like pelvic fins and grasping mouth (Fukui 1979). This goby in the Ota-gawa River experiences low winter water temperature from December to March that limits their activity while they have low condition factor (Iida et al. 2013). During their oceanic larval duration, some individuals from throughout the species range seem to disperse widely along the Kuroshio Current from Taiwan to northern Japan (Watanabe et al. 2006; Iida et al. 2010).

An interesting aspect of amphidromous fishes in Japan is that they are present all the way from the temperate zone in the north to the subtropical zone of the oceanic islands in the south. These types of fishes are also widespread in regions of the southern hemisphere with various degree oceanic dependency (Watanabe et al. 2014). Some regions include multiple species and a variety of particularly gobies can be found in a single river. This is also true in Japan, such as on Ishigaki-jima and Iriomote-jima islands where there are 40 and 48 species of diadromous fishes, respectively (Yoshigo 2014); and a recent study of the Arida-gawa River on the Pacific coast of the Kii Peninsula of southern Honshu found the presence of 14 possibly amphidromous species and compared the life history characteristics of six of the more abundant species (Tanaka et al. 2020).

13.4 Diversity of Migratory Fishes in Japan

Migratory fishes are distributed worldwide, but as is overviewed in this book, Japan represents a unique combination of geographic factors that have resulted from its landmasses being surrounded by the sea and its archipelago of islands stretching across 25° of latitude, with the climate environments ranging from subtropical to purely temperate. Mainland Japan (Hokkaido, Honshu, Shikoku and Kyushu) is the only group of large islands that occur along the path of a western boundary current (Imawaki et al. 2013), so these types of factors and the geomorphology of the rivers and lakes of Japan have likely helped to shape the characteristics and diversity of migratory fishes in and around Japan. Since Japan is surrounded by the sea, the migrations of the oceanodromous, anadromous and catadromous fishes found there can occur on a large scale in the Pacific Ocean. The migratory species that use freshwater for at least part of their life histories can range from purely tropical species to totally temperate species that experience near-arctic conditions during winter if they remain in freshwater.

The previous sections showed that Japan has a diverse fauna of migratory fishes, which remarkably includes all the different categories of migrations. While beyond the scope of this chapter to clearly evaluate this possibility, Japan may likely have the greatest diversity of native migratory species in the world. There are more than 200 species of freshwater fishes in Japan (Yuma et al. 1998) in its rivers and freshwater lakes

(Yoshimura et al. 2005). This number of species is relatively high compared to that of other large island countries, but is much lower than that of the major regions of freshwater fish diversity such as North America and the Amazon basin. However, about 37% of the freshwater fish species in Japan are diadromous (Yuma et al. 1998).

Japan has a diverse fauna of tropical amphidromous fishes such as gobies that live in places including Iriomote-jima (Suzuki and Mori 2016) and Okinawa-jima islands (Yoshigo 2014), and temperate gobies and Ayu live in the northern areas of the Pacific coast of the main islands (Harada et al. 2002; Iguchi 1993). Anadromous salmon species live in northern Honshu and Hokkaido, and migrate widely in the North Pacific (Morita 2014). Two species of catadromous anguillid eels overlap in their distributions that range from the southernmost islands of Japan to northern Honshu and spawn offshore in the North Equatorial Current (Kumai et al. 2020). There are also a variety of oceanodromous fishes that have migration loops of various distances between their southern spawning areas and northern feeding areas along both sides of Japan (Yatsu 2019). Although there are no potamodromous species with large-scale freshwater migration, Lake Biwa has resulted in the evolution of 16 endemic species (Tabata et al. 2016), several of which are potadromous species (Hosoya 2020). There are also landlocked forms of various diadromous taxa such as Ayu (Tsukamoto et al. 1987) that migrate between spawning and feeding areas.

One important factor in the species compositions and diversity of migratory species across the Japanese Archipelago is the transport of warm water of the Kuroshio and Tsushima currents to higher latitudes. This characteristic is clearly a factor that has influenced the life histories of many of the major marine fisheries species such as Pacific Bluefin Tuna and Yellowtail that spawn in the southern Kuroshio region (Kitagawa et al. 2010; Tan et al. 2012), but use more northern regions for feeding and growth. The flow of warm water to the north is also likely to be deeply related to the history of colonization and diversification of diadromous fishes of the Japanese Archipelago and the success of the larvae that use coastal waters for larval growth. One of the characteristics of migratory fishes in Japan is the abundance and diversity of freshwater amphidromous fishes. Approximately 68 amphidromous fish species (nine families and 30 genera) have been found in Japan (Tanaka et al. 2020), which represent approximately 15% of fishes recorded in freshwater environment (River Environment Database: http://www.nilim.go.jp/lab/fbg/ksnkankyo/).

Similar diadromous species are found in other regions of the world, but only one of the amphidromous fish species found in Japan (Red Tailed Parrot Goby, *Sicyopterus lagocephalus*) is widely distributed and found across the Indo-Pacific (Watson et al. 2000; Keith et al. 2005; Lord et al. 2012). The catadromous eel, *Anguilla marmorata*, is similarly widespread, and has several different spawning populations (North Pacific population members recruit to Japan: Ishikawa et al. 2004; Minegishi et al. 2008; Watanabe et al. 2008, 2009). The two main islands of New Zealand are somewhat similar to mainland Japan except for the proximity to the western boundary currents of each ocean basin. New Zealand has two widespread species of catadromous anguillid eels, but amphidromous galaxiids (southern circum-temperate Osmeriformes, family not found in Japan) appear to occupy a similar niche compared to the amphidromous gobies in other regions (McDowall 1988, 2010a; Waters et al. 2000). But New Zealand does not have any native anadromous salmon species and may not have similarly large populations of oceanodromous fishes in the surrounding marine environment compared to those that use the Kuroshio Current and Kuroshio Extension near Japan. The nearby more-tropical large island of New Caledonia also has a diverse fauna of catadromous eels and amphidromous gobies (Keith et al. 2014), as does Madagascar (Fricke et al. 2018), but the diversity migratory fishes on these large islands is similar or lower than in Japan.

Interestingly, because of its island nature and range from tropical to temperate latitudes, Japan seems to have the ideal characteristics for all three groups of diadromous fishes. Small steep rivers such as those found in some areas of Japan, assist the downstream migration of the larvae of Ayu, galaxiids, sculpins and gobiid fishes, which prevents them from exhaustion of larval energy reserves before feeding can begin in coastal waters and that reduces the period of exposure to predators (Iguchi and Mizuno 1990; Tsukamoto 1991; McDowall 2004, 2007, 2009b, 2010b; Watanabe et al. 2014). Therefore, it is likely that the similar environmental features found in Japan and other regions have promoted the independent evolution of amphidromous life histories in both temperate and tropical islands (Goto et al. 2015).

The impact of humans on the aquatic habitats including constructions of blockages in rivers has been causing serious problems for migratory fishes in Japan because the diadromous migrations of fishes depend on the connectivity of freshwater and marine environments without blockages to upstream or downstream migration (Drouineau et al. 2018; Clemens et al. 2020). Therefore, the success of the diadromous life cycle depends on maintaining rivers and estuaries to allow movements between both habitats. It is also necessary to understand the migrations of these fish species and to develop management and restoration strategies to protect the health of the unique fauna of migratory fishes into the future.

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14

Adaptive Phenotypic Divergence in Fishes of Japan: Potential Model Systems for Ecological and Evolutionary Genomics

Tomoyuki Kokita

Abstract

Recent progress in ecological and evolutionary genomics has provided insight into why and how so many phenotypes and species evolved in the wild. Teleost fishes harbor extraordinary diversity both in phenotypes and species, and therefore have potential as model vertebrate systems for exploring the patterns, processes, and mechanisms of adaptation, phenotypic diversification, ecological speciation, and adaptive radiation at the gene and genome levels. Thus, ecological and evolutionary genomics are of increasing importance in modern natural history studies, however, these lines of research are limited to a few model systems such as threespine stickleback and cichlids. The advent of next-generation DNA sequencing technologies, the growing use of omics approaches, and the spread of genome-editing technology could answer fundamental questions using ecologically and evolutionarily fascinating non-model fishes. The Japanese Archipelago stretches a considerable distance from north to south and is bounded by sea on all sides. In addition, there are a variety of freshwater environments in Japan. Japanese waters harbor a great diversity of fishes, which have long aroused the interest of fish biologists because of their extraordinary species diversification and phenotypic diversity of ecologically relevant traits. This chapter describes several model systems in Japanese fishes suitable for exploring adaptive phenotypic diversification and speciation using ecological and evolutionary genomics approaches and reviewing the pattern of phenotypic divergence in each system.

Keywords

Adaptive evolution · Ecological speciation · Adaptive radiation · Stickleback · Goby · Gudgeon · Medaka · Bitterling

14.1 Introduction

Natural populations inhabiting different ecological environments diverge in a variety of phenotypic traits that influence survival and reproduction (Endler 1986). Such adaptive phenotypic divergence can initiate reproductive isolation, suggesting that it is the first sign of ecological speciation (Schluter 2000; Nosil 2012). Thus, examination of adaptive phenotypic divergence in response to environmental conditions is a key topic in ecology and evolutionary biology. However, documenting adaptive divergence is a challenge in evolutionary ecology and requires carefully designed experiments that measure components of fitness for individuals

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from different populations across a range of environments (Endler 1986). Modern integrated research has uncovered the genetic and genomic bases underlying phenotypic divergence, which are key to understanding how organisms adapt to changing environments in the wild (Stapley et al. 2010; Elmer and Meyer 2011; Seehausen et al. 2014). Identifying the genomic regions that have been subject to natural selection will provide insight into the adaptive evolutionary change of organisms. Thus, ecological and evolutionary genomics are of increasing importance in modern natural history studies (Van Straalen and Roelofs 2012; Orsini et al. 2013).

Teleost fishes show striking diversity in ecologically relevant traits, and this extraordinary diversity has attracted considerable interest from researchers across several biological disciplines, especially ecology and evolutionary biology (Volff 2005; Smith and Wootton 2016). In general, phenotypic diversification among geographical populations within species or between closely related species is a rigorous framework for testing the role of natural selection in phenotypic evolution (Elmer and Meyer 2011; Byers et al. 2017). Two fish groups harboring broad phenotypic variation coupled with recent divergence are threespine stickleback fishes in marine, brackish, and freshwater habitats of the Northern Hemisphere (Bell and Foster 1994; McKinnon and Rundle 2002; Östlund-Nilsson et al. 2006) and cichlid fishes in tropical lakes of Africa and Central America (Seehausen 2006; Henning and Meyer 2014). These systems experienced adaptive radiation and have yielded insight not only into how natural selection shapes evolutionary diversification, but also how the influence of natural selection can be constrained. Another model system, Mexican Tetra (*Astyanax mexicanus*), is an ideal target for understanding the evolutionary mechanisms underlying adaptation to extreme environments (Keene et al. 2015). For these systems, genetic mapping, genome-wide analyses, and genome projects have flourished in recent decades (e.g., Jones et al. 2012; Brawand et al. 2014; McGaugh et al. 2014; Peichel and Marques 2017). New rapidly advancing technologies, including next-generation DNA sequencing and genome editing, enable researchers to study ecologically and evolutionarily interesting non-model lineages from genetic and genomic standpoints (Ellegren 2014; Matz 2018; Burnett et al. 2020). Therefore, studies of ecological and evolutionary genomics using these non-model fishes could provide insight into adaptation, phenotypic diversification, and speciation in more general framework.

The Japanese Archipelago stretches a considerable distance from north to south (approximately 3000 km) and is bounded by seawater on all sides. In addition, there are a variety of freshwater environments in Japan. Therefore, Japanese waters harbor a great diversity of fishes (Fujikura et al. 2010; Watanabe et al. 2016), which have attracted the attention of fish biologists because of their extraordinary species diversification and phenotypic diversity of ecologically relevant traits (e.g., Mizuno and Goto 1987; Nakazono and Kuwamura 1987; Goto and Maekawa 1989). Japan's geography allows for great diversity in physicochemical environmental conditions and ecosystems on both large and small geographical scales, indicating an important role for adaptive phenotypic divergence in fishes under different selective regimes. As mentioned above, studying closely related lineages is an excellent means of understanding the factors promoting and constraining adaptive phenotypic evolution. The typical method of developing evolutionary inferences for a group of organisms is to measure phenotypic variation and relate it to various geographical and environmental factors, although phenotypic variation in the wild may not accurately reflect genotypic variation caused by differing selective regimes, because both genetic and environmental factors contribute to phenotypic variance (Conover et al. 2009).

This chapter describes several model systems in Japanese fishes suitable for exploring adaptive phenotypic diversification and speciation using an ecological and evolutionary genomics approach, reviewing the pattern of phenotypic divergence in each system. This chapter focuses on five topics: phenotypic endemism in the Sea of Japan; phenotypic adaptation to the Lake Biwa environment; freshwater threespine stickleback in

Japanese spring-fed habitats; phenotypic divergence among populations of medaka, a model fish from Japan; and highly diverged reproductive traits in two Japanese fish systems. In this chapter, I provide an overview of the current understanding of phenotypic divergence in these systems and propose future directions in phenotypic evolutionary studies.

14.2 Phenotypic Endemism in the Sea of Japan

Physical barriers to gene flow that theoretically prevent genetic divergence among populations are less common in marine environments compared to terrestrial and freshwater environments (Puebla 2009; Bernardi 2013; Bowen et al. 2013). However, molecular phylogeographic studies have revealed that geographical isolation by low sea levels associated with Pleistocene glacial cycles has often resulted in allopatric genetic divergence, even in marine environments, although absolute allopatric barriers have disappeared at present (e.g., Maggs et al. 2008; Wilson and Eigenmann Veraguth 2010; Ni et al. 2014; DiBattista et al. 2016). In general, the Pleistocene glacial episodes caused extinctions and repeated changes in the ranges of those taxa that survived. These range shifts likely involved considerable demographic change and have provided opportunities for phenotypic adaptations to the associated severe environments (Davis and Shaw 2001; Davis et al. 2005). A historically enclosed sea basin therefore might have been an evolutionary driver of adaptive population divergence, thereby promoting high phenotypic endemism. However, few studies have explored the divergence of fitness-related phenotypic traits between isolated seas and the surrounding marine areas during the Pleistocene glacial periods.

Divergent allopatric lineages have appeared inside and outside of the Sea of Japan, providing a valuable opportunity to explore marine phenotypic evolution and speciation in relation to Pleistocene glacial isolation. Environments in the Sea of Japan, a young marginal basin located between Japan and the Asian continent, connected to the Pacific Ocean and two neighboring marginal seas in the present day, have changed markedly in relation to shifts in sea level as a result of repeated glaciations (Chinzei 1991; Oba et al. 1991; Gorbarenko and Southon 2000). The Sea of Japan, which was almost isolated from the surrounding seas multiple times during the Pleistocene, has experienced extreme environmental conditions, being characterized by low salinity and low temperature regimes during the Last Glacial Maximum. The Sea of Japan may be a potential hotspot of lineage-specific adaptation, especially for coastal and diadromous species inhabiting shallow areas. Here, I refer to two systems studied in the context of divergence in ecologically relevant traits between the Sea of Japan and the surrounding ocean and seas.

Perhaps the most famous example of this phenomenon is two divergent lineages—namely, the Sea of Japan lineage (SJ lineage) and the Pacific Ocean lineage (PO lineage)—of the marine (anadromous) threespine stickleback (*Gasterosteus aculeatus*) around the Japanese Archipelago (Higuchi and Goto 1996; Kitano et al. 2007; Fig. 14.1). The derived SJ lineage has been described as the taxonomically separate species *Gasterosteus nipponicus* based on morphological differences (Higuchi et al. 2014), and the presence of reproductive isolation in sympatry supports the notion that the two taxa are distinct species (Kitano et al. 2009). Threespine stickleback has been described as a super-model organism, and is used in research on adaptation and speciation in the wild with modern genetic and genomic techniques (Gibson 2005; Barber and Nettleship 2010). This fish is distributed in cold freshwater and marine habitats in North America and from Northern Europe to East Asia (Bell and Foster 1994), and *G. nipponicus* is suggested to have diverged from the ancestral PO lineage of *G. aculeatus* during periods of Pleistocene geographical isolation between the Sea of Japan and the Pacific Ocean (Higuchi and Goto 1996; Kitano et al. 2007). In present-day Japan, marine *G. aculeatus* and *G. nipponicus* are mainly found along the coasts of the Pacific Ocean and the seas of Japan and Okhotsk,

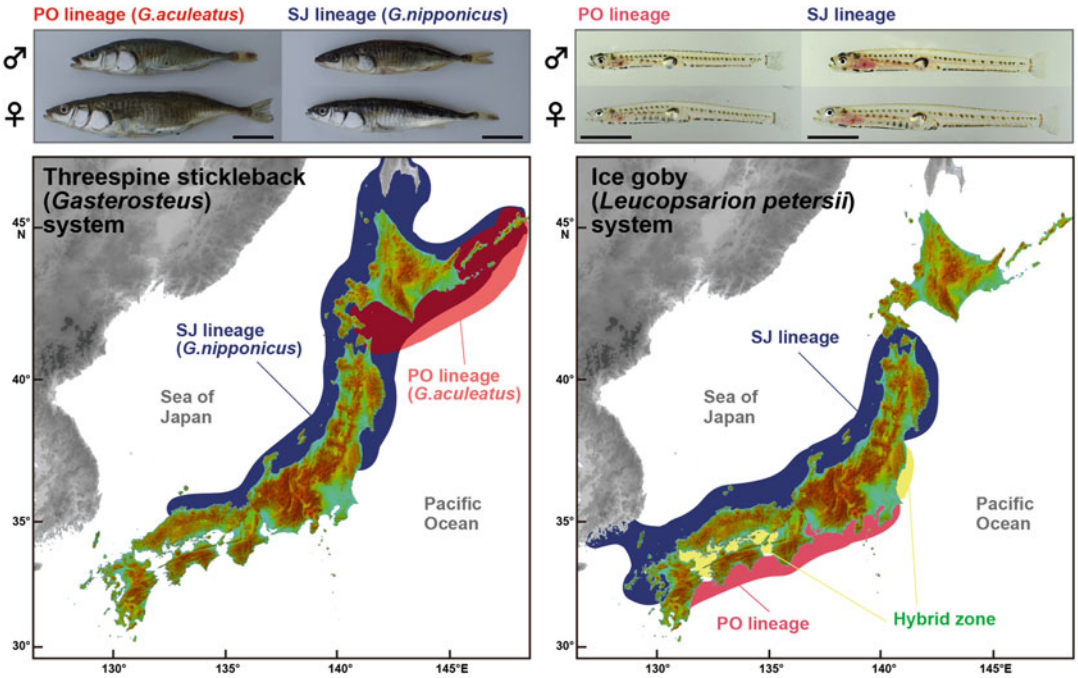

Fig. 14.1 Present day distribution of two phenotypically and genetically distinct lineages of the marine threespine stickleback (Photo by J. Kitano) and the ice goby around the Japanese Archipelago. *Scale bar* = 1 cm. (These elevation maps were used with permission from the Geospatial Information Authority of Japan, http://www.gsi.go.jp/)

respectively. The latter lineage is endemic to the Sea of Japan and the Sea of Okhotsk. A recent study using whole-genome sequencing data indicated that the two lineages split approximately 0.68–1 million years ago (Mya) but have continued to exchange genes at a low rate throughout divergence (Ravinet et al. 2018). Detailed ecological and genetic analyses of a population within a secondary contact zone of the two lineages—that is, a region of sympatry (see Fig. 14.1)—elucidated that the two lineages are reproductively isolated in the wild (Kitano et al. 2009). Thus, the speciation process of this system is nearly complete, and the two lineages are a sister-species pair with accumulated genetic differentiation.

Ecologically relevant traits, including many ecomorphological, life history, and behavioral traits, are diverged between the two species, although whether some of these diverged phenotypes have a heritable component is unclear. First, among ecomorphological traits, *G. nipponicus* has a smaller body size and more slender body shape than *G. aculeatus* (see Kitano et al. 2007, 2009). In addition, there is a clear difference in lateral plate pattern between the two species, and in *G. nipponicus*, the heights of the lateral plates decrease dramatically from the trunk (above the anus) to the caudal peduncle (Kitano et al. 2007; Higuchi et al. 2014). The lateral plate pattern of threespine stickleback is a prominent example of morphological traits under natural selection (see Sect. 14.4). Furthermore, *G. nipponicus* has more gill rakers, a good indicator of trophic ecology (Kitano et al. 2007). In general, fishes with a more planktivorous feeding mode have more gill rakers than those that exploit benthic prey (Berner et al. 2008; Kahilainen et al. 2011). In fact, divergence in diet and foraging behavior between the two species is confirmed; *G. aculeatus* consumes more benthic prey and demonstrates improved prey handling, which is consistent with divergence in this foraging morphology (Ravinet et al. 2014). Second, among life history and physiological traits, *G. nipponicus* produces many smaller-sized eggs compared to *G. aculeatus*, suggesting the existence of a trade-off between clutch and egg size in this species pair, which is an important component of life history strategy (Kume 2011). In addition, in the sympatric area, the two species have diverged in their breeding habitats by using different salinity regimes within a single watershed, suggesting that they have evolved different reproductive characteristics in response to the differing salinities and properties of their environments (Kitano et al. 2009; Kume et al. 2010). The two species also differ in their ability to survive in freshwater environments—*G. nipponicus* has lower freshwater tolerance (Ishikawa et al. 2016). Third, there is divergence in some reproduction-related behaviors between the two species (Kitano et al. 2007, 2008b). The divergence in male courtship behavior is noteworthy; *G. aculeatus* performs the zigzag dance that has become a synonym for the threespine stickleback, whereas *G. nipponicus* performs the rolling dance. In addition, dorsal pricking display during male courtship behavior is greatly exaggerated in *G. nipponicus* but relatively weak in *G. aculeatus*. The reproductive isolation between these species consists both of multiple premating and postmating isolating barriers, including eco-geographical isolation (breeding sites), seasonal isolation (the timing of breeding), sexual isolation resulting from divergence in male body size and male dorsal pricking behavior, ecological selection against migrants, hybrid male sterility, and ecological selection against hybrids (Kume et al. 2005, 2010; Kitano et al. 2007, 2009; Yoshida et al. 2019). Kitano et al. (2009) reported that *G. nipponicus* has a neo-sex chromosome system, which was created by Y-autosome fusion, and this sex-chromosome divergence between the two lineages contributes to the above-mentioned sexual isolation and hybrid male sterility. Thus, *G. nipponicus* evolved several novel phenotypic traits—such as neo-sex chromosomes and courtship behaviors—different from those of *G. aculeatus* in this unique sea basin, thereby contributing to the evolution of a new threespine stickleback.

Although there are many landlocked threespine stickleback populations derived independently from the ancestral marine *G. aculeatus* throughout its distributional range (see Sect. 14.4), no freshwater populations derived from *G. nipponicus* have been reported thus far (Ravinet et al. 2014). Recently, the reason underlying this phenomenon was elucidated. Ishikawa et al. (2019) showed that deficiency in docosahexaenoic acid (DHA), an essential $\omega - 3$ fatty acid, can constrain freshwater colonization by marine fishes, and gene duplications of the fatty acid desaturase gene (*Fads2*), which encodes an enzyme crucial for fatty acid synthesis, increased their ability to synthesize DHA and survive on DHA-deficient diets in freshwater environments. Genomic analyses of both species revealed multiple independent duplications of *Fads2* in *G. aculeatus*, which subsequently colonized and radiated in freshwater habitats, but not in *G. nipponicus*, which failed to colonize. *Gasterosteus nipponicus*, lacking an increased number of *Fads2* gene copies, cannot compensate for the dearth of dietary fatty acids such as DHA in freshwater, thus resulting in no freshwater populations. Thusly, this species pair has already greatly contributed to our knowledge of evolutionary mechanisms of speciation and colonization of new ecological niches in a general framework.

Furthermore, lineage divergence between the Sea of Japan and the Pacific Ocean was found in several anadromous and coastal fish species, including five gobiid fishes *Pterogobius elapoides*, *Pterogobius zonoleucus*, *Leucopsarion petersii*, *Chaenogobius annularis*, and *Chaenogobius gulosus* (reviewed by Hirase 2021). However, these fishes are essentially temperate-water species, and their distribution range differs from that of the marine threespine sticklebacks, which are essentially cold-water species. Although the divergence time between the SJ and PO lineages of these species has not been estimated by whole-genome sequencing, the divergence time estimated by neutral DNA markers appears to be comparable to (or older than) that of the threespine stickleback species pair in Japan (Kokita and Nohara 2011; Hirase and Ikeda 2014; Akihito et al. 2016; Hirase et al. 2016). Among these systems, phenotypic divergence of ecologically relevant traits between the PO and SJ lineages was examined in detail in Ice Goby *L. petersii* (Fig. 14.1). *Leucopsarion petersii* is a paedomorphic bony fish characterized by a larval-like form that includes a slender translucent and scaleless body and has an anadromous life history. Adults ascend to the lower reaches of rivers for reproduction, and newly hatched larvae descend to the marine environments where they grow in coastal waters (Matsui 1986). This annual fish species is distributed widely in shallow coastal areas within the Japanese Archipelago and the southern part of the Korean Peninsula. The SJ and PO lineages are estimated to have diverged during the late-Early to Middle Pleistocene (<1 Mya) (Kokita and Nohara 2011). The SJ lineage of this fish has a larger body size than the PO lineage and the body size divergence has a heritable basis; the SJ lineage had rapid growth rates, partly resulting from a higher innate capacity for food consumption, and consequently evolved toward a larger size (Kokita and Nohara 2011; Kokita et al. 2017). Furthermore, the body size-related traits may be targets of natural selection for the SJ lineage (Kokita et al. 2013). If this is the case, temperature may be an important selective agent of evolution toward larger body size. Modern temperatures of shallow coastal waters are generally lower in the Sea of Japan than along the Pacific coast around the Japanese Archipelago (Fujikura et al. 2010). Also, during the Last Glacial Maximum, the sea was covered by extremely cold water (10 °C colder than today), whereas relatively moderate environmental conditions were maintained on the Pacific coast (Chinzei 1991; Oba et al. 1991; Oba and Murayama 2004). This suggests that the SJ fish were exposed to extremely cool environments during the late Pleistocene. Thus, the SJ lineages have lived under cool conditions in both past and present environments. Therefore, body size-related traits of the SJ lineage may be interpreted as physiological adaptations to lower water temperatures because this fish is essentially a temperate-water species. If so, the SJ lineages of other temperate fishes may show similar patterns, that is, evolution toward a larger body size. Examining the patterns of body size divergence for the other temperate systems mentioned above could provide insight into physiological adaptation in the historically enclosed sea basin.

Although divergence in female mate-choice patterns between the two lineages of the ice goby was detected—SJ females demonstrated preferences for larger and same-lineage males, whereas PO females did not—reproductive isolation between them has not evolved and there are hybrid populations in two secondary contact zones between the PO and SJ lineages (Kokita et al. 2017; Hirase et al. 2020; Fig. 14.1). This situation differs appreciably from that of the Japanese stickleback species pair, although the divergence time appears to be comparable between the ice goby and stickleback systems. In addition, hybrid populations exist in secondary contact zones between the PO and SJ lineages of other systems including *P. elapoides* and *P. zonoleucus* (see Nohara 2009), *C. annularis* (see Hirase et al. 2021), and *C. gulosus* (S. Hirase, unpublished data). Thus, different systems determine the position of a particular diverging pair on the speciation continuum. The Japanese marine threespine stickleback has attained a complete reproductive isolation state, whereas the state of the ice goby falls at the beginning of phenotypic divergence without reproductive isolation. Therefore, the patterns of genetic and phenotypic divergence along the speciation continuum must be examined for other systems. There are numerous unpublished and unexplored examples of allopatric genetic divergence between populations in the Sea of Japan and the surrounding ocean and seas, especially the Pacific Ocean. The Sea of Japan may be a potential hotspot of phenotypic novelty for ecologically important traits in cold- and temperate-water species.

In summary, allopatric divergence inside and outside the Sea of Japan provides an opportunity to understand not only adaptive phenotypic evolution in a marine environment with historical climate change, but also the processes and mechanisms of marine allopatric speciation and the formation of new species. This will be an exciting exploration of convergent evolution in the marine realm.

14.3 Phenotypic Adaptation to the Lake Biwa Environment

Ancient lakes are ideal model systems for exploring the ecological and genetic bases of adaptive phenotypic diversification in the wild (Schön and Martens 2004; Cristescu et al. 2010). In fact, cichlids in the Great Lakes of East Africa (Seehausen 2006; Turner 2007) and sculpins in Lake Baikal (Sherbakov 1999; Goto et al. 2015) are examples of explosive adaptive radiation in ancient lakes. The cichlids are a traditional model system in adaptive radiation research and enable hypotheses on adaptive radiation to be tested at the genomic level (e.g., Malinsky et al. 2018; McGee et al. 2020; Ronco et al. 2021). Lake Biwa, located in central Japan, is a representative ancient lake in East Asia. It is the largest lake in Japan in terms of surface area (670.3 km^2) and volume (27.5 km^3) and its origin dates back at least 4 Mya (Yokoyama 1984; Kawabe 1994). The lake consists primarily of the northern and the southern lake basins, and the northern basin has a large, deep pelagic zone (maximum depth 104 m) and complex littoral zone with various substrate types including sands, pebbles, and rocks (Fig. 14.2). This lake environment started to develop approximately 0.4 Mya (Yokoyama 1984; Kawabe 1994). Lake Biwa is the center of adaptive diversification in freshwater environments of western Japan (Okuda et al. 2014), and this section describes especially suitable fish model systems for ecological and evolutionary genomic studies.

Like other ancient lakes, Lake Biwa harbors many endemic species of a variety of organisms. Although 16 endemic or semi-endemic species/subspecies (hereafter species) of fishes of diverse taxa occur in and around Lake Biwa, including Salmonidae, Cobitidae, Cyprinidae, Siluridae, Gobiidae, and Cottidae, the number of endemic forms is smaller than in other ancient lakes (Okuda et al. 2014). Thus, the fish assemblage of Lake Biwa lacks "species flocks," which are species groups—such as those found in the cichlids of the African Great Lakes or the sculpins of Lake Baikal—generated via explosive adaptive radiation. However, compared with closely related species, most of these endemic species in Lake Biwa evolved distinct phenotypes that are considered the products of adaptations to the habitats of the lake including the extensive pelagic area, deep zone, and littoral rocky area. Tabata et al. (2016) investigated the origins of the endemic fishes of Lake Biwa and inferred the historical demography using a dataset of mitochondrial DNA (mtDNA) sequences from a large number of fish species in and around the lake. Their phylogenetic analysis suggested that some endemic species diverged from their closest relatives earlier than the period in which the present environmental characteristics of the lake started to develop, whereas others diverged more recently. In addition, their historical demographic analysis suggested that population expansion of almost all endemic species occurred after the development of the present lake environment, resulting in a time lag between phylogenetic divergence and population establishment and possible phenotypic adaptation of some endemic species. Therefore, the lineages of some endemic species originated before the formation of the present lake environment; however, the current phenotypic traits of these species are presumed to have differentiated from their ancestral riverine species by ecological adaptation after the formation of the present northern basin environment. Several sets of "endemic species inhabiting the lake–nonendemic ancestral species distributed around the lake"—namely, parapatric species pairs—exist in the present Lake Biwa system. I propose three systems as suitable models for studying adaptive phenotypic divergence and eventual ecological speciation in this ancient lake: the *Gnathopogon* (Cyprinidae) system, the *Gymnogobius* (Gobiidae) system, and the *Sarcocheilichthys* (Cyprinidae) system (Fig. 14.2).

The Lake Biwa endemic cyprinid *Gnathopogon caerulescens* is a typical limnetic

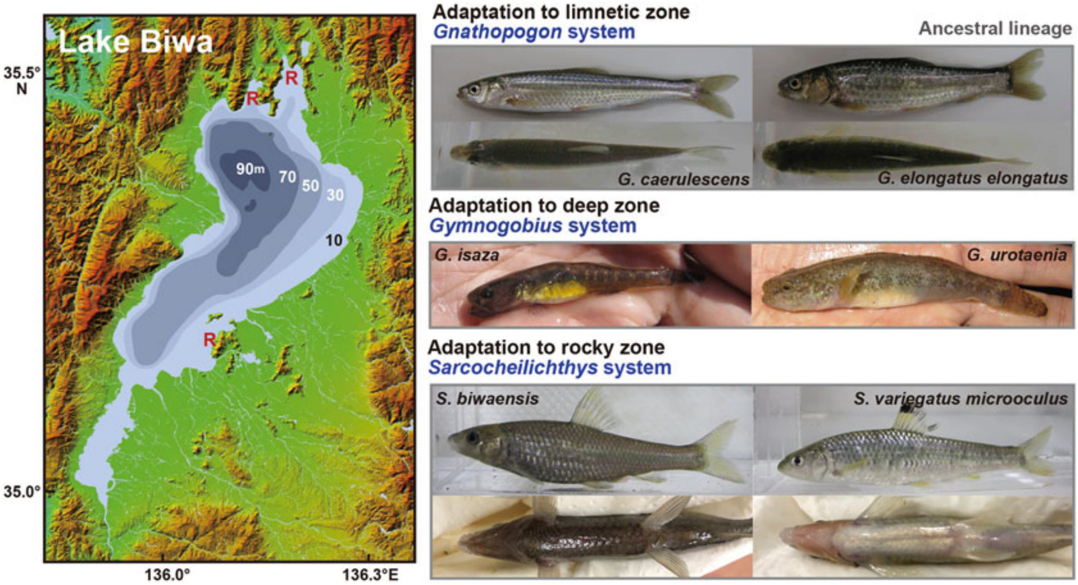

Fig. 14.2 Topography of Lake Biwa and phenotypic adaptation of three endemic fish systems to Lake Biwa environments. *R* indicates the littoral rocky zone in Lake Biwa. (This elevation map was used with permission from the Geospatial Information Authority of Japan, http://www.gsi.go.jp/)

species with an exclusively pelagic lifestyle in the lake and forages for zooplankton (Nakamura 1969; Hosoya 1987). Another taxonomic *Gnathopogon* species (*Gnathopogon elongatus*) also inhabits the Japanese Archipelago. This species is widely distributed in rivers and ponds of western to central Japan, and feeds on zoobenthos and benthic algae (Nakamura 1969; Hosoya 1987). In the Lake Biwa system, *G. elongatus* inhabits mainly rivers flowing into Lake Biwa and lagoons connected to Lake Biwa. A molecular phylogenetic study using mtDNA sequences identified four major lineages among these Japanese *Gnathopogon* fishes, including *G. caerulescens*, which diverged from a geographical lineage of *G. elongatus* occurring in western Japan, including around Lake Biwa (Kakioka et al. 2013b). This *Gnathopogon* system in Lake Biwa is a typical case of ecological speciation in that colonization of ancestral riverine *G. elongatus* populations into the extensive pelagic environment of this lake led to ecological diversification followed by speciation. There is distinct phenotypic divergence in ecomorphological traits, including swimming- and foraging-related traits, between the two *Gnathopogon* species, and *G. caerulescens* has a set of morphological features specialized to the limnetic lifestyle in Lake Biwa (e.g., slender body, upward-pointing mouth, and fine gill rakers) (Hosoya 1987; Kakioka et al. 2015). A similar phenomenon is found in the lake–stream threespine stickleback species pair in postglacial lakes (Hendry et al. 2002; Roesti et al. 2012). The two *Gnathopogon* species can be interbred easily by artificial insemination (Nakamura 1969) and are conducive to quantitative genetic approaches for investigating the evolutionary genetic basis of the diverged ecomorphological traits. Kakioka et al. (2013a, 2015) investigated the genetic architecture underlying the interspecific variation of complex morphological traits by quantitative trait locus (QTL) analysis and found a genetic signature of directional selection in the body shape of *G. caerulescens*. Therefore, the slender body shape of *G. caerulescens* is a product of adaptive evolution to the pelagic lifestyle.

The Lake Biwa floating goby *Gymnogobius isaza* is a representative inhabitant of the deep pelagic zone of Lake Biwa. *G. isaza* lives on the lake bottom deeper than 30 m to almost the deepest area of the lake (Takahashi 1981; Kumagai 2008). This species has a unique ecological characteristic, that is, it performs vertical diel migration from the deep bottom to near the surface for foraging amphipods and other macrozooplankton (Takahashi 1981). This species diverged from congener *Gymnogobius urotaenia*, which is an amphidromous and partly freshwater species distributed widely in Japan, including in the Lake Biwa system, as supported by a phylogenetic analysis using allozyme polymorphisms (Aizawa et al. 1994). A molecular phylogenetic study using mtDNA sequences showed that *G. isaza* was derived not from *G. urotaenia*, but from the common ancestor of *G. urotaenia* and *Gymnogobius petschiliensis*, another amphidromous congener (Harada et al. 2002; Tabata and Watanabe 2013), causing the difficult issue of the origin of *G. isaza*. However, a more recent phylogenetic analysis based on transcriptome sequences revealed that *G. isaza* was inferred to be a sister species of *G. urotaenia*, as expected (R. Ito et al., unpublished data). Because *G. urotaenia* inhabits mainly rivers flowing into Lake Biwa and part of the littoral zone of the Lake Biwa system, the *Gymnogobius* system is an example of a species pair along a depth gradient. In the context of ecological speciation and adaptive radiation, divergence along depth gradients is often associated with the evolution of reproductive isolation in marine and freshwater species (Ingram 2011; Baillie et al. 2016). Although ample knowledge of the life history of *G. isaza* has accumulated, the adaptive phenotypic evolution associated with the acquisition of this offshore life history in a wide, deep pelagic environment is unclear. Because deep water is an extreme environment, especially for essentially riverine fishes including *Gymnogobius* species, it is assumed to pose an array of physiological and ecological challenges to organisms. Low water temperature, high hydrostatic pressure, low levels of dissolved oxygen, and a lack of ambient light result in characteristic selection pressures below 50 m depth (Sebert and Macdonald 1993). Therefore, some physiological adaptations are necessary for successful colonization of the deep zone. For example, in the cichlids of the Great Lakes of East Africa, the adaptive divergence of genes encoding visual pigment proteins (opsins) and oxygen-transport proteins (hemoglobins) is associated with different depth ranges (e.g., Terai et al. 2006, 2017; Seehausen et al. 2008; Hahn et al. 2017). Surprisingly few studies have addressed this question for the *Gymnogobius* system. However, Suito et al. (2018) performed a comparative analysis of phospholipids and triacylglycerols in the *Gymnogobius* species pair in Lake Biwa. The novel lipid profile of *G. isaza* reflects its adaptation to benthopelagic life in Lake Biwa. Investigating this *Gymnogobius* system will provide insight into the adaptive evolution of fishes to deep-water environments.

The gudgeon *Sarcocheilichthys* is a genus of cyprinid fishes found mainly in rivers of eastern Asia. *Sarcocheilichthys* species usually swim close to the bottom (subbenthic habitat) and forage for prey (mainly benthic invertebrates) from substrates (Zhang et al. 2008). Three taxonomic species/subspecies—*Sarcocheilichthys variegatus variegatus*, *Sarcocheilichthys variegatus microoculus*, and *Sarcocheilichthys biwaensis*—inhabit Japanese inland freshwaters, and the latter two species are endemic to Lake Biwa (Hosoya 1982). These two species have divergent body colors and distributional patterns (Nakamura 1969; Hosoya 1982; Komiya et al. 2011). *Sarcocheilichthys variegatus microoculus* has a yellow-grayish body and occurs throughout the littoral zone including in sandy, pebbly, and rocky areas and in rivers flowing into Lake Biwa. By contrast, *S. biwaensis* has a brownish body with yellow-brownish and brownish-black coloration, and occurs strictly in and around rocky areas. These two *Sarcocheilichthys* species are presumed to have evolved from the ancestral riverine *S. variegatus variegatus*, which is widely distributed in western Japan, except in Lake Biwa (Hosoya 1982). Phylogeographic analyses using neutral DNA markers have suggested that the Lake Biwa population was created by multiple colonizations of this lake by the riverine lineages (Komiya et al. 2014). Although these two fishes have been treated taxonomically as separate species, previous phylogeographic and population genetic analyses using mtDNA and microsatellite markers have suggested no genetic differentiation between these species and the panmictic status of *Sarcocheilichthys* in Lake Biwa (Komiya et al. 2014). In addition, *S. biwaensis* has been taxonomically described as an independent species, primarily based on its body (and fin) color, body shape, and head morphology. This species has a longer head and deeper body than its congener. However, the ecomorphological traits of *S. variegatus microoculus*, which uses several bottom environments including sandy, pebbly, and rocky areas, show continuous variation in relation to habitat types, and its head and body shapes in rocky areas largely overlap with those of *S. biwaensis* (see Komiya et al. 2011). These traits of both species inhabiting rocky areas are advantageous for capturing cryptic and/or attached prey in rocky areas with complex structure (Komiya et al. 2011). Thus, sympatric *S. variegatus microoculus* and *S. biwaensis* exhibit similar morphologies, except for body coloration, and cannot be distinguished by neutral DNA markers. *Sarcocheilichthys variegatus microoculus* displays a sharp typical countershading coloration and *S. biwaensis* is darkly pigmented all over the body, including the ventral region, and lacks a countershading pattern. Kokita et al. (2021) reported that this color divergence was primarily controlled by a single-locus, two-allele Mendelian-inheritance pattern by crossing experiments in the laboratory and a genome-wide association analysis using wild caught individuals. Moreover, except for the region near the locus potentially associated with color divergence, there was no genome-wide divergence between the two species in a co-occurring rocky area. This implies that the two taxonomic species show genetic color polymorphism within a single interbreeding population or two incipient species with weak premating isolation. The melanistic *S. biwaensis* is a rock-dwelling specialist inhabiting around darker colored substrates; conversely, the countershaded *S. variegatus microoculus* occurs almost entirely in the littoral area and uses a wide variety of bottom environments, including sandy and pebbly zones with lighter substrates. Therefore, the uniform dark coloration of *S. biwaensis* is speculated to serve as camouflage, albeit briefly, in dark rocky environments (Hosoya 1982; Komiya et al. 2011). Therefore, this *Sarcocheilichthys* system provides an opportunity for testing hypotheses on functional aspects of countershading coloration and its loss in aquatic environments. It will also enable investigation of the processes and mechanisms underlying the evolutionary maintenance of color polymorphism in spatially heterogeneous littoral environments of this lake.

Further studies of these endemic systems based on ecological, genetic, and genomic analyses are needed to explore phenotypic adaptation to unique environments and consequent ecological speciation in this ancient lake.

14.4 Freshwater Threespine Stickleback in Japanese Spring-Fed Habitats

As per the previous section (Sect. 14.2), the threespine stickleback *Gasterosteus aculeatus* is an excellent model system for ecology and evolutionary biology (Hendry et al. 2013). This species has attracted attention as a vertebrate model because of its phenotypic (e.g., morphological, ecological, physiological, and behavioral) diversification of freshwater populations derived independently from the ancestral marine (anadromous) populations. Most freshwater populations in North America and northern Europe were founded at the end of the last glacial period when marine sticklebacks began to colonize new freshwater habitats (Bell and Foster 1994). Distinct freshwater populations typically have unique phenotypes, and some Japanese populations have intriguing characteristics not found in other populations (Mori 1997; Kitano and Mori 2016; Fig. 14.3). A recent comprehensive phylogenomic study evaluated the phylogenetic relationships among these Japanese populations and their freshwater colonization history (Kakioka et al. 2020). In Japan, the

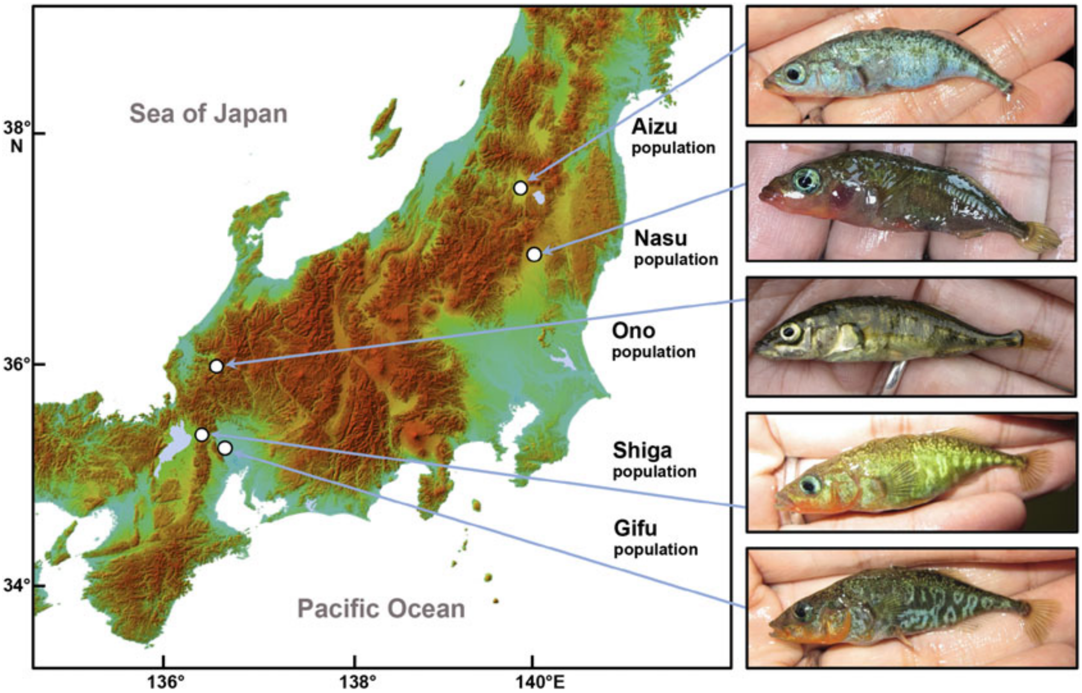

Fig. 14.3 Freshwater threespine stickleback populations inhabiting spring-fed habitats in central and southwestern Honshu Island, Japan. Gifu and Shiga populations are called as the Hariyo lineage in Japan. (This elevation map was used with permission from the Geospatial Information Authority of Japan, http://www.gsi.go.jp/)

freshwater colonization occurred in multiple waves, each of which may reflect different interglacial isolations. The oldest freshwater populations from southwestern Honshu Island, the largest of the four main islands of Japan, were estimated to have colonized freshwater approximately 0.17 Mya. This lineage, which is called “Hariyo” stickleback in Japan (Watanabe et al. 2003; Kitano and Mori 2016), is the oldest extant freshwater lineage of the species reported to date. The next wave of independent colonization likely occurred about 0.1 Mya, and consequently, three distinct freshwater lineages exist in central Honshu Island such as in the Aizu Basin (Fukushima Prefecture), the Nasu region in the northern part of the Kanto Plain (Tochigi Prefecture), and the Ono Basin (Fukui Prefecture), respectively (Fig. 14.3). Other freshwater populations from northern Honshu Island and Hokkaido Island (northernmost of the four main islands of Japan) have diverged more recently and their phylogenetic positions are nested among marine populations. Therefore, these Japanese stickleback systems differ from those in the Pacific Northwest of North America and northern Europe in terms of divergence time and history. Stickleback populations in the Japanese Archipelago offer an opportunity to study evolutionary processes on historical and contemporary timescales.

Freshwater populations in central and southwestern Honshu Island, which were derived from the oldest or subsequent waves of colonization, inhabit spring-fed ponds and streams. The genus *Gasterosteus* is associated with the high-latitude cold zone of the Northern Hemisphere and is distributed in cold freshwater and marine habitats in North America and from northern Europe to East Asia (Wootton 1976; Bell and Foster 1994). Thus, this species are generally cold-water fish, and optimal temperatures for their growth and reproduction are usually below 20 °C (Ikeda

1933; Wootton 1984). Although most freshwater environments in Honshu Island become hot during summer and therefore are not suitable for threespine stickleback (Mori 1997), the spring-fed environments with cold underground spring water have a constant year-round temperature below 20 °C, allowing the fish to avoid heat in summer. Habitats of the Hariyo lineage are located in the southern range limit of the global natural distribution of freshwater populations (Watanabe et al. 2003; Kitano and Mori 2016). These freshwater lineages in Honshu Island, which are relatively old in terms of divergence, tend to have more specialized morphology (Ishikawa et al. 2019). The oldest freshwater Hariyo lineage has unique characteristics—including a cloud-like pattern of melanin pigmentation on the body side (Mori 1985, 1993; see Fig. 14.3)—among all freshwater populations globally.

In the threespine stickleback, adaptive divergence in the number of lateral armor plates, a defensive trait, between freshwater and marine populations has been studied (Bell 2001). The process and mechanism of this adaptive phenotypic evolution have been investigated ecologically and genetically (e.g., Colosimo et al. 2005; Kitano et al. 2008a; Barrett et al. 2008). Parallel reduction in the armor plate in multiple freshwater populations of young origins in North America and Europe is caused by repeated fixation of the same allele of the ectodysplasin (*Eda*) gene. By contrast, armor plate reduction in the Japanese Hariyo lineage is caused by independent mutations of *Eda* (O'Brown et al. 2015; Yamasaki et al. 2019). Parallel phenotypic changes of several morphological traits, including shortened spine lengths and increased body depths, were also found in the Hariyo lineage and other freshwater populations worldwide. However, similar to lateral armor plates, the evolutionary genetic and genomic bases may differ between the Hariyo lineage (older origin) and other freshwater populations (younger origin). Therefore, the Hariyo lineage could be used to investigate diversity in genetic and genomic mechanisms underlying parallel evolution in the wild.

In addition to its morphological traits, the Hariyo lineage has unique reproductive characteristics. First, these populations exhibit nearly year-round reproduction in the wild (Mori 1985). The threespine stickleback typically only reproduces in spring or summer in most of its geographic range (Wootton 1976; Bell and Foster 1994). Therefore, the year-round reproduction of the Hariyo populations is distinct, although this reproductive pattern has also been reported in the California population in North America (Baskin 1974), as well as in the Ono population, which is located close the Hariyo populations (Yamamoto et al. 2020; see Fig. 14.3). The stable environmental conditions of their habitats—including a constant water temperature—are likely responsible for enabling the stickleback to reproduce almost year-round (Mori 1985). In general, reproductive timing and duration are critical determinants of individual reproductive success for a variety of organisms (Williams et al. 2017). If this prolonged duration of reproduction is genetically determined, the Hariyo lineage could be a novel model system for exploring the evolutionary mechanism underlying variation in this fitness-related trait.

The breeding system and reproductive behavioral ecology of the Hariyo lineage were explored in the wild (Mori 1985, 1987, 1993). Although the threespine stickleback has been a model vertebrate in ethology and behavioral ecology, and many reproductive behavioral experiments have been conducted in the laboratory (Bell and Foster 1994; Östlund-Nilsson et al. 2006), detailed field studies are rare in populations other than the Hariyo lineage. The Hariyo lineage harbors two geographically and genetically distinct populations: the Gifu and Shiga populations (Watanabe et al. 2003; Ishikawa et al. 2019; see Fig. 14.3). Divergence in breeding system, male mating strategy, and female spawning strategy was found between the two populations by detailed field observation (Mori 1987, 1997). Although both populations dwell spring-fed streams, the Shiga population inhabits high-gradient streams with considerably faster water velocity compared to the Gifu population. Therefore, the Shiga population is exposed to relatively severe environmental conditions: unsteady flow of water, few inlets in which males build nests for reproduction, unstable water level, high fluctuations in water temperature, and a gravelly bottom substratum. By contrast, the Gifu population is found in lowland areas with many standing water areas in which males build nests as well as temporospatially stable environmental conditions including temperature and food supply. Therefore, the interpopulation variation in breeding strategy is considered to reflect adaptations to the divergent environmental conditions of their habitats. Such divergence in male and female reproductive strategies could provide insight into how genetic variation affects reproductive traits, including behavioral phenotypes. Thus, due to the ease of direct observation, the Japanese freshwater populations inhabiting transparent spring-fed habitats could be model systems for integrated studies of behavioral ecology and evolutionary genomics (Rittschof and Robinson 2014; Bengston et al. 2018; Rubenstein et al. 2019).

14.5 Phenotypic Divergence Among Populations of Medaka, a Model Fish from Japan

The Japanese rice fish "medaka" (*Oryzias latipes*) is a tiny freshwater fish native to East Asia, including the Japanese Archipelago, and is mainly found in standing and slow-flowing waters such as rice paddies, ponds, and agricultural channels. Phylogeographic analyses using allozyme and mtDNA data showed that the medaka is divided into at least four major lineages: the northern Japanese, southern Japanese, eastern Korean, and western Korean/Chinese groups (e.g., Sakaizumi et al. 1983; Takehana et al. 2003, 2004; Katsumura et al. 2009). Therefore, there are two genetically distinct lineages of medaka in Japan; the northern group is distributed along the Sea of Japan coast of central and eastern Japan, and the southern group is distributed along the Pacific coast of eastern Japan and throughout western Japan (Takehana et al. 2003). The northern group has been recently described as a new species, *Oryzias sakaizumii*, based on its morphological characteristics (Asai et al. 2011). *Oryzias latipes* and *O. sakaizumii* were estimated to have diverged several Mya (Takehana et al. 2003; Katsumura et al. 2019; but see Setiamarga et al. 2009). However, their specific status is controversial (Oda 2016; Katsumura et al. 2019; see also Saitoh 2019) because *O. sakaizumii* is not reproductively isolated from *O. latipes* (see Sakaizumi et al. 1992), and therefore repeated gene introgression and mating between the two taxonomic species have occurred in the wild (Iguchi et al. 2018). Therefore, the medaka is now frequently referred to as the *Oryzias latipes* species complex. Because this section does not address their species status, I refer to the northern group as *O. sakaizumii* and the southern group as *O. latipes*. Because a recent review described the phenotypic diversity of the medaka and its relatives in an evolutionary context (Hilgers and Schwarzer 2019), I here summarize the potential of this system in ecology and evolutionary biology briefly.

The medaka has been reared in Japan as an ornamental fish from as early as the seventeenth century (Edo era in Japan), and populations derived from wild individuals have been maintained in universities and research institutes in Japan since 1985 (Shima and Mitani 2004; Kinoshita et al. 2009). Japanese biologists have used this fish as a model organism, like the zebrafish (*Danio rerio*), for physiology, embryology, and genetics studies. This fish is an ideal laboratory organism with short generation times and is easy to maintain due to its small body size and simple dietary and habitat requirements and can be bred in captivity. Therefore, genetically based phenotypic divergence between the two Japanese medaka species has been detected not only for morphological traits—including brain morphology, craniofacial anatomy, vertebral regionalization and number, and rate of fin development (Ishikawa et al. 1999; Kimura et al. 2007, 2012; Kawajiri et al. 2009)—but also for potentially fitness-related traits such as body size, low and high temperature tolerance, degree of sexual dimorphism of the dorsal fin, and aggressive and startle behaviors (Hirayama et al. 2010; Asai et al. 2011; Kagawa 2014; Tsuboko et al. 2014; Kawajiri et al. 2015; Yassumoto et al. 2020).

As is the often the case with Japanese fish species, each medaka species shows a wide latitudinal distribution in the Japanese Archipelago. Therefore, noticeable climatic differences exist between the southern and northern ends of their distribution, resulting in exposure to various selective pressures according to the latitudinal environment. Thus, phenotypic variation including life history traits is often reported among latitudinal populations in Japanese fishes because latitude is the basis of a conspicuous environmental gradient (e.g., Iguchi 1993; Kokita 2003; Tamate and Maekawa 2006). In general, the potential for local adaptation is determined by the interplay between the selection differential and the level of gene flow among locations (Kawecki and Ebert 2004; Savolainen et al. 2013). Because mountain ridges and seas generally restrict migration and prevent gene flow between local populations, especially for freshwater fishes, they likely undergo local adaptation, including medaka. In fact, heritable variation in some ecologically relevant traits among latitudinal populations of *O. sakaizumii* has been documented, which is explained in the context of adaptation to local climate (e.g., Yamahira et al. 2007; Yamahira and Nishida 2009; Suzuki et al. 2010; Sasaki and Yamahira 2016). For example, higher-latitude individuals grow faster than lower-latitude individuals across all temperatures examined, suggesting that this faster growth rate compensates for a shorter growing season further north. However, faster growth, which is achieved by higher feeding rates, is accompanied by greater vulnerability to predation. Hence, different growth capacities in the northern population likely evolved in response to the length of the growing season and predation pressure. Such latitudinal compensation was investigated in Atlantic Silverside (*Menidia menidia*), which shows latitudinal heritable variation of fitness-related traits (Conover 1998). This phenomenon in medaka is important for exploring its evolutionary mechanism at the gene and genome levels because medaka is amenable to a variety of molecular genetics approaches, together with population and evolutionary ecological approaches in the wild. Therefore, this small fish, frequently used as a model fish in the laboratory, could also enable investigation of the ecological, genetic, and genomic bases of latitudinal phenotypic variation in relation to the ecogeographic rules in the wild.

14.6 Highly Diverged Reproductive Traits in Two Japanese Fish Systems

Maternal reproductive traits, including egg morphology, fecundity and reproductive output, and allocation between egg size and number, are fundamental traits that females adopt to maximize fitness (Wootton and Smith 2015). Phenotypic divergence in egg phenotypes, including egg size and shape, among local populations or closely related species has long attracted the attention of ecologists and evolutionary biologists (Hendry et al. 2001; Kamler 2005). Therefore, it is a well-studied topic for many organisms including fishes, and the traits appear to be optimized by natural selection (Einum et al. 2004; Teletchea et al. 2009; Krist 2011). For example, fish egg size often varies with latitude at the intraspecific population and species levels (Thresher 1988; Chambers 1997). In addition, it often differs between landlocked populations and ancestral marine (diadromous) populations (Baker et al. 2008; Closs et al. 2013). Furthermore, egg shape variation in birds is correlated with variation in their flight ability (Stoddard et al. 2017). However, the evolutionary genetic basis and evolutionary potential of diversification in egg morphology are not well understood despite the phenomenon being widespread and potential ecological drivers of the diversification having been discussed. Among the Japanese freshwater fishes, “Yoshinobori” goby and “Tabira” bitterling, can be used to address the above questions. In this section, I propose these systems harboring extreme diversification in egg phenotypes as model systems for integrated ecology, genetics,

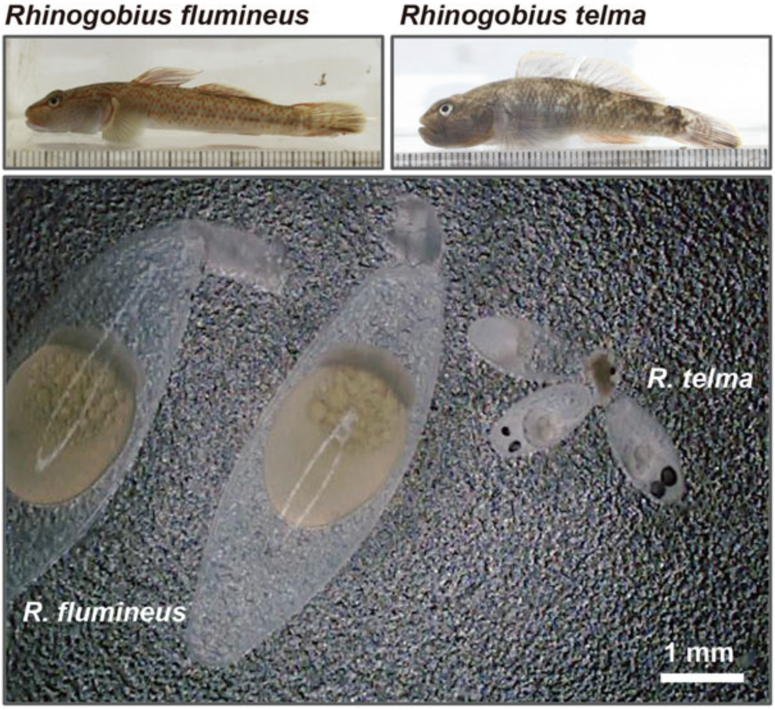

Fig. 14.4 Two sister species of *Rhinogobius* exhibiting notable divergence in egg size. (Photos by Y. Y. Yamasaki)

and genomics studies of the adaptative evolution of egg phenotypes (Figs. 14.4 and 14.5).

One example is the large-scale and repeated egg size evolution in relation to migration-related life history in a goby lineage (Yoshinobori goby; genus *Rhinogobius*) (Nishida 1994, 2001). *Rhinogobius* fishes are widely distributed in East and Southeast Asia, and consist of more than 85 species, representing the most species-rich group of freshwater gobies (Oijen et al. 2011). In Japan, this group is distributed widely from Hokkaido to the Ryukyu Islands, and a total of 18 Yoshinobori goby species are known from the Japanese Archipelago (Suzuki et al. 2020). Although their species status has been evidenced by morphological, ecological, behavioral, and genetic analyses, some are taxonomically uncertain, and their scientific names have not yet been decided; only the standard Japanese names have been given. There are three types of migration-related life histories—namely, amphidromous, fluvial, and lentic forms—among Yoshinobori goby species in Japan. The most common type is the amphidromous life history, in which newly hatched larvae in the river flow down to marine environments and grow there, returning to the river at the juvenile stage to grow and reproduce. Landlocked fluvial and lentic forms complete their life cycles in running freshwater such as rivers and streams and in standing freshwater such as lakes and marshes, respectively. Males of the Yoshinobori gobies make nests and care for the oviposited and fertilized eggs under a stone until hatching, and their eggs are demersal and elliptical like other gobies. The egg size of Yoshinobori goby species in Japan ranges from 0.6 to 2.1 mm in the major axis, and amphidromous and lentic species produce small eggs, whereas fluvial species spawn larger eggs (reviewed by Yamasaki et al. 2015). The extreme egg size variations associated with their migration ecology are the product of adaptative evolution in relation to survival during the larval period (Nishida 1994, 2001; McDowall 2007; Closs et al. 2013). At the expense of egg number spawned, the fluvial species may need to produce larger eggs and larvae that can persist in running water, and that utilize large prey items in rivers, which are relatively harsh and unproductive environments. By contrast, the large number of

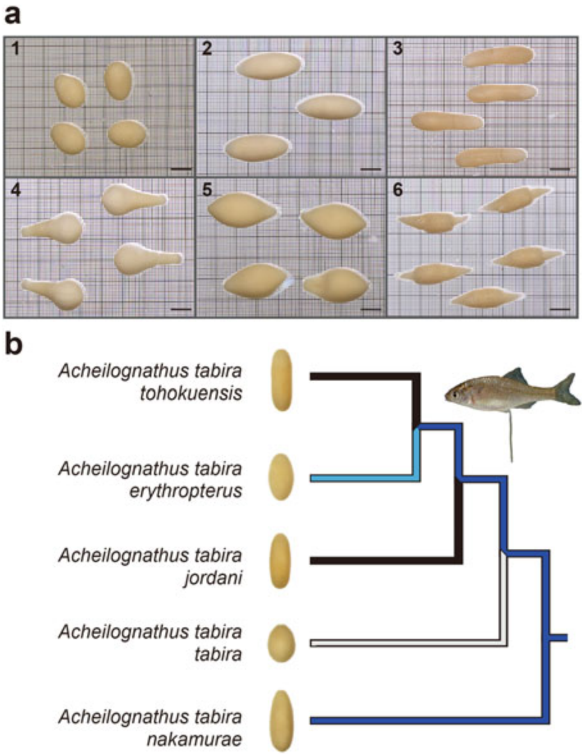

Fig. 14.5 Eggs of brood parasitic bitterling fishes. (**a**) Extreme diversity of egg shape in bitterling fishes (1: *Acheilognathus tabira tabira*; 2: *Acheilognathus typus*; 3: *Acheilognathus cyanostigma*; 4: *Rhodeus ocellatus kurumeus*; 5: *Tanakia lanceolata*; 6: *Tanakia himantegus*). *Scale bar* = 1 mm. Photo by J. Kitamura. (**b**) Evolutionary pattern of egg shape in the Tabira bitterling (*Acheilognathus tabira*). (Topography is based on Kitamura et al. 2012)

small eggs and larvae produced by the amphidromous and lentic species seem to be adaptive to standing water with abundant small-sized plankton, such as the sea near a river mouth and lakes or ponds, where strong swimming ability is not necessary.

Yamasaki et al. (2015) showed by comprehensive molecular phylogenetic analyses that the evolutionary change from amphidromous to fluvial life, accompanied by egg size change, occurred independently in at least three lineages (*Rhinogobius flumineus*, *Rhinogobius* sp. BB, and *Rhinogobius* sp. YB), and the change from amphidromous to lentic life with no clear egg size change occurred in one lineage that thereafter diverged into two lentic species [*Rhinogobius biwaensis* (formerly *Rhinogobius* sp. BW) and *Rhinogobius tyoni* (formerly *Rhinogobius* sp. BF)]. In addition, an interesting pattern of life history transformation from the fluvial to the lentic type, involving a possible reversal evolution in egg size, was found in a lineage within *Rhinogobius*. In this lineage, egg size changed from small (ancestral amphidromous species) to large (fluvial species *R. flumineus*) and back to small [*Rhinogobius telma* (formerly *Rhinogobius* sp. TO)]. Thus, a notable interspecific difference in egg size was associated with these life history types (Fig. 14.4). Although increased egg size of landlocked populations is also known in an ecological and evolutionary model fish, threespine stickleback (Mori 1987; Baker et al. 2008), the difference is of considerable magnitude for the Yoshinobori goby system, which is probably not found among closely related species of other fish groups.

Reproductive isolation of Yoshinobori goby species is achieved mainly by premating isolation mechanisms, including differences in spawning habitat in the river course, assortative mating based on nuptial coloration and courtship behavior, or both (Mizuno 1987). In fact, introgressive hybridization has occurred contemporarily among some landlocked Yoshinobori species following artificial transplantation (Mukai et al. 2012). This phenomenon implies that postmating isolation between the species is weak or absent, and artificially interspecific crosses can be created by artificial insemination in the laboratory. Therefore, forward genetic approaches such as QTL analysis are applicable for exploring the genetic architecture underlying egg size variation, and this system is suitable for studying adaptive diversification of egg size in nature.

There is marked inter- and intraspecific diversification in egg shape in a cyprinid lineage known as the bitterling (subfamily Acheilognathinae). Bitterling fishes are distributed in temperate regions of Europe and East Asia and comprise approximately 40 species or subspecies worldwide (Banarescu 1990). The group is characterized by a unique reproductive strategy: it is an obligatory brood parasite of freshwater mussels (Reichard 2003). Bitterling fishes deposit their eggs on the gills of living mussels using a long ovipositor, and embryonic and larval development is completed in the gill chamber of the host bivalve. Some species of bitterling are host specialists, whereas others are generalists that use a range of host mussel species (Smith et al. 2004; Reichard et al. 2007; Kitamura 2007). Although investigation of bitterling reproductive ecology has been conducted in Europe, only a single species, the European bitterling (*Rhodeus amarus*), is present in Europe. By contrast, the bitterling shows notable species diversity in East Asia, and multiple species often occur sympatrically. The Japanese Archipelago harbors 16 species or subspecies of bitterling, most of which are endemic (Kitamura and Uchiyama 2020), and can be regarded as a hotspot of bitterling species diversification. Divergence in a variety of ecologically relevant traits is known among bitterling fishes and is the product of adaptive evolution in relation to ecological and reproductive niche divergences.

There is marked diversity in egg shape among bitterling species, suggesting relevance to host mussel use (Nakamura 1969; Kitamura and Uchiyama 2020; Fig. 14.5). The bitterling species that use small mussels belonging to the subfamily Unionidae typically produce round eggs, whereas those using large mussels belonging to the subfamily Anodontinae exhibit elongated or uniquely bulb-shaped eggs. Such extreme variation is rarely seen, at least among closely related species of fishes. Mussel gill structure varies among species, and it is hypothesized that bitterling egg shape is adaptive in ensuring eggs remain wedged within the host gill (Liu et al. 2006; Reichard et al. 2007). Egg shape can play a vital role in securing the lodging of eggs in the gill cavity until hatching because mussels respond to bitterling oviposition by rapidly contracting their valves and expelling the eggs. Eggs that are expelled before completing development are quickly eaten or die (Kitamura 2005). Therefore, an elongated egg shape may be advantageous only for bitterlings that use large-sized mussels. The shape may bear some cost in terms of its ability to be deposited into small shells and a reduced egg number deposited per oviposition trial.

Although large-scale variation in egg shape was confirmed across bitterling species, there is similar intraspecific variation within a lineage (Tabira bitterling: *Acheilognathus tabira*) native to the Japanese Archipelago (Arai et al. 2007; Fig. 14.5). *Acheilognathus tabira* is divided into five subspecies; three lotic inhabitants (*Acheilognathus tabira erythropterus*, *Acheilognathus tabira nakamurae*, and *Acheilognathus tabira tabira*) and two lentic inhabitants (*Acheilognathus tabira jordani* and *Acheilognathus tabira tohokuensis*). There is egg shape variation along a continuum from the roundest shape in *A. t. tabira* to the most elongated in *A. t. tohokuensis*. Lentic subspecies spawn elongated eggs and the eggs of lotic subspecies are relatively round compared with lentic species. Most Tabira populations use mussels of the Unioninae or Anodontinae subfamilies; lotic and lentic populations frequently use Unioninae and Anodontinae mussels, respectively. Therefore, differences in host mussel taxa likely influence variations in egg shape. Based on a robust phylogeny of *A. tabira* populations, Kitamura et al. (2012) demonstrated that the evolution of egg shape occurred repeatedly in the Tabira bitterling, correlating with host differences, and suggested that egg shape can undergo divergent selection. In Tabira bitterling, deposited eggs are found mainly in the mussel's suprabranchial cavity, which is connected to the exhalant siphon (Kitamura and Morosawa 2010). Because the suprabranchial cavity is larger in Anodontinae than in Unioninae, a more elongated egg shape with a larger surface area may have been selected for in Tabira populations using Anodontinae to enable firm attachment of the egg to the cavity wall, thus reducing the probability of eggs being expelled.

Because premating and postmating isolation mechanisms did not evolve among Tabira subspecies, we can easily perform artificial crosses (Suzuki 1985). Therefore, as is the case with Yoshinobori gobies, experimental genetic studies can provide insight into the genetic architecture of egg shape divergence. In addition, measures of reproductive success by egg shape manipulation using experimental hybridizations between subspecies would also be useful to document the ecological significance in egg shape divergence. Combined with ecological and behavioral experiments in the laboratory or in the wild, as well as functional genetics and genomics, the Tabira bitterling enables ecological evolutionary developmental studies of egg shape evolution in nature.

14.7 Conclusion

Although the mechanisms of adaptation and speciation have been a focus of interest in ecology and evolutionary biology, until recently, this line of research was limited to a few ecological and evolutionary model systems such as, for fishes, three stickleback and cichlids. These model systems enable investigation of the genetic and genomic mechanisms underlying phenotypic adaptation and adaptive radiation in the wild. However, we are far from being able to predict common evolutionary patterns, processes, and mechanisms of adaptation and speciation at the gene or genome level. Studies using a variety of non-model organisms could provide insight into why and how so many phenotypes and species have evolved in the wild. In addition, these non-model organisms enable addressing a series of scientific questions that cannot be solved using ecological and evolutionary model systems. The advent of next-generation DNA sequencing technologies, omics approaches, and genome-editing technology could enable fundamental questions to be answered using ecologically and evolutionarily fascinating non-model organisms.

Among Japanese fishes, there are many potential model systems whose natural history has been explored other than those mentioned in this chapter. These systems enable hypotheses on adaptation and speciation to be tested using contemporary approaches. De novo whole-genome sequencing and assembly has been conducted for several non-model Japanese fishes, including ice goby, *Sarcocheilichthys* gudgeon, Yoshinobori goby, and Tabira bitterling. Moreover, ecological and evolutionary genomics research using these species is ongoing. Thus, the integrated studies of natural history and modern life science will enhance our understanding of the evolutionary mechanisms underlying phenotypic and species diversification of fishes.

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Ecological Diversity of Larval Fishes: Ontogeny of Deep-Sea Demersal Species

15

Munehiro Takami

Abstract

This chapter introduces the ecological diversity of larval and juvenile stages of fishes, using, as an example, the ontogeny of deep-sea demersal species, one of the least known groups with regard to early life history. To clarify the latter in such fishes, a near-bottom sampling survey was conducted on the upper continental slope of Suruga Bay. The larval fish fauna in the near-bottom layer of the bay was clarified for the first time, and ontogenies of three species (*Leptoderma lubricum*, *Leptoderma retropinnum*, and *Paraliparis dipterus*) highly dependent upon the near-bottom layer were described herein. The collected deep-sea demersal fishes were separated into three types based on their distribution patterns in the near-bottom layer and water column: Type A, all developmental stages occurring only in the near-bottom layer; type B-1, early juvenile stage occurring mainly in the water column, thereafter the near-bottom layer; and type B-2, juvenile stage only collected from near-bottom, no larvae collected from the near-bottom layer or water column. The characteristics and significance of the ontogeny of these types are discussed, and the current status of larval fish taxonomy in Japan is summarized. Some suggestions are made to increase the number of larval fish descriptions in the future.

Keywords

Ontogeny · Larvae · Juvenile · Deep-sea demersal fishes · Near-bottom layer

15.1 Introduction

The taxonomic study of larval fishes has progressed greatly since 1980, many atlases and identification guides having been published, including Leis and Rennis (1983), Ozawa (1986), Okiyama (1988b, 2014), Leis and Trnski (1989), Moser (1996), Neire et al. (1998) and Leis and Carson-Ewart (2000) (Indo-Pacific); Oliver and Fortuño (1991), Richards (2006) and Fahay (2007a, b) (Atlantic); Kellermann (1989) (Antarctic). While these reports described larvae and juveniles of ca. 325 families, the differences in the amount of information available depending on the taxon was inescapable, being abundant for coastal and offshore pelagic taxa, but very scarce for other taxa, such as Alepocephalidae, Macrouridae, and Liparidae. Most of the species belonging to the latter taxa are deep-sea demersal fishes that are highly dependent upon the seafloor and are distributed in the deep-sea above the upper continental slope (200–1000 m depth), in contrast to mesopelagic species, also deep-sea

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fishes but for which a wealth of knowledge on larval stages exists.

Why are the larvae of deep-sea demersal fishes rarely reported? Since the exploratory voyage of *HMS Challenger* in 1872–1876, collecting efforts for larval fishes have concentrated mainly in the upper water column. More than a century of collecting efforts have revealed the larval stages of commercially important coastal and offshore fishes, coral reef fishes, and mesopelagic fishes. In addition, the larval stages of some deep-sea demersal fishes are known, including some in Ipnopidae and Ophidiidae. Such larvae occur in the surface zone, unlike the adults, which are associated with the sea bottom. On the other hand, surveys of larval stages in the near-bottom layer have been conducted only in shallow waters (Yamamoto et al. 2004; Yagi et al. 2009), rather than the deep-sea, the neglect of the latter having arisen from a number of inherent difficulties, e.g., the sampling device either contacting the bottom or detaching far from it. Most larval stages of deep-sea demersal fishes are thought to be distributed in the near-bottom layer, where most collection efforts have not reached.

Suruga Bay, located on the Pacific coast of central Honshu, is the deepest bay in Japan, reaching 2245 m depth. The geography of Suruga Bay is precipitous and complex, with the Suruga Trough extending north-south in the center of the bay, and numerous submarine canyons to the east and west of the trough. The species composition of fishes in Suruga Bay indicates that deep-sea fishes account for a large proportion, about 38% of the known species (more than 1200 species) (Fukui 2015). Since 2002, a monthly near-bottom larval sampling program has been conducted on the upper continental slope of Suruga Bay to clarify the ontogeny of resident deep-sea demersal fishes.

15.2 Sampling Stations and Near-Bottom Layer Survey Method

Near-bottom sampling in Suruga Bay was conducted off Miho and the mouth of Fujikawa River (Fig. 15.1), although the former was the main area sampled, such being conducted from shallower to deeper water, since the irregular seafloor topography off Miho precluded the towing of nets along isobath lines. Two sampling areas were established off Miho: the Hagoromo submarine canyon and associated slope, in a depth of approximately 200–1000 m (st. I), and the South-Komagoe submarine canyon and associated slope, in a depth of about 500–1000 m (st. J). Off the Fujikawa River, six stations were established along isobath lines (possible due to the flattened seafloor topography), at depths of about 350, 500, 600, 700, 800, and 900 m. Where possible, each station was sampled once per month.

Figure 15.2 shows the near-bottom sampling device designed for fish larvae. The larval net had a diameter of 1.3 m, and side lengths of 3 m (cylindrical part) and 4 m (conical part). Net mesh size was 2 mm for the anterior 2 m, 1 mm for the next 1 m, and 0.53 mm for the conical section, because sand and mud disturbed by the weight when landing on the bottom could enter the net and clog it. A large cod end bucket attached to the end of the net prevented damage to collected material. The net frame was equipped with a flow meter, depth, temperature, and salinity recorders (Compact-TD and Infinity-CT; JFE Alec Co. Ltd., Tokyo, Japan), and 14 deep-sea floats (Viny 5A-12; Institute of Cellular Materials Co. Ltd., Osaka, Japan) to prevent undue sinking of the net when towed. The weight comprised a large depressor and columnar weight, totaling 271 kg. The net was attached to a releaser between the wire and subsequent 0.8 m chain, the latter being joined to the depressor.

Towing was conducted as follows: (1) Towing commenced just after the columnar weight contacted the seafloor (determined by hand from the tow wire tension), the wire (or rope) released equaling “bottom depth + ca. 5–10 m”; (2) Following contact of the weight with the seafloor, the wire was slightly extended, taking into account the seafloor topography, and the net towed at a speed of about 1.7 kt (while keeping the weight on the bottom); (3) Whenever the wire length reached “bottom depth + 50–70 m,” or the tow

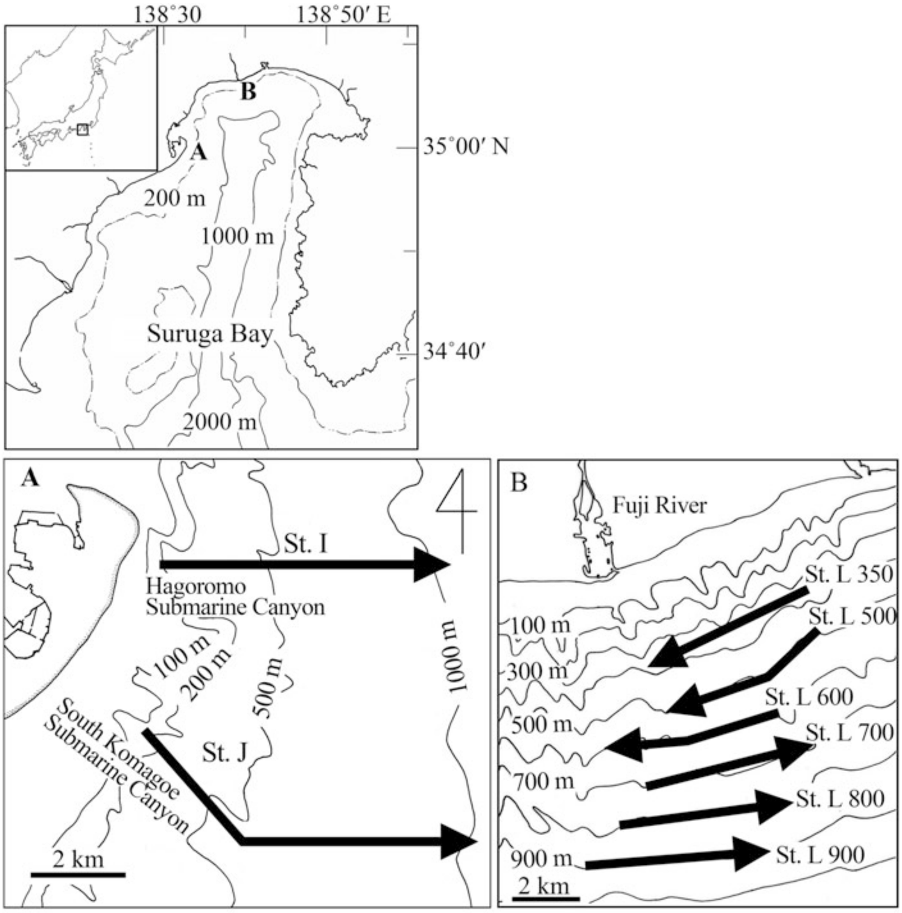

Fig. 15.1 Sampling stations for the near-bottom layer in Suruga Bay, southern Japan. *A* off mouth of Fuji River; *B* off Miho. Arrowed lines indicate range and direction of towed larval net

wire tension indicated that the weight was about to rise from the seafloor, the ship was slowed and the wire reeled in to "depth + 5–10 m"; (4) After confirming subsequent landing of the weight, towing at about 1.7 kt was recommenced; and (5) "Towing speed and deceleration" and "tow wire unreeling and reeling" were repeated while towing the net to a predetermined depth (or distance). This towing technique enabled the larval net to be towed ca. 1–8 m above the seafloor at depths of 200–1000 m (Fig. 15.3).

15.3 Deep-Sea Demersal Fishes Collected from the Near-Bottom Layer

The results of 74 tows completed during the monthly survey program off Miho from October 2006 to June 2009 and off the mouth of Fujikawa River from July 2009 to February 2010 are presented. Because no apparent differences in fish fauna were found between the off Miho and the mouth of Fujikawa River surveys, all results were combined below.

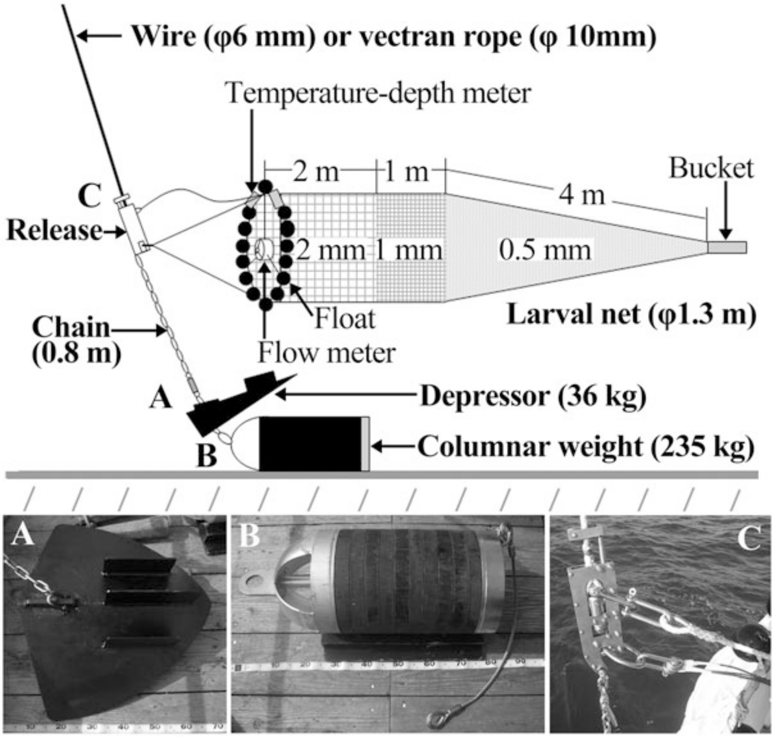

Fig. 15.2 Illustrations of the sampling device for the near-bottom layer. *A* Depressor; *B* columnar weight; *C* releaser

A total of 582 fishes, representing 57 species (plus unidentified taxa) in 38 genera (23 families), were collected by near-bottom sampling. Species and individual numbers were highest for adults (53.3%, 55.0% respectively), followed by juveniles (29.4%, 39.8%) and larvae (17.3%, 5.2%) (including postflexion, flexion, preflexion, and yolk-sac stages) (Fig. 15.4). Larval and juvenile stage individuals numbered 261 in 27 species (and unidentified taxa) in 15 genera (12 families). All taxa represented deep-sea demersal species.

Macrouridae was the most abundant family, accounting for 25.0% of the total number of specific taxa (Fig. 15.5a), followed by Synaphobranchidae (14.4%), Alepocephalidae and Ophidiidae (10.7% each), and Neoscopelidae and Liparidae (7.1% each). These six families accounted for 75.0% of the total. The remaining seven families, Notacanthidae, Nettastomatidae, Phosichthyidae, Moridae, Hoplichthyidae, and Psychrolutidae were each represented by a single species (3.6%). However, Phosichthyidae was

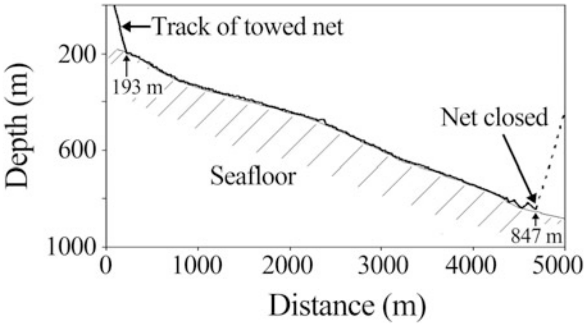

Fig. 15.3 Relationship between the towed larval net track and bottom depth in the near-bottom layer survey (st. I, 8 April 2009). (Reproduced from Takami and Fukui 2010)

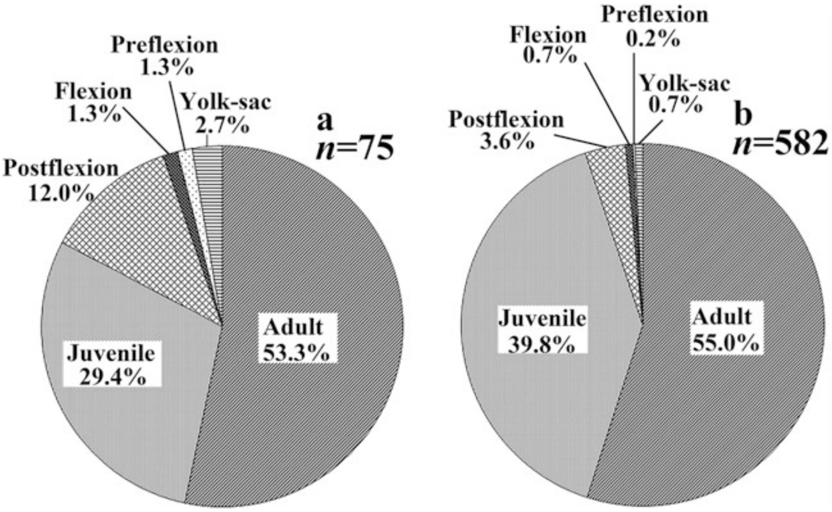

Fig. 15.4 Species (including unidentified taxa) (**a**) and individual (**b**) numbers in each developmental stage of deep-sea fishes occurring in the near-bottom layer of the upper continental slope in Suruga Bay

most abundant in terms of individuals, accounting for 29.0% of the total (Fig. 15.5b), followed by Macrouridae (23.7%), Synaphobranchidae (21.4%), Alepocephalidae (11.8%), Liparidae (7.6%), and Ophidiidae (10.7%). These six families accounted for 95.8% of the total. The remaining seven families (Notacanthidae, Neoscopelidae, Nettastomatidae, Moridae, Hoplichthyidae, Psychrolutidae, and Zoarcidae) each had fewer than three individuals (1.1%).

The top seven species for individual numbers (≧5%) were *Polymetme elongata* (Phosichthyidae) (*n* = 76), *Coelorinchus kishinouyei* (Macrouridae) (*n* = 55),

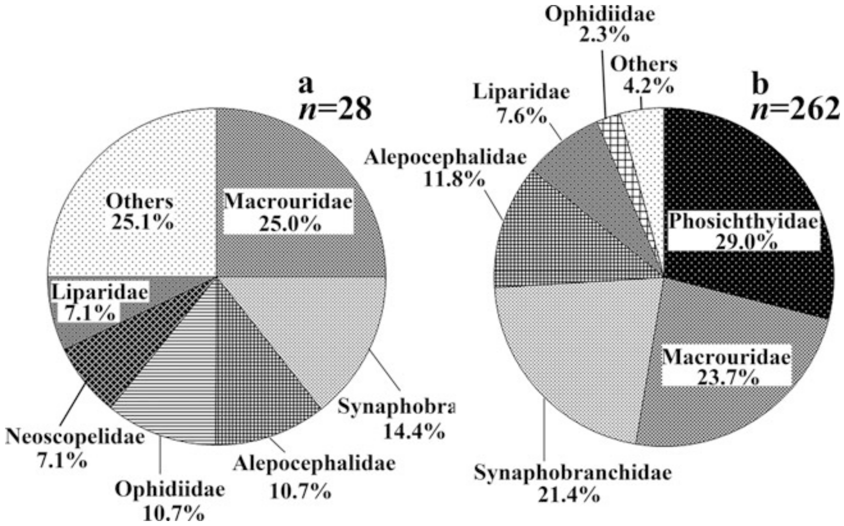

Fig. 15.5 Species (including unidentified taxa) (**a**) and individual (**b**) numbers in each family of larvae and juveniles occurring in the near-bottom layer of the upper continental slope in Suruga Bay

Synaphobranchus sp. 1 (Synaphobranchidae) (*n* = 33), *Simenchelys parasiticus* (Synaphobranchidae) (*n* = 17), *Paraliparis dipterus* (Liparidae) (*n* = 15), *Leptoderma lubricum* (Alepocephalidae) (*n* = 14), and *Leptoderma retropinnum* (*n* = 13). The first recorded larval or juvenile stages by near-bottom sampling were found for *Polymetme elongata*, *Leptoderma lubricum*, *Leptoderma retropinnum*, *Coryphaenoides marginatus* (Macrouridae) (*n* = 2), *Coelorinchus kishinouyei*, *Dicrolene tristis* (Ophidiidae) (*n* = 4) *Paraliparis dipterus*, and *Careproctus rhodomelas* (Liparidae) (*n* = 5), the total number for these eight species accounting for about 70% of the total number of collected larvae and juveniles.

Although the larval net (1.3 m in diameter) used in this study was at the small size range for collecting fish larvae and juveniles, many large-sized adult stages were collected. These included *Chlamydoselachus anguineus* (Chlamydoselachidae) (*n* = 1, 1058 mm TL), *Mitsukurina owstoni* (Mitsukurinidae) (*n* = 1, 1210 mm TL), *Coryphaenoides marginatus*, *Bathygadus antrodes*, and other species (Macrouridae) (*n* = 98, 83.9–486 mm TL), and *Synaphobranchus kaupii* (Synaphobranchidae) (*n* = 80, 236–478 mm TL). Net avoidance of the near-bottom sampling method in this study seemed to be low because many large-sized adult stage fishes were collected.

15.4 Characteristics of Larval and Juvenile Fishes in the Near-Bottom Layer and Water Column

Water column sampling included 277 species or unidentified taxa (*n* = 5518) representing 55 genera (29 families) (excluding coastal epipelagic species), collected by Isaacs-Kidd Midwater Trawl (IKMT) and 1.3 m larval net in and adjacent to Suruga Bay in depths less than approximately 540 m (100–2160 m above the seafloor).

Comparing the habitat categories, only 7.5% of all species collected were deep-sea demersal fishes, 70.9% being mesopelagic fishes in the water column (the remaining 21.6% of collected fishes were classified into the habitat category unknown group). Differences in developmental stages between the near-bottom layer and water column were also clear. In the near-bottom layer, the number of taxa and individuals were lowest for larval stage (17.3% and 5.2%, respectively) and highest in the adult stage (53.3% and 55.0%, respectively), whereas in the water column, the number of taxa was highest for larval stage (76.0%), followed by the juvenile stage (19.3%), and number of individuals highest for the juvenile stage (65.3%), followed by the larval stage (31.3%).

The 27 species or unidentified taxa of larvae and juveniles that appeared in the near-bottom layer were separated into the following three categories, based on their appearance in the near-bottom layer and water column (Table 15.1). Type A included all developmental stages collected in the near-bottom layer and not occurring in the water column (note, however, that adults of *Leptoderma lubricum* were also distributed in the water column). This type does not undergo ontogenic vertical migration (three species: *L. lubricum*, *L. retropinnum*, and *Paraliparis dipterus*). Type B-1 included larval to early juvenile stages in the water column, and the juvenile stage (including the larval stage just before metamorphosis) in the near-bottom layer. This type demonstrated ontogenic vertical migration, the vertical distance migrated varying among species (nine species: *Polymetme elongata*, unidentified species of Moridae, *Coryphaenoides marginatus*, *Coelorinchus kishinouyei*, *Coelorinchus* sp., three unidentified species of Macrouridae, *Hoplobrotula armata*). Type B-2 included juveniles and adults collected in the near-bottom layer, but had no larvae collected from either the near-bottom layer or water column (16 species: *Notacanthus abbotti*, *Simenchelys parasiticus*, *Ilyophis brunneus*, *Synaphobranchus affinis*, *Synaphobranchus* sp., *Nettastoma parviceps*, unidentified species of Alepocephalidae, *Neoscopelus macrolepidotus*, *Neoscopelus* sp., unidentified species of Macrouridae, *Dicrolene tristis*, unidentified species of Ophidiidae, unidentified species of

Table 15.1 Occurrence type based on each developmental stage of near-bottom layer species

			Near-bottom						Water column			
Type	Family	Species (types)	Y	Pre	Flex	Post	J	A	Pre	Flex	Post	J
A	Alepocephalidae	*Leptoderma lubricum*				+	+	+				
		Leptoderma retropinnum	+			+	+	+				
	Liparidae	*Paraliparis dipterus*	+		+	+	+	+				
B-1	Phosichthyidae	*Polymetme elongata*					+				+	+
	Moridae	unidentified sp. of Moridae		+					+			
	Macrouridae	*Coryphaenoides marginatus*[a]					+	+			+	+
		Coelorinchus kishinouyei[a]				+	+				+	
		Coelorinchus sp.[a]				+					+	+
		unidentified sp. 1 of Macrouridae[a]				+					+	
		unidentified sp. 2 of Macrouridae[a]				+					+	
		unidentified sp. 3 of Macrouridae[a]				+					+	
	Ophidiidae	*Hoplobrotula armata*					+				+	+
B-2	Notacanthidae	*Notacanthus abbotti*					+					
	Synaphobranchidae	*Simenchelys parasiticus*					+	+				
		Ilyophis brunneus					+	+				
		Synaphobranchus affinis					+	+				
		Synaphobranchus sp.					+					
	Nettastomatidae	*Nettastoma parviceps*					+	+				
	Alepocephalidae	Unidentified sp. of Alepocephalidae				+						
	Neoscopelidae	*Neoscopelus macrolepidotus*					+					
		Neoscopelus sp.					+					
	Macrouridae	unidentified sp. 4 of Macrouridae					+					
	Ophidiidae	*Dicrolene tristis*					+	+				
		Unidentified sp. of Ophidiidae					+					
	Hoplichthyidae	Unidentified sp. of Hoplichthyidae					+					
	Psychrolutidae	*Ebinania* sp.					+					
	Liparidae	*Careproctus rhodomelas*					+	+				
	Zoarcidae	*Melanostigma orientale*					+	+				

Y yolk-sac stage, *Pre* preflexion stage, *Flex* flexion stage, *Post* postflexion stage, *J* juvenile stage, *A* adult stage
[a] Larval stage includes postflexion stage

Hoplichthyidae, *Ebinania* sp., *Careproctus rhodomelas*, and *Melanostigma orientale*).

15.5 Ontogeny of Deep-Sea Demersal Fishes

This section presents the ontogeny of three species determined as type A (above, all developmental stages in the near-bottom layer); *Leptoderma lubricum* and *L. retropinnum* (Alepocephalidae) and *Paraliparis dipterus* (Liparidae).

15.5.1 *Leptoderma lubricum* and *L. retropinnum*

The family Alepocephalidae (Alepocephaliformes) comprises benthic and pelagic deep-

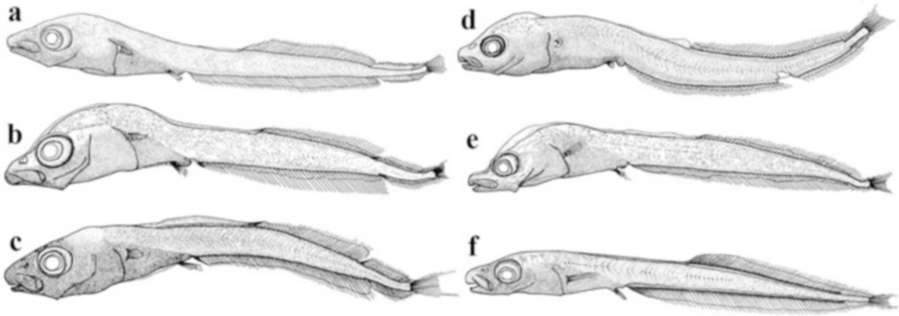

Fig. 15.6 Larvae and juveniles of *Leptoderma lubricum* (**a**–**c**) and *Leptoderma retropinnum* (**d**–**f**). (**a**) 26.9 mm SL, postflexion stage; (**b**) 31.8 mm SL, juvenile stage; (**c**) 42.9 mm SL, juvenile stage; (**d**) 22.2 mm SL, yolk-sac stage; (**e**) 28.4 mm SL, juvenile stage; (**f**) 57.6 mm SL

sea fishes, included in about 23 genera with at least 90 species (Markle and Quéro 1984; Nelson et al. 2016). Adults are characterized by the head usually lacking scales, gill membranes separated from the isthmus, one or two supramaxillae, the tongue lacking teeth, the dorsal-fin base origin located posterior to the midpoint of the body, and the absence of an adipose fin, swim bladder and luminous gland on the postcleithrum (McEachran and Fechhelm 1998; Sazonov and Markle 1999). Identification of larvae and juveniles in the family is difficult, even at the generic level, owing to the lack of good representative series of specimens at early life history stages (Richards and Hartel 2006). In fact, alepocephalid larvae and juveniles are known for only six species belonging to four genera (Holt and Byrne 1908; Badcock and Larcombe 1980; Markle and Krefft 1985; Ambrose 1996), all possessing a translucent occipital region, horizontally elongate eyes, and a black head (except upper surface) and abdominal cavity (Holt and Byrne 1908; Badcock and Larcombe 1980; Markle and Krefft 1985; Ambrose 1996). Alepocephalids are thought to spawn large, presumably demersal eggs (2–8 mm in diameter) (Markle and Quéro 1984; Sazonov and Williams 2001), but other aspects of their spawning ecology are essentially unknown.

Leptoderma is a relatively medium-sized alepocephalid genus [ca. 26 cm in maximum standard length (SL)], comprising six species (Sazonov and Ivanov 1980; Markle and Quéro 1984; Angulo et al. 2016). All are characterized by a remarkably elongate blackish or grayish-blue body, almost circular eyes, the anal-fin base origin anterior to the dorsal-fin base origin, the procurrent caudal-fin rays close to the vertical-fin rays, and a lack of scales, except on the lateral line (Sazonov and Ivanov 1980; Markle and Quéro 1984; Sazonov and Markle 1999). Two species, *L. lubricum* and *L. retropinnum*, are distributed in Japanese waters, differing from each other in membrane morphology between the vertical-fin rays and procurrent caudal-fin rays (Nakabo and Kai 2013a).

A total of 31 larval and juvenile alepocephalids were collected from the near-bottom layer. These were divided into three types, according to meristic characters and membrane morphology between the vertical-fin rays and procurrent caudal-fin rays. Among them, two types were identified as *L. lubricum* (26.9–69.0 mm SL, *n* = 14) and *L. retropinnum* (21.1–67.2 mm SL, *n* = 13), respectively, on the basis of separation (*L. lubricum*) or otherwise (*L. retropinnum*) of the membrane between the vertical-fin rays and procurrent caudal-fin rays, and dorsal- and anal-fin ray numbers (Fig. 15.6). The ontogeny of *L. lubricum* and *L. retropinnum* are outlined here, including adult specimens [*L. lubricum* (*n* = 4), 170.7–229.9 mm SL; *L. retropinnum* (*n* = 13), 87.8–202.9 mm SL].

The smallest specimens of *L. lubricum* and *L. retropinnum* (26.9 mm SL and 21.1 mm SL, respectively) were already at the postflexion stage, the two smallest (21.1 and 22.2 mm SL) of *L. retropinnum* having the yolk-sac occupying about half of the abdominal cavity. Therefore, it is conceivable that species of *Leptoderma* reach the postflexion stage very early, shortly after hatching. The smallest specimens of both species already possessed general adult characters, such as a remarkably elongate body, the relative position of the dorsal- and anal-fin bases, and fin ray complement [except procurrent caudal (*L. lubricum*) or pectoral-fin (*L. retropinnum*)]. Only three morphological differences were evident between the larval and adult stages of both species; a horizontally elongate eye, translucent occipital region, the head below the upper orbital margin, and the abdominal cavity densely covered by melanophores. Pectoral-fin rays were completed (juvenile stage) at 28–30 mm SL, with no discontinuous morphological changes observed. Subsequently, the eyes gradually become round with growth [completed at 61.4 mm SL (late juvenile stage in *L. lubricum*) and 163.1 mm (adult stage) in *L. retropinnum*]. The translucent occipital region gradually became covered with melanophores, to be colored similarly to the rest of the head. Accordingly, the ontogeny of *Leptoderma* can be characterized by the acquisition of general adult characters before and during the postflexion stage (before complete absorption of the yolk-sac in *L. retropinnum*), with indistinct transformation thereafter and the retention of few larval characters during the juvenile stage, similar to other known larval and juvenile fishes of Alepocephalidae (Holt and Byrne 1908; Badcock and Larcombe 1980; Markle and Krefft 1985; Ambrose 1996).

The onset of the juvenile stage in *Leptoderma* (28.4 mm SL in *L. retropinnum*; 29.7 mm SL in *L. lubricum*) is the smallest known among Alepocephalidae [35–36 mm SL in *Alepocephalus bairdii* (see Holt and Byrne 1908), <40 mm SL in *Bajacalifornia megalops* (see Markle and Krefft 1985), 58.5 mm SL in *Talismania bifurcate* (see Ambrose 1996), and 66.6 mm SL in *Bajacalifornia burragei* (see Ambrose 1996)]. However, the lengths at onset of the juvenile stage are unrelated to maximum adult lengths, being 18–26 cm SL in two species of *Leptoderma* (see Sazonov and Ivanov 1980; Machida 1984), *T. bifurcate* (see Parr 1951), and *B. burragei* (see Markle and Krefft 1985), ca. 40 cm SL in *B. megalops* (see Markle and Sazonov 1990), and 100 cm SL in *A. bairdii* (see Markle and Sazonov 1990). These adults are distributed mainly near bottom in the deep sea, similar to *Leptoderma* (see Markle and Quéro 1984; Ambrose 1996). The larvae and juveniles of the two present species of *Leptoderma* and *A. bairdii* (see Holt and Byrne 1908) (≤36 mm SL at juvenile onset) are distributed near bottom, whereas those of two species of *Bajacalifornia* and *T. bifurcate* (>37 mm SL) rise to the water column (Markle and Krefft 1985; Ambrose 1996). That is to say, onset juveniles reflect the early stage habitats of Alepocephalidae, those in the near-bottom layer together with adults having a small SL at the juvenile stage, whereas those in the water column separated from adults are characterized by a large juvenile stage SL, although the latter still lack specialized pelagic lifestyle morphology.

Larval and juvenile *Leptoderma lubricum* were collected when the maximum net depth reached 633–937 m, but not when it was shallower than 607 m. Those of *L. retropinnum* were collected at maximum net depth 607–966 m, but not when shallower than 575 m. The distribution depth of adult *L. lubricum* is 1000–1700 m, and of adult *L. retropinnum*, 500–1786 m (Nakabo and Kai 2013a), the surveys suggesting that early stage *L. lubricum* occurred in shallower depths than the adult stage, and that the habitats of larvae and juveniles of the two species of *Leptoderma* overlapped.

Gut contents were found in all examined larvae and juveniles of the two species of *Leptoderma* (11 individuals of each). Food items in both species were mostly benthic or near-bottom species, including those of Polychaeta, Harpacticoida, Cumacea, and Amphipoda, suggesting that the early life history of both species of *Leptoderma* is strongly dependent on the near-bottom habitat. On the other hand, inter-specific differences in the dominant prey taxa [Radiolaria (72.8%) in juvenile *L. lubricum* vs. Harpacticoida (72.1%) in juvenile *L. retropinnum*] implied differences in food selectivity and/or degree of near-bottom dependence, adult *L. lubricum* having been frequently collected from the water column, unlike adult *L. retropinnum*.

Adults of both species (one of *L. lubricum*; eight of *L. retropinnum*) had ovarian eggs. The total fecundities of each species were 4898 (*L. lubricum*) and 1883–3026 (average ± standard deviation, 2389.0 ± 475.7) (*L. retropinnum*), the number of well-developed ovarian eggs being 69 (maximum diameter 3.45 mm) and 22–46 (34.3 ± 7.6) (maximum diameter 3.56 mm), respectively. These results suggested that *Leptoderma* has large mature eggs, as in other alepocephalids, and spawns very few eggs at any time. In addition, the occurrence of *L. retropinnum* with developed ova in January, March–May, August–October, and December indicated that the species spawns year-round.

15.5.2 Paraliparis Dipterus

The liparid genus *Paraliparis* includes benthic, benthopelagic, and pelagic species, occurring from 100 m to abyssal depths. *Paraliparis* is characterized by a single nostril and one or (rarely) two suprabranchial pores on each side, a ventral sucking disk with pseudobranchs absent, six branchiostegal rays, no skin flaps or barbels on the head, the gill slit either entirely above the pectoral-fin base or above it and extending ventrally over a number of fin rays, and the pectoral-fin lower lobe comprising more than two rays (Kido 1988; Stein and Tompkins 1989; Stein et al. 2001; Stein 2012; Takami and Fukui 2012; Murasaki et al. 2020). Although about 140 species are known to date, occurring in all of the world's oceans (Murasaki et al. 2020), larval and juvenile *Paraliparis* have rarely been collected, resulting in scarce knowledge of larval morphology represented only by four species; *Paraliparis holomelas* (North Pacific) (Busby and Cartwright 2006), *Paraliparis cephalus* (eastern Pacific) (Ambrose 1996), and *Paraliparis calidus* and *Paraliparis copei* (both western North Atlantic) (Able et al. 1986). Among them, post-yolk-sac larval development in *P. holomelas* and flexion larvae of *P. calidus* have been reported, the former possessing a flexed notochord tip while retaining the yolk, in addition to a full complement of fin rays (except pectoral-fin) and the gill opening positioned similarly to that in adults, both developing directly.

Near-bottom sampling collected 28 adult (17.2–47.2 mm SL) and 18 flexion stage with yolk-sac to juvenile (5.6–16.5 mm SL) specimens (Fig. 15.7). Larval and juvenile *P. dipterus* can be distinguished from the other 13 Japanese species of *Paraliparis* by the number of dorsal- (54–58), anal- (48–54), and caudal-fin rays (6), the horizontal mouth, a coronal pore present, and the gill slit extending ventrally to the 1st–4th pectoral-fin ray base (Kido 1988; Nakabo and Kai 2013b; Murasaki et al. 2018, 2019, 2020; Kai et al. 2020).

The smallest specimen collected (5.6 mm SL) had a large yolk-sac, indicating that it had been recently hatched. The specimen had already attained general adult characters, except the remarkably short pectoral-fin and slightly posteriorly positioned anus. Body proportions in the specimens were almost conserved from the larval to adult stages, except pectoral-fin length and pre-anal length. Notochord tip flexion was completed at 9.4 mm SL. Full numbers of the upper and lower pectoral-fin rays were complete at 7.3 mm SL and 11.1 mm SL, respectively. The pectoral-fin upper lobe continuously elongated until about 30 mm SL (adult stage). The anus position continued to move anteriorly until 24.5 mm SL (adult stage). Minute melanophores were scattered dorsally on the trunk and laterally around the midpoint of the tail, with the abdominal cavity blackish, at 5.6 mm SL. Subsequently, melanophores progressively increased in number with development, being densely distributed on the entire body, expect posteriorly on the head and the posterior 1/5 of the tail. Accordingly, the ontogeny of *P. dipterus* is characterized by the general acquisition of adult characters during

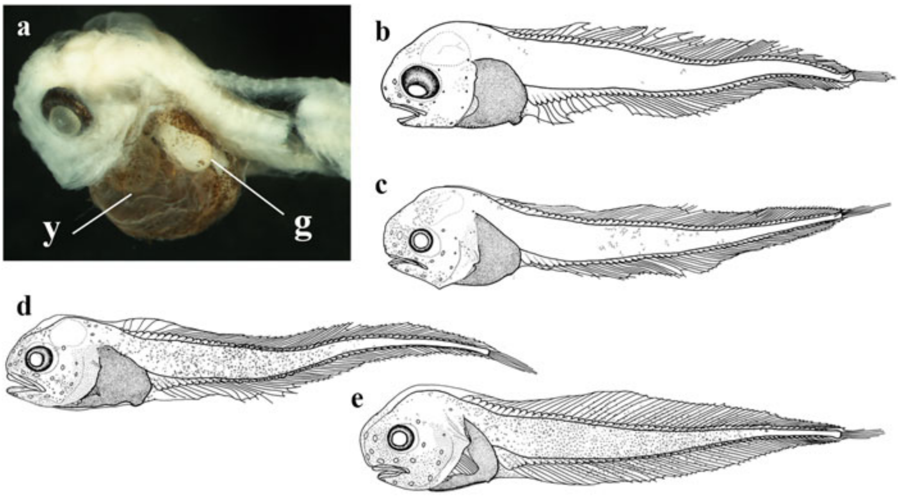

Fig. 15.7 Larvae and juveniles of *Paraliparis dipterus*. (**a**) photograph of 5.6 mm SL, yolk-sac stage; (**b**) 6.4 mm SL, yolk-sac stage; (**c**) 7.3 mm SL, flexion stage; (**d**) 10.1 mm SL, postflexion stage; (**e**) 11.2 mm SL, juvenile stage. *y* Yolk-sac, *g* gut

the larval stage, followed by indistinct transformation thereafter, with some characters changing subtly throughout the juvenile to adult stages.

Larval and juvenile *P. dipterus* were collected from 174 to 802 m depth, a range similar to collected depths of adults (185–965 m), suggesting that larvae and juveniles are sympatric with adults. Gut contents were not observed in yolk-sac larvae ($n = 2$), but were found in three out of five larvae after yolk-sac absorption and all juveniles ($n = 7$). Food items included four taxa, Radiolaria (20.6%), Calanoida (8.8%), Harpacticoida (26.5%), and other copepods (except Calanoida and Harpacticoida) (26.5%). The dominant prey taxa of *P. dipterus*, as in *Leptoderma*, were Radiolaria and Harpacticoida.

The collected adults of *P. dipterus* included 18 females (17.2–47.2 mm SL). The maximum diameter of ovarian eggs was 2.3 mm, with total fecundities ($\geqq$0.1 mm in diameter) of 322–735 (507.3 ± 160.5). Ova could be subdivided into “undeveloped” (0.1–0.8 mm diameter classes, translucent to milky white in color) and “developed” (0.9–2.3 mm, bright yellow to yellow) groups, based on the size distribution of ovarian eggs. Moreover, the “developed” group comprised only one ($n = 3$) or two ($n = 1$) size distributions, the ova in each distribution numbering 8–18 (13.4 ± 4.1, $n = 5$). According to Stein (1980), who noted the relationship between the maximum number of “developed” eggs and spawning patterns, *P. dipterus* is a continuous spawner due to the low numbers (8–18) in each distribution of the “developed” ova group. The periods during which both yolk-sac larvae (February and June) and adults possessing “developed” eggs were present (June, July, November, and December) suggest that *P. dipterus* spawns year-round.

15.6 Characteristics and Ecological Significance of the Ontogeny of Deep-Sea Demersal Fishes

A comparison of larval and adult presence in the near-bottom layer and water column showed that larval and juvenile fishes collected from the near-bottom layer could be classified into three types (Fig. 15.8) Type A was the most dependent on the near-bottom layer. The three species of this type (*Leptoderma lubricum*, *L. retropinnum*, and *Paraliparis dipterus*) do not have ontogenetic vertical migration and live only in the near-

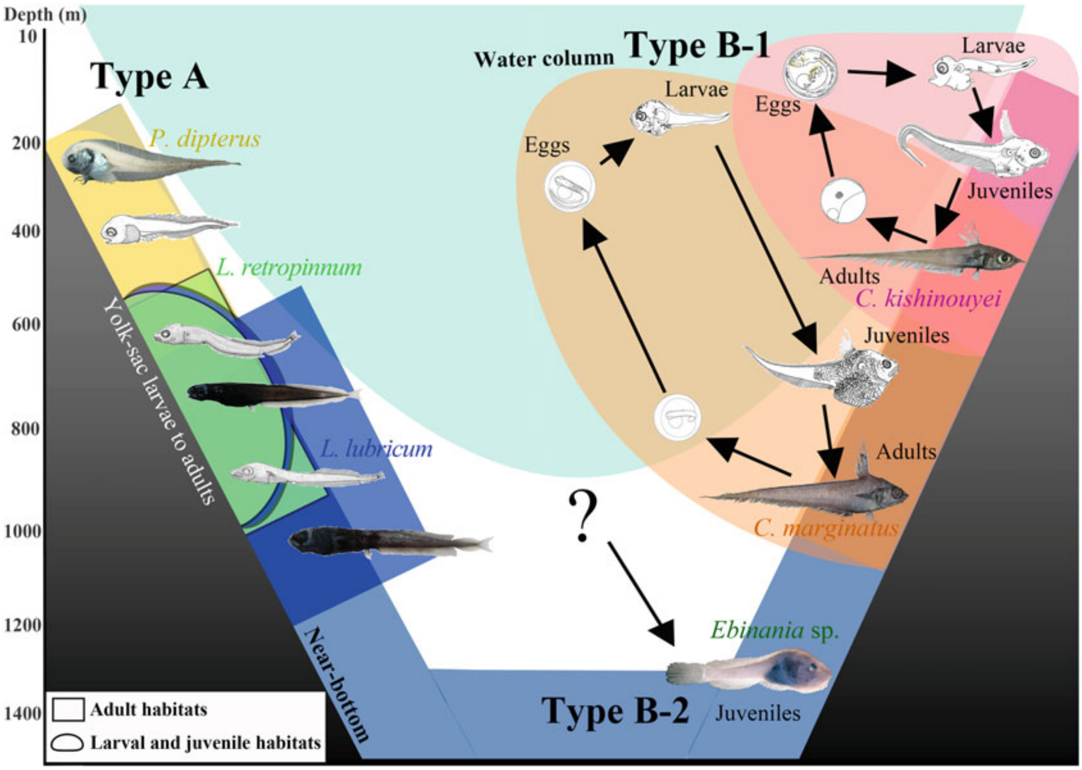

Fig. 15.8 Illustration of three ecological types based on the ontogeny of near-bottom layer species on the upper continental slope of Suruga Bay. *Leptoderma lubricum* and *Leptoderma retropinnum*: Takami and Fukui (2010); *Paraliparis dipterus*: Takami and Fukui (2012); *Coryphaenoides marginatus*: Fukui et al. (2008); *Coelorinchus kishinouyei*: Fukui et al. (2010)

bottom layer throughout their life history. On the other hand, type B-1 has ontogenetic vertical migration, rising to shallower depths in the water column during the egg and larval stages, and returning to the near-bottom layer mainly after the late juvenile stage.

Significant differences occur between the ontogeny of types A and B. Type A spawns a limited number of large demersal eggs. In general, ascent to shallower depths during early life history occurs mainly during the egg stage. However, the egg characteristics of type A are consistent with the absence of ontogenetic vertical migration. Large eggs increase the size of hatched larvae, which acquire many adult morphological characteristics, such as fin ray complement, from the early larval stage. These are linked to improved swimming ability from early development. The three species of type A are all suggested as year-round spawners. Although the distribution depth of *P. dipterus* was slightly shallower than the other type A species, the distribution depth of the larval and juvenile stages overlapped among the three species. Food items of the latter were also commonly dominated by Radiolaria and Harpacticoida, the overall indication being that the larvae and juveniles of the three species share spatial-temporal distribution, and are in a competitive relationship. However, both the number of species and individual larvae and juveniles in the near-bottom layer of the upper continental slope of Suruga Bay were very low, suggesting that the competitive relationship between the different species and within a single species in the layer may differ from that in the epipelagic zone used by many larvae. On the other hand, the number of species and individuals in the near-bottom layer was highest for the adult stage, followed by the juvenile stage, and lowest for the larval stage. This suggests that feeding pressure from more developed fishes is higher for near-bottom larvae. The completion of many adult morphological characters at a smaller body size in type A larvae and juveniles may also aid against predation (reduction of predation pressure).

Type B-1 species spawn large numbers of pelagic eggs, of smaller size than in type A. In addition, type B-1 undergoes ontogenetic vertical migration, hatches at an immature state, and has a distinct metamorphic stage. For example, the diameter of pelagic eggs of *Coryphaenoides marginatus* is 1.14–1.31 mm (Fukui et al. 2008), the number of mature ovarian eggs being about 54,000. Similarly, pelagic egg diameters of *Coelorinchus kishinouyei* are 1.18–1.31 mm (Fukui et al. 2010), with about 6000 mature ovarian eggs. The spawning period of type B-1 is not year-round, as in type A, being September to April in *C. marginatus* and April to September in *C. kishinouyei*. The depth layer reached by ontogenetic vertical migration varies with species, most eggs of *C. kishinouyei* rising to a depth of 100–200 m, whereas most of *C. marginatus* rise only to 200–350 m (Fukui et al. 2008, 2010). Both species hatch at about 3 mm TL, with mouths unopened, and develop in depths of 350 m or less (but not at the surface). Subsequently, larvae sink to the seafloor, appearing in the near-bottom layer from around 20 mm TL (*C. kishinouyei*) and 30 mm TL (*C. marginatus*).

In species in the third type (type B-2), only juvenile stage individuals appeared in the near-bottom layer of the upper continental slope, with no larval stages collected from either the near-bottom layer or the water column. One possible reason for this phenomenon is that the species spawns and develops outside the study area, entering Suruga Bay after the juvenile stage, as in Anguillidae. However, it is unlikely that all type B-2 species have such an early life history. The two species of Alepocephalidae collected in this study were type A, which complete their life history in the near-bottom layer, but some Alepocephalidae larvae have been collected from the mesopelagic zone (Markle and Krefft 1985; Ambrose 1996). The collection of near-bottom layer specimens in this study was limited to those occurring 1–8 m above the seafloor, there being a significant interval without collecting effort between the sampled water column (shallower than 540 m depth) and the near-bottom layer. It may be that larval stages of the type B-2 species are distributed over a wider range of near-bottom layer than considered in this study or in the meso-bathypelagic zone, where collecting efforts are infrequent. It is important to increase collection efforts in near-bottom and meso-bathypelagic zones so as to clarify the overall picture of deep-sea demersal fish species ontogeny.

15.7 Current Status of Larval Fish Taxonomy in Japan

The beginnings of larval fish taxonomy in Japan can be traced back to the end of the nineteenth century. Subsequently, from the middle of the twntieth century, large scale larval fish surveys under the auspices of the Fisheries Agency resulted in publications by Uchida et al. (1958) and Mito (1966) (Okiyama 1988a). Subsequently, atlases of early stage Japanese fishes were published by Okiyama (1988b, 2014). However, the number of species of larval and juvenile stage fishes published in Okiyama (2014) was 1544, about one-third of the total number of Japanese fishes. In fact, about half of the marine fish families (149 families) in Japanese waters have less than 50% of species for which larvae have been described. The percentages of the number of described larvae in each family of Japanese marine fishes and larvae not identified at the species level out of the total number of described larvae are summarized in Table 15.2 [based on Nakabo 2013; Okiyama 2014].

To date, 24 families recorded from Japan have had no larvae reported from Japanese waters, although 15 have had larvae reported from elsewhere (Leis et al. 1993; Lamkin 1997; Okiyama

Table 15.2 Percentages of Japanese marine fish species with larval descriptions, and unidentified larvae (at species level) relative to the number of larvae described [based on Nakabo 2013; Okiyama 2014]

Percentage of species with described larvae	Percentage of larvae not identified to species level relative to number of larvae described			
	0	≦30	>30 to ≦70	>70
Larvae undescribed from Japan	Myrocongridae, Colocongridae, Monognathidae[a], Ariidae[a], Paraulopidae[a], Melanonidae[a], Macrouroididae, Aphyonidae[a], Solenostomidae[a], Plectrogenidae, Parabembridae, Bembridae, Pseudochromidae[a], Banjosidae, Glaucosomatidae[a], Bathyclupeidae, Drepanidae[a], Ariommatidae[a], Parabrotulidae, Clinidae[a], Xenisthmidae[a], Citharidae[a], Aracanidae[a], Triodontidae[a]			
≦10	Bythitidae, Liparidae, Zoarcidae, Tripterygiidae, Balistidae		Pomacanthidae	Ogcocephalidae, Peristediidae
>10 to ≦20	Ateleopodidae, Syngnathidae, Tetrarogidae, Aploactinidae, Plesiopidae, Epigonidae, Lethrinidae, Branchiostegidae, Callionymidae, Triacanthodidae	Alepocephalidae, Macrouridae, Serranidae, Pomacentridae, Pinguipedidae, Acanthuridae	Antennaridae, Nemipteridae, Mullidae, Labridae, Scaridae, Ptereleotrinae	Ophichthidae, Chlorophthalmidae, Linophrynidae, Oneirodidae, Cetomimidae, Holocentridae, Triglidae, Hoplichthyidae
>20 to ≦30	Aulopidae, Howellidae, Echeneidae, Caristiidae, Gerreidae, Embiotocidae, Cyclopteridae, Percophidae, Uranoscopidae, Chaenopsidae, Draconetiidae, Microdesmidae, Siganidae, Monacanthidae, Tetraodontidae	Gobiidae	Leiognathidae	Polymixiidae, Notocheiridae, Kraemeriidae
>30 to ≦40	Platytroctidae, Moridae, Synanceiidae, Acropomatidae, Symphysanodontidae, Emmelichthyidae, Sciaenidae, Cepolidae, Kyphosidae, Soleidae, Cynoglossidae, Ostraciidae	Carapidae, Sebastidae, Apogonidae, Chaetodontidae, Blenniidae	Lophiidae, Ambassidae, Ephippidae	Synaphobranchidae, Diceratiidae
>40 to ≦50	Muraenesocidae, Derichthyidae, Plotosidae, Chauliodontidae, Veliferidae, Lophotidae, Caulophrynidae, Melamphaidae, Anomalopidae, Gobiesocidae, Samaridae, Diodontidae, Sphyraenidae, Psychrolutidae, Parazenidae, Zeniidae, Zeidae, Grammicolepididae, Macroramphosidae, Centriscidae, Mugillidae, Dactylopteridae, Latidae, Ostracoberycidae, Scombropidae, Pempheridae, Stromateidae, Polynemidae, Ereuniidae	Synodontidae, Atherinidae, Cottidae	Muraenidae, Sternoptychidae, Melanostomiidae, Trachichthyidae, Scorpaenidae, Opistognathidae	Albulidae, Serrivomeridae, Idiacanthidae, Himantolophidae, Neosebastidae

>50 to ≦60	Argentinidae, Teraponidae, Creediidae	Ophidiidae, Priacanthidae, Carangidae, Lutjanidae, Haemulidae, Stichaenidae, Trichiuridae	Astronesthidae, Platycephalidae	
>60 to ≦70	Nemichthyidae, Clupeidae, Diretmidae, Pegasidae, Cheilodacthylidae, Bathymasteridae, Pholidae, Trichonotidae, Caproidae, Gempylidae	Bregmacerotidae, Malacanthidae, Paralichthyidae,	Congridae, Ceratiidae, Callanthiidae,	Notacanthiformes[b], Chaunacidae
>70 to ≦80	Neoscopelidae, Trachipteridae, Gadidae, Sparidae, Sillaginidae, Pentacerotidae, Centrolophidae, Molidae	Phosichthyidae, Myctophidae, Cirrhitidae, Bothidae	Malacosteidae, Champsodontidae	Gigantactinidae
>80 to ≦90	Opisthoproctidae, Paralepididae, Exocoetidae, Bramidae, Ammodytidae	Microstomatidae, Caesionidae, Agonidae, Scombridae	Chiasmodontidae	
>90	Elopidae, Megalopidae, Pterothrissidae, Anguillidae, Eurypharyngidae, Engraulidae, Chirocentridae, Chanidae, Gonorynchidae, Salangidae, Stomiidae, Pseudotrichonotidae, Giganturidae, Bathysauridae, Bathysauroididae, Scopelarchidae, Evermannellidae, Sudidae, Alepisauridae, Lampridae, Regalecidae, Merlucciidae, Centrophrynidae, Neoceratiidae, Melanocetidae, Rondeletiidae, Barbourisiidae, Gibberichthyidae[c], Berycidae, Monocentridae, Anoplogastridae, Oreosomatidae, Hypoptychidae, Aulothynchidae, Aulostomidae, Fistulariidae, Belonidae, Scomberesocidae, Sebastolobidae, Apistidae, Centrogeniidae, Lateolabridae, Polyprionidae, Giganthiidae, Rachycentridae, Coryphaenidae, Menidae, Lobotidae, Monodactylidae, Scorpididae, Oplegnathidae, Microcanthidae, Girellidae, Nomeidae, Tetragonuridae, Anoplopomatidae, Hexagrammidae, Trichodontidae, Rhamphocottidae, Hemitripteridae, Cryptacanthodidae, Anarhichadidae, Ptilichthyidae, Zaproridae, Icosteidae, Scatophagidae, Luvaridae, Zanclidae, Scombrolabracidae, Istiophoridae, Xiphiidae, Pleuronectidae, Poecilopsettidae, Triacanthidae	Gonostomatidae, Notosudidae, Hemiramphidae	Moringuidae, Chlopsidae, Nettastomatidae, Ipnopidae	

[a] Larvae reported from other than Japanese waters

[b] Including only Lipogenyidae and Notacanthidae

[c] Not listed in Nakabo (2013)

and Kato 1997; Pironet and Neira 1998; Sabatés 1998; Leis and Carson-Ewart 2000; Johnson and Britz 2005; Richards 2006; Sado and Kimura 2006; Lima et al. 2013; Leis 2015; Matsuura and Middleton 2016; Zavala-Muñoz et al. 2016; Poulsen et al. 2018). Collection data (location, time, season, and method of collection) for these families elsewhere should assist in the discovery of larvae around Japan (except Glaucosomatidae: larval stage described from reared specimens). Six of the nine families for which no larvae have been described are represented by deep-sea demersal species (Myrocongridae, Colocongridae, Macrouroididae, Plectrogenidae, Parabembridae, Bembridae, and Bathyclupeidae). In order to detail larval development in these families, it seems necessary to increase collection efforts in the aforementioned near-bottom layer and meso-bathypelagic zone with reference to previously recorded depths and distribution. Of the remaining families, a juvenile stage only of Banjosidae has been reported from Japan (Matsunuma and Motomura 2017), and Parabrotulidae is known to be viviparous, with adults distributed in the meso-bathypelagic zone (Miya and Nielsen 1991).

Families with less than 10% of larvae described are thought to spawn demersal eggs or be viviparous. It is also interesting to note that some of these families include species in which the eggs are guarded by an adult until they hatch (eggs of deep-sea Liparidae are protected in the gill cavity of crabs) (Shiogaki and Dotsu 1973; Kawase 1998; Nelson et al. 2016; Gardner et al. 2016). In these families, larvae may be distributed in the same layer as adults. For example, deep-sea near-bottom layer surveys may be useful for deep-sea Liparidae, Zoarcidae, and Bythitidae, and investigations of the near-bottom layer or crevices of coral reefs and rocky shores for Tripterygiidae, Balistidae, and shallow water Bythitidae. However, surveys of the near-bottom layer or crevices of coral reefs and rocky shore areas with existing methods (nets) for collecting larval fishes are difficult. New collection methods and devices need to be considered. There are now examples of diving and submersible observations and collections that have contributed to the clarification of larval fish morphology (Endo et al. 2010; Matsuura and Middleton 2016; Nonaka et al. 2021). It is likely that such methods will continue to be effective in the discovery of previously unknown fish larvae.

The occurrence of diel and ontogenetic vertical migration during early life stages, with the larvae of some species appearing in a deeper layer (below the surface layer), has been long known, with larval sampling in the epipelagic zone (≦200 m depth) or deeper having been conducted around Japan for several decades (Okiyama 1965; Tanaka 1981; Ozawa 1986; Kitagawa and Okiyama 1997). In recent years, high-performance mid-water trawl gear has been developed and used for resources and ecological studies in the epipelagic and mesopelagic zones (Oozeki et al. 2004, 2012a, b; Sassa 2019; Miller et al. 2020). However, most families including species that are rarely collected from the surface and more often from a layer deeper than the upper epipelagic zone (deeper than about 100 m) (including oblique tows to the surface), belong to the 10–50% group (Platytroctidae, Alepocephalidae, Chlorophthalmidae, Polymixiidae, Macrouridae, Zeniidae, deep-sea Sebastidae and Scorpaenidae, Synanceiidae, Psychrolutidae, Cepolidae, Nemipteridae, Branchiostegidae, Opistognathidae, Pinguipedidae, Percophidae, Uranoscopidae) (Okiyama 2014). This indicates a lack of collecting effort for larval taxonomic studies in depths below than the upper epipelagic zone in Japan. In addition, despite the inclusion of species that occur rarity at the surface, families with abundant larval stage information (Microstomatidae, Myctophidae, and Scopelarchidae) are offshore groups, while the aforementioned families include many coastal species, suggesting an offshore bias in collection effort at depths bellow the upper epipelagic zone.

Most of the families with a high percentage of larvae unidentified at the species level are characterized by overlapping meristic characters among species and a lack of unique morphological characteristics in the larval stages (for example, Mullidae, Labridae, Holocentridae, Callionymidae, and Acanthuridae). Because larvae are usually not described if they cannot be identified to species level, such families are included in the 0% type ratio group. Identification by DNA analyses should contribute greatly to clarification of larval stage morphology of these taxa. As Leis (2015) noted, it is important to describe the morphology of larvae identified by DNA analysis. In the case of such larvae, that have poor morphological characteristics and are difficult to identify only from conventional larval characters (e.g., melanophores and meristic characters), it is necessary to discover new diagnostic characters. For example, it may be useful to observe fresh body coloration (e.g., xanthophores, erythrophores, and iridophores), which has not been widely used because of its rapid disappearance after fixation (Smith 1995; Fujita et al. 2000; Baldwin 2003; Baldwin et al. 2009; Baldwin and Johnson 2014). In addition, it may also be valuable to pay attention to characteristics that are easily damaged. The underwater photographs of larvae and juveniles taken during diving often show a delicate morphology that is not apparent due to damage to the specimens when collected by net, although the latter are mainly used in larval taxonomic studies (Nonaka et al. 2021). However, DNA analysis and concurrent morphological observations on various taxa are difficult following typical net collection of specimens, in which a large number of larval fish and other plankters are collected at the same time, due to larvae being small and fragile, and prone to rapid decay. The sharing of small innovations in procedures and methods for sorting, specimen preparation, and photography among researchers should dramatically increase the efficiency of this work.

Even in species for which larval morphology has been reported, attention should be paid to whether or not fresh body coloration has been described, in addition to all developmental stages. Most descriptions of larvae and juvenile stages to date have been based on preserved specimens, there having been few descriptions of body coloration other than melanophores. Baldwin (2013) suggested that the ontogeny of pigment patterns in marine fishes may be an even riper source of phylogenetic information, yet to be tapped. In addition, improved information on fresh body coloration of larvae and juveniles will contribute to the accuracy of identification of larval photographs. Studies of fish fauna and biogeography have been conducted on adults using the Image Database of Fishes in the Kanagawa Prefectural Museum of Natural History, including photographs taken by many divers, in addition to fish collection and literature (Senou et al. 1997, 1998, 2006). If similar studies could be conducted for larval stages, our knowledge of the appearance and distribution of early life stages would be greatly enhanced. Because there are many species for which only a few developmental stages have been described, the discovery of an undescribed developmental stage, even if representing only a brief period of development, is worth reporting. Such records, even if representing intermittent periods, can be important for elucidating a complete picture of the early life history of a species. While a report on many developmental stages simultaneously is most desirable, such may require years of investigation. This is because many fishes inhabit specific habitats at each developmental stage or at different times of day. In addition, post-juvenile stages become more difficult to collect due to their increased swimming ability. Therefore, in order to cover all the developmental stages, a variety of collection methods may be necessary. Furthermore, many fishes have specific spawning seasons, each developmental stage appearing only in a specific season. In other words, if the appropriate collecting method for the larval type in particular season is not used, the next opportunity to collect specimens will be a year later! As described above, the ecological diversity of larval fishes both delights researchers and makes difficult the clarification of their early life history.

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Morphological Diversity of the Lateral Line System in Teleostei

16

Mao Sato

Abstract

The morphological diversity of the lateral line system in Teleostei is reviewed, referring especially to morphological, phylogenetic, and taxonomic studies for the system. The system comprises a number of sensory organs denominated neuromasts, along with associated tubular structures (lateral line canals) passing through specific bones and scales. Each component of the system (viz., the canals, scales, and neuromasts) varies in its morphology among the fishes, reflecting their respective habitats, habits, and phylogenetic backgrounds. In this chapter, a representative condition is introduced for lateral line canals, neuromasts, and associated cranial nerves, followed by derivative conditions observed in specific taxa. A heterochronic change, which is a mechanism leading to produce the morphological diversity of the system, is also mentioned. Furthermore, recent progresses in anatomical studies of the system in Apogonidae, Gobioidei, Kurtidae, and Pleuronectiformes are briefly reviewed.

Keywords

Mechanosensory system · Neuromasts · Scales · Lateral line nerves · Anatomy

16.1 Introduction

The lateral line system, a sensory system for detecting water motion, is present in fishes and aquatic stages of amphibians (Russell 1976; Northcutt 1989; Schlosser 2002). In fish, the lateral line system can detect unidirectional flows and oscillatory waves, but also relative flows owing to own movements (i.e., swimming). Therefore, the system plays a critical role in various behaviors of fishes such as prey/predator detection, avoidance, rheotaxis, and communication (for the association between the system and behaviors, see Bleckmann et al. 1989; Janssen 2004; Coombs and Montgomery 2014; Montgomery et al. 2014; Mogdans 2019). Hence, many aspects of the system have been attracting attention in various disciplines, such as behavioral ecology, evolutionary biology, developmental biology, and phylogenetic systematics.

Morphologically, the lateral line system comprises lateral line canals and neuromasts. The lateral line canals are ossified or cutaneous tubular structures passing through specific dermal bones and serial trunk scales (termed lateral line scales), with each canal having small openings to the body surface (Figs. 16.1 and 16.2) (Webb 1989a; Voronina and Hughes 2013, 2018). The neuromasts are sensory organs found on the body surface (superficial neuromasts) or within the lateral line canals (canal neuromasts) (Fig. 16.1). Reflecting habitats, habits, and phylogenetic

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backgrounds in fishes, the system is morphologically various among species or groups, specifically in courses and shapes of the canals, as well as the number and distribution of neuromasts.

Histologically, each neuromast includes mechanosensory hair-, support-, and mantle cells, and a gelatinous part (termed cupula) which projects toward water from the body surface (Reno 1969; Owens et al. 2007; Becker et al. 2016). A cluster of hair cells (sensory strip) is positioned at the center of neuromast; each hair cell includes kinocilium and stereocilia, collectively called sensory bundle (Fig. 16.1b), which are embedded in the cupula (Reno 1969; Owens et al. 2007; Becker et al. 2016). Afferent and efferent fibers of the lateral line nerves innervate each hair cell (Rouse and Pickles 1991; Münz 1979; Faucher et al. 2003). The support cells intervene among the hair cells (Reno 1969; Münz 1979; Rouse and Pickles 1991; Owens et al. 2007). The mantle cells surround the sensory strip and are thought to secrete the cupula (Webb 2014b). This histological structure is common in both canal and superficial neuromasts. However, the size and shape of the neuromasts, sensory strip, and cupula differ between the two types of neuromasts as well as among fishes (see Webb 2014a; Becker et al. 2016). Each neuromast detects water motion when the cupula receives physical stimuli caused by water motion. Physiologically, deflection of the cupula leads to the change in tensions of the sensory

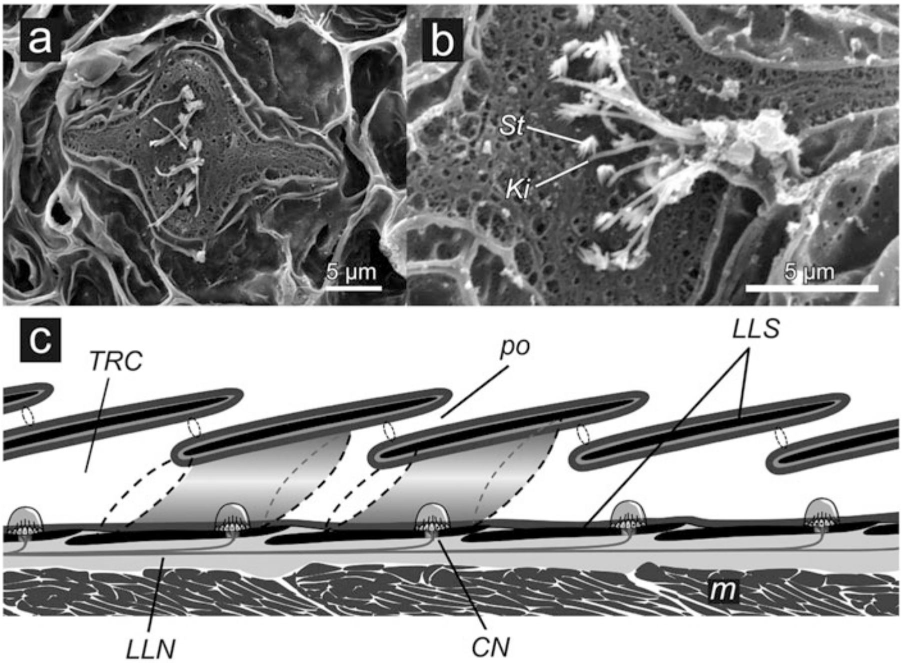

Fig. 16.1 (**a**) A superficial neuromast on the trunk of *Kurtus gulliveri* in SEM observation. (**b**) Sensory bundles (each consisting of kinocilium and stereocilia) in a superficial neuromast on the trunk of *K. gulliveri*. (**c**) A schematic diagram of the trunk canal in horizontal plane (along the longitudinal axis of the canal; the left is rostral), in which the lateral line scales (*black*) with the canal segments (depicted in 3D for two scales) sit beneath the epidermis (*gray*) at a shallow angle in the dermis (*light gray*); the anterior and posterior openings of the canal segments are represented by *large dashed cercles*; *small dashed cercles* are pores opening to the body surface. *CN* canal neuromast, *cs* canal segment, *Ki* kinocilium, *LLN* posterior lateral line nerve, *m* trunk muscle, *po* pore, *sp* scale plate, *St* a bundle of stereocilia, *TRC* inside of the trunk canal. (**a**, **b:** Adapted from Sato et al. 2021a in Ichthyology & Herpetology and **c**: adapted from Webb and Ramsay 2017 in Copeia by the American Society of Ichthyologists and Herpetologists, under CC BY 4.0)

bundles, and this causes a change in the membrane potential of the hair cells, which is transmitted as a neural signal in the afferent neurons (Reno 1969; van Netten and Kroes 1989; van Netten and McHenry 2014). Each neuromast has the highest physiological sensibility to water flows along a direction and its opposite direction (reviewed in Chagnaud and Coombs 2013). This directionality of sensibility (physiological sensory orientation) in a neuromast can be inferred on the basis of a positional relationship of the kinocilium and stereocilia, under scanning electron microscopy (SEM) observation (van Netten and Kroes 1989; van Netten and McHenry 2014).

In this chapter, the morphological diversity of the lateral line system in Teleostei is reviewed, with a special focus on the lateral line canals and distribution pattern of neuromasts. Since the lateral line system consists of several components (lateral line canals, scales, canal and superficial neuromasts, and associated nerves) and each of these differs in morphology among taxa, this chapter has sections that introduce each of the components. In each section, a representative condition of the component is explained, followed by its derivative conditions seen in specific species (in Sects. 16.2 and 16.3). Heterochrony on the system (i.e., variations in developmental timing and stages) and the putative functional significances of respective lateral line morphologies are also briefly introduced (in Sects. 16.4 and 16.5, respectively), as both topics relate to evolutional backgrounds of the morphological diversity of the system. Since several previous papers reviewed the lateral line canals and their developmental processes in detail (Coombs et al. 1988; Webb 1989a, b, 2014a, b), this chapter devotes space to the distribution and innervation of neuromasts with specific examples, given that these two relatively have not been focused on before. Additionally, recent progresses in the morphological studies of four teleostean taxa (Apogonidae, Gobioidei, Kurtidae, and Pleuronectifomes) are also mentioned (in Sect. 16.6). Some of these later studies were carried out with fishes distributed in Japan using the DiASP vital-staining method for observing neuromasts (Collazo et al. 1994; Nakae et al. 2012). For the lateral line system in extant higher taxonomic groups other than Teleostei, see respective descriptive studies, due to distinctiveness of the system in each (reviewed by Northcutt 1989; for Agnatha, see Fernholm 1985; Northcutt 1989; for Chondrichthyes, see Fields et al. 1993; Maruska 2001; Lisney 2010; Gardiner and Atema 2014; for Sarcopterygii, see Webb and Northcutt 1997; Northcutt 1989; for Cladistia, see Allis 1922; Piotrowski and Northcutt 1996; Webb and Northcutt 1997; Rizzato et al. 2020; for Chondrostei, see Norris 1925; for Holostei, see Allis 1889; Norris 1925; Song and Northcutt 1991).

16.2 Morphological Diversity of the Lateral Line System

16.2.1 Canal Topography on the Head

On the head of teleosts, the lateral line canals pass through specific dermal bones, each canal with either pores, tubular branches or both, these opening to the body surface. Due to the association between the head canals and cranial bones, courses of the canals (hereafter termed canal topography) are highly conservative in teleosts, showing roughly the same topography among species. Specifically, eight canals are present: supraorbital, infraorbital, otic, preopercular, mandibular, postotic, and supratemporal canals and the temporal portion of the trunk canal (sensu Webb 1989a). Here, the topography in *Lateolabrax japonicus* (Percoidei *incertae sedis*) is presented as a typical condition (Fig. 16.2).

The supraorbital canal courses along the dorsal margin of the orbit, from a point posterodorsal to the eye (junction of the frontal, infraorbital, and pterotic bones; termed supraorbital-infraorbital junction), to the snout, passing through the frontal and nasal bones; the canals on the left and right sides are interconnected on the interorbital space. The infraorbital canal courses along the lower margin of the orbit from that junction to the lateral surface of the snout, passing through the infraorbital bones. The otic canal extends from the supraorbital-infraorbital junction to a middle

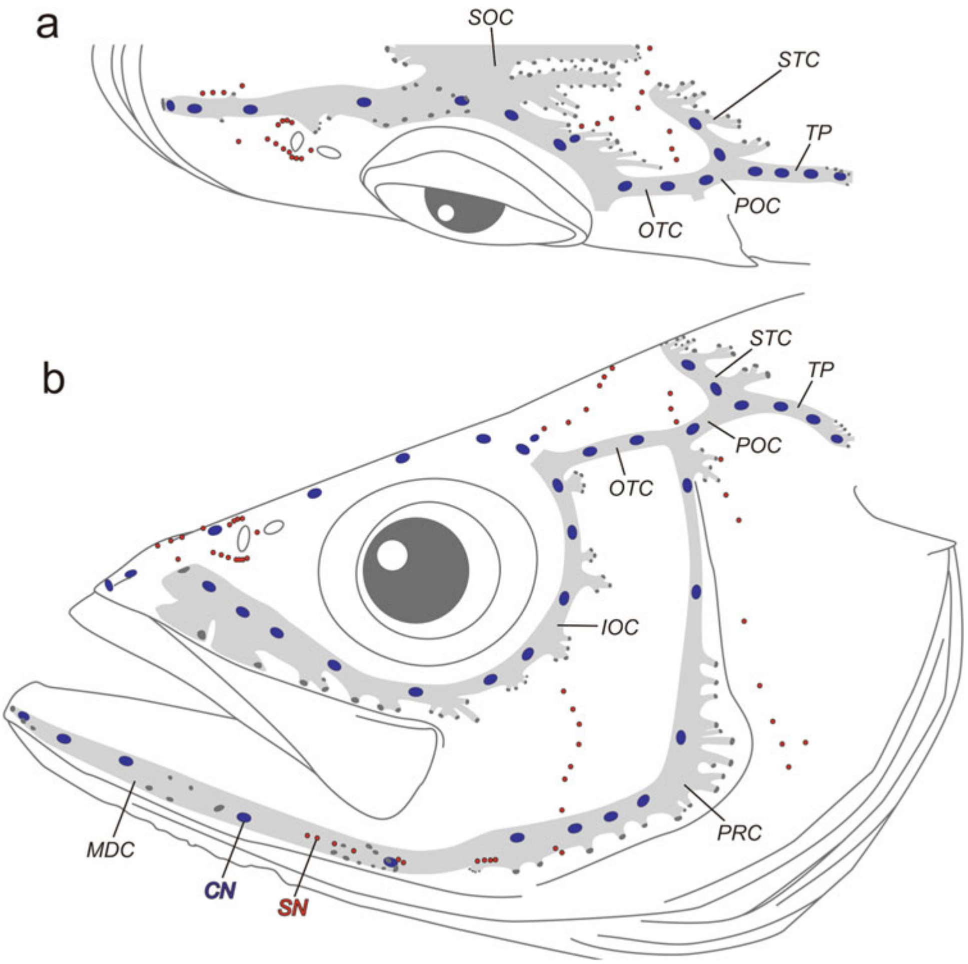

Fig. 16.2 Lateral line canals and neuromasts on the head of *Lateolabrax japonicus*; (**a**) dorsal and (**b**) lateral views. *IOC* infraorbital canal, *MDC* mandibular canal, *OTC* otic canal, *POC* postotic canal, *PRC* preopercular canal, *SOC* supraorbital canal, *STC* supratemporal canal, *TP* temporal portion of trunk canal. *Dark gray* indicates pore openings. *Large navy* and *red small dots* indicate canal and superficial neuromasts, respectively. (Adapted from Sato et al. 2017 with permission from the Ichthyological Society of Japan)

point of the pterotic bone (otic-preopercular junction), passing through the pterotic bone. The preopercular canal passes through the preopercular bone from the otic-preopercular junction to the mandibular canal which passes though the dentary and anguloarticular bones. The postotic canal is short, between the otic-preopercular junction and postotic-supratemporal junction (in the posterior extrascapular bone), through the pterotic and the posterior extrascapular bones. The supratemporal canal courses dorsally from the postotic-supratemporal junction though the extrascapular bones, terminating on the parietal region as pores. The temporal portion of the trunk canal, which connects to the trunk canal consisting of lateral line scales, courses from the postotic-supratemporal junction to the trunk canal through the extrascapular, posttemporal, and supracleithrum bones.

The above head canal topography is widely seen in teleosts, although slight differences exist

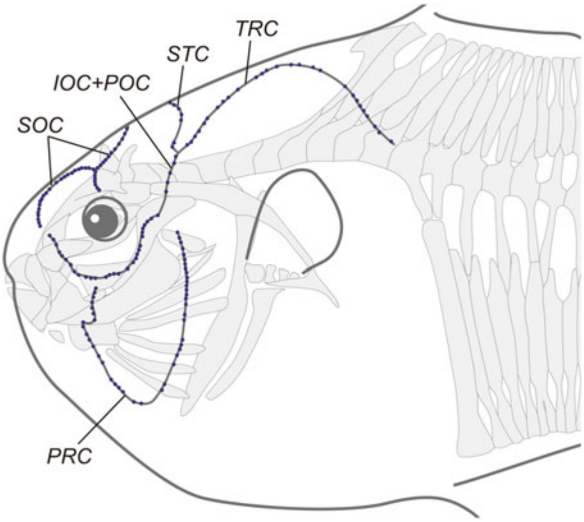

Fig. 16.3 Lateral line canals present as inconspicuous grooves, with canal neuromast homologues in *Mola mola* (Molidae). *IOC + POC* Infraorbital and otic canals, *PRC* preopercular canal, *SOC* supraorbital canal, *STC* supratemporal canal, *TRC* trunk canal (including the temporal portion of the trunk canal). *Navy dots* indicate canal neuromast homologues (depicted slightly larger than actual size). (Illustrated by the author based on Nakae and Sasaki 2006 with permission from the Ichthyological Society of Japan)

among fishes due to their respective skull morphologies (for Elopomorpha, see Nelson 1972; Dario 2004; Nakae et al. 2021; for Osteoglossomorpha, see Nelson 1969, 1972; Verçoza et al. 2021; for Otocephala, see Lekander 1949; Illick 1956; Reno 1969; Arratia and Huaquin 1995; Ito et al. 2017; Rizzato and Bichuette 2017; Pastana et al. 2020; for Protacanthopterygii, see Nelson 1972; Sanford 2000; Nakae and Hasegawa 2021; for Osmeromorpha, see Marranzino and Webb 2018; for Ateleopodomorpha, see Sasaki et al. 2006; for Cyclosquamata, see Johnson et al. 1996; for Scopelomorpha, see Freihofer 1970; Lawry 1973; for Paracanthopterygii, see Cole 1898; Garman 1899; Marshall 1965; Schwarzhans 2014; for Acanthopterygii, see Webb 1989a). In Elopiformes, Anguilliformes, and Clupeiformes, a short canal (ethmoidal sensory canal) or a canal commissure ["rostral organ" in Nelson 1984] are found on the snout tip (Allis 1902; Nelson 1972, 1984; Dario 2004; Dario and de Pinna 2006; Nakae et al. 2021).

Exceptional cases for the conservativeness of the canal topography are Tetraodontiformes and Lophiiformes, where the head canals develop as grooves passing on the body surface thus leaving from the dermal bones and show a characteristic topography in the respective orders (Fig. 16.3) (Nakae and Sasaki 2005, 2006, 2010). In Pleuronectiformes, the canal topography is asymmetric between the ocular and blind sides, owing to distortion of the cranial bones (discussed in Sect. 16.6.4; reviewed by Voronina et al. 2021).

16.2.2 Morphology of Head Canals, and Canal Neuromasts

The structural complexity of the head canals (viz., width, number of pores and branches, and ossification degree of the canals) is significantly different among taxa. Webb (1989a) recognized four representative types in variation of the canal morphology: simple (narrow), branched, widened, and reduced. The simple (narrow) type is the most common; the canals are well ossified and embedded in the dermatocranium, with either small pores, less-branched tubules or both. As an unusual example for the simple type, in some species of Anguilliformes, the head canals contain pouch-like parts which are without any pores, instead of tubules (Allis 1902; Nakae et al. 2021). In the branched type, the canals give off highly branched tubules which each terminate on the body surface as a large number of pores. This type is also widely seen in Teleostei, being particularly conspicuous in Clupeiformes and Scombroidei (Wohlfahrt 1937; Webb 1989a; Dario 2004; Dario and de Pinna 2006; Nakae et al. 2013). In the widened type, the canals are broad compared to the simple (narrow) canals, and generally accompanied by incompletely-ossified (epithelial) canal roofs (Webb 1989a). For example, in Trachichthyidae, Macrouridae, and Melamphaidae, the head canals are widened and occupy the entire snout, cheek, and parietal regions, in contrast to the simple canals that do not reach these regions (Marshall 1965, 1996; Jakubowski 1974). In addition, roofs of their widened head canals are not ossified, thus the canals are present as grooves on the dermal bones enclosed by epithelium. The reduced type is defined by total or partial absence of the head canals (Webb 1989a). In Tetraodontiformes and Lophiiformes, the head canals develop as inconspicuous grooves without roofs, containing homologues of associated canal neuromasts as superficial neuromasts linearly arranged on the grooves (Nakae and Sasaki 2005, 2006, 2010).

In the head canals of teleosts, total ca. 30–60 canal neuromasts are arranged at roughly even intervals (Fig. 16.2) (Cole 1898; Allis 1902; Jakubowski 1963, 1966, 1974; Marshall 1965; Freihofer 1970, 1978; Bird and Webb 2014; Becker et al. 2016; Sato et al. 2017). Each canal neuromast occurs on the proximal surface (floor) of the canal (Fig. 16.1c) (Bird and Webb 2014; Becker et al. 2016) and has a directional sensitivity parallel to the long axis of the canal course containing it, to detect the movements of water passing though the canal (Bird and Webb 2014). In the widened canal type, each canal neuromast is generally large, diamond shaped, and positioned in a slight constricted part of the widened canals (Garman 1899; Jakubowski 1974; Marshall 1965, 1996). Although in the reduced type, the canals are absent or incompletely formed, homologues of the canal neuromasts associating such lost parts are found as row(s) or cluster(s) of superficial neuromasts ("replacement neuromasts" in Coombs et al. 1988) at the site where the canals were supposed to be formed. For example, in Esocidae, the head canals are partly absent in many species, but with many superficial neuromasts along the lacking portions of the canal courses (Webb 1989a; Nelson 1972). In Gobioidei, most parts of the head canals are absent but the associated canal neuromast homologues develop as many superficial neuromasts arranged in rows (discussed in Sect. 16.6).

16.2.3 Canal Topography on the Trunk

Typically a single canal runs along the trunk of teleosts, but its course is variable among fishes. This is in contrast to the head canals which course conservatively specific routes. Nevertheless, multiple trunk canals are present in several taxa (Figs. 16.4 and 16.5). According to Webb (1989a), eight representative types are recognized in variation of the trunk canal topography: straight, dorsal displacement, ventral displacement, arched, disjunct, incomplete, multiple, and absent. In addition, zigzag, wavy, ramified, and mesh-like types are found only in a small number of taxa in each.

As a primary course of the trunk canal, the single straight canal runs from the temporal region (the posterior end of the temporal portion of the trunk canal) to the caudal fin base or onto a scaled caudal fin membrane, coursing along the horizontal septum (Fig. 16.5a) (Coombs et al. 1988; Webb 1989a; Northcutt et al. 2000). The dorsal and ventral displacement types are

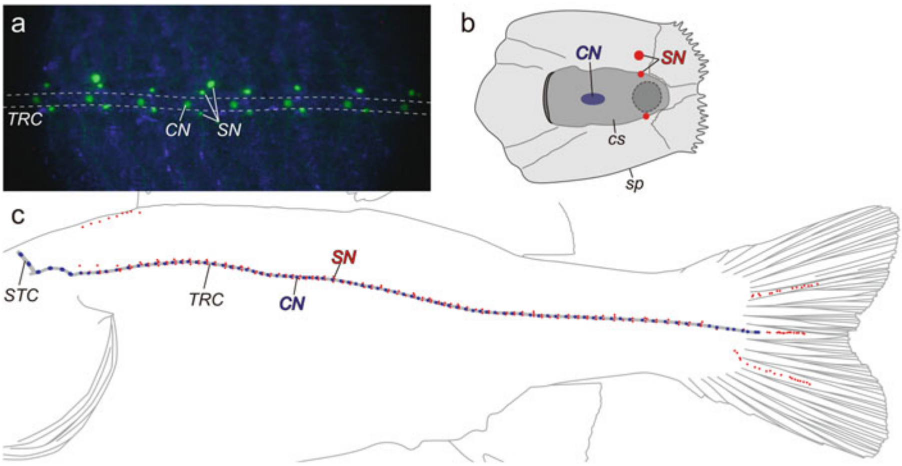

Fig. 16.4 Lateral line system on the trunk and caudal fin of *Lateolabrax japonicus*. (**a**) Canal and superficial neuromasts stained with DiASP; *dashed lines* indicate the course of the trunk canal. (**b**) A lateral line scale. (**c**) Course of the trunk canal and the distribution pattern of canal and superficial neuromasts. *CN* canal neuromast (under the roof of canal segment), *cs* canal segment, *SN* superficial neuromast, *sp* scale plate, *STC* supratemporal canal, *TRC* trunk canal. (**a**: The author's observation; **b**, **c**: adapted from Sato et al. 2017 with permission from the Ichthyological Society of Japan)

characterized by the trunk canal positioned on the dorsal and ventral margins of the trunk, respectively (Fig. 16.5b, c). The dorsal displacement type is represented by some species of Uranoscopidae, in which the trunk canal passes close to the dorsal fin base (Coombs et al. 1988; Webb 1989a, 1990; Fricke 2018). The ventral displacement type is widely found in Cyprinidae, Zoarcidae, and Beloniformes (Webb 1989a; Hirota et al. 2014; Balushkin and Orlovskaya 2019). In the arched type, seen in derived teleosts (e.g., acanthomorphs), the trunk canal arches in its anterior part, over the pectoral fin which is located on the lateral side of the body, while its posterior part is along the horizontal septum (Fig. 16.5d) (Coombs et al. 1988; Webb 1989a; Yamanaka et al. 2010). The disjunct and incomplete types are defined by the partial absence of the canal in its middle and posterior parts, respectively (Fig. 16.5e, f) (Webb 1989a, 1990). The absent type is a complete truncation of canal formation (Fig. 16.5l) (Coombs et al. 1988; Webb 1989a), similarly to the reduced type of head canals. In a small number of taxa, the canal runs in zigzag (in Balistidae) or wavy (in Scombroidei, particularly *Lepidocybium flavobrunneum*) (Fig. 16.5g, h) (Jones and Silas 1961; Coombs et al. 1988; Nakae and Sasaki 2010). Each of the above topographies can be recognized as a positional derivation of the straight trunk canal (Webb 1989a).

Multiple trunk canals occur in some species of Notothenioidei, Plesiopidae, Hexagrammidae, Stichaeidae, and Cynoglossidae, running parallelly along the trunk (Fig. 16.5j, m) (Jordan and Snyder 1902; Yatsu et al. 1978; Hardy 1984; Balushkin 1996; Wonsettler and Webb 1997; Yokogawa et al. 2008; Fukuda et al. 2010; Clardy et al. 2015). Stichaeidae includes species with four longitudinal trunk canals (e.g., *Ernogrammus zhirmunskii*; Yamanaka et al. 2012), but the third and fourth canals are connected in most species. In the family, a mesh-patterned canal is spread on the entire trunk surface in species of *Stichaeopsis* and *Dictyosoma* (Fig. 16.5k) (see Jordan and Snyder 1902; Yatsu et al. 1978; Clardy et al. 2015); this mesh seems to be formed of four long longitudinal canals and many short transverse canals linking the longitudinal ones. In the scombrid

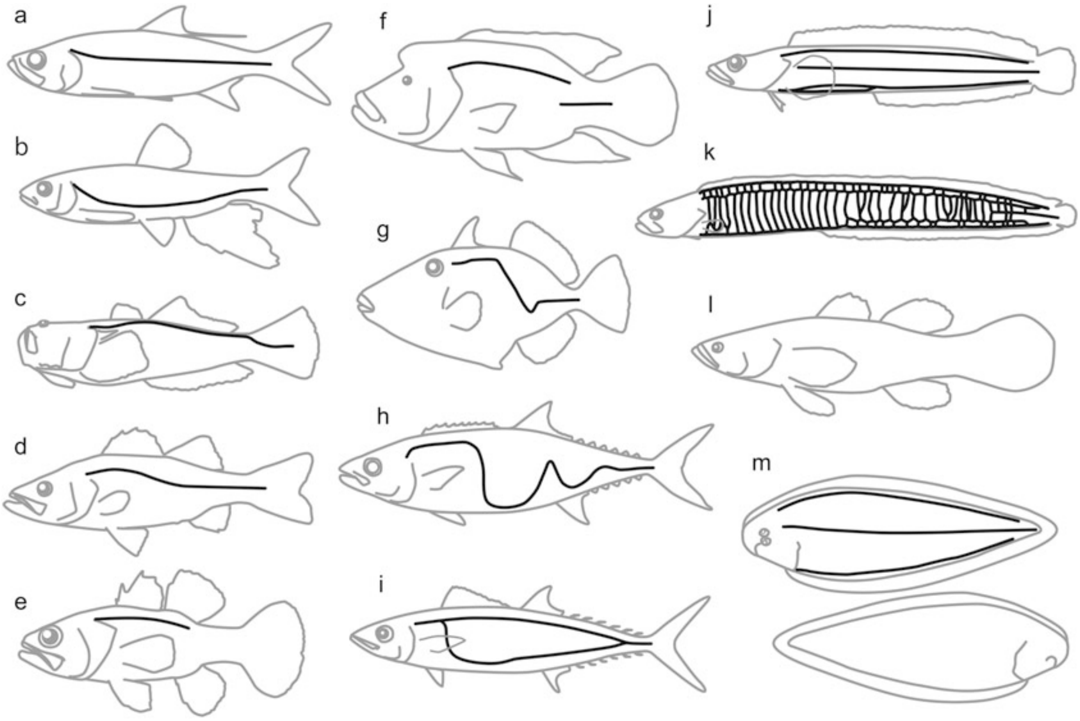

Fig. 16.5 Trunk canal topographies (*black lines*) in Teleostei. (**a**) Straight–*Megalops cyprinoides* (Megalopidae), (**b**) ventral displacement–*Opsariichthys platypus* (Cyprinidae), (**c**) dorsal displacement–*Uranoscopus japonicus*, (**d**) arched–*Lateolabrax japonicus* (Percoidei), (**e**) incomplete–*Fowleria variegate* (Apogonidae), (**f**) disjunct–*Cheilinus undulatus* (Labridae), (**g**) zigzag–*Rhinecanthus aculeatus* (Balistidae), (**h**) wavy–*Lepidocybium flavobrunneum* (Gempylidae), (**i**) bifurcated–*Grammatorcynus bilineatus* (Scombridae), (**j**) multiple–*Ernogrammus hexagrammus* (Stichaeidae), (**k**) mesh-like–*Dictyosoma burgeri* (Stichaeidae), (**l**) absent–*Bunaka gyrinoides* (Eleotridae), (**m**) asymmetric–*Cynoglossus ochiaii* (Cynoglossidae): three trunk canals are present on the ocular side, while absent on the blind side. (Illustration based on the author's observations)

Grammatorcynus bilineatus, the trunk canal bifurcates in its anterior part, merging again on the caudal peduncle, thereby forming a loop in the trunk canal (Fig. 16.5i) (Collette and Gillis 1992). One of the most unique conditions in the trunk canal(s) is in species of Cynoglossidae, where the canal topography is asymmetric: two or three trunk canals develop on the ocular side (i.e., multiple type) but no canals are present on the blind side. This character may be a combination of the multiple- and absent types. Therefore, the topography of the trunk canal varies according to its heterotopic change (i.e., changes in developmental place on the trunk). Furthermore, duplication of the trunk canal seems to be acquired in some taxa.

16.2.4 Morphology of the Trunk Canal(s) and Canal Neuromasts

In general, the trunk canal consists of a series of scales, each with a canal segment (called lateral line scales). Typically, each lateral line scale is composed of a scale plate and canal segment, the latter being positioned on or piercing through the scale plate (Fig. 16.4c). Each canal segment is connected with adjacent ones via cutaneous tubules; generally, it has pore(s) or tubular branches, and/or a pore is present on each cutaneous tubule. Therefore, the trunk canal with pore openings at regular intervals, which passes through the lateral line scale series, is found on the trunk (Fig. 16.1c) (reviewed in Voronina and Hughes 2013, 2018; Webb and Ramsay 2017).

An interspecific difference of the lateral line scales arises from a combination of the presence or absence of the scales plate and canal segment, as well as respective shapes and positional relationship of the two. Because shape of the scale plate apparently associates with other trunk scales (possibly owing to developmental constraints), morphology of the lateral line scales is apparently affected by intra- and interspecific variations of the trunk scales. Voronina and Hughes (2018) categorized various lateral line scale morphologies into four representative types (the tubular-scalar, integrated, tubular, and non-tubular lateral line scale types) on the basis of a relationship between the canal segment and the scale plate. For instance, the tubular-scalar lateral line scales comprise externally distinguishable elasmoid scale plate and tube (canal segment) in each; in the integrated lateral line scale type, the scale plate and canal segment are integrated with no clear boundary between them; the tubular lateral line scale is a canal segment without scale plate; conversely, the non-tubular lateral line scale is the scale plate without canal segment (Voronina and Hughes 2018). Specifically, the lateral line scale of *L. japonicus*, apparently consisting of the scale plate and canal segment, is the tubular-scalar type (Fig. 16.4b). In *Anguilla japonica* (Anguillidae), the lateral line scales are of the tubular type, and occur medial to the trunk scales in a different ontogenetic timing to the trunk scales (Nakae et al. 2021).

In general, a canal neuromast occurs within the canal segment in each lateral line scale (Fig. 16.1c). The physiological sensory orientation of this canal neuromast is parallel to the canal course (i.e., longitudinal in the fish) (Webb 1989c; Faucher et al. 2003), as same with the case of the canal neuromasts of the head canals. In lateral line scales without canal segment [i.e., the non-tubular lateral line scale in Voronina and Hughes 2018], a homologue of the canal neuromast is present as a superficial neuromast (s) (Sato et al. 2017). Accordingly, the absence of apparent trunk canal, generally described as “no lateral line” in taxonomic context, does not mean that the species completely lost neuromasts in the trunk. Lateral line scales each containing the canal segment but no canal neuromast [in Hexagrammidae and *Pseudamia gelatinosa* (Apogonidae)] or those each with multiple canal neuromasts within the canal [in *Rhyacichthys aspro* (Rhyacichthyidae)] were reported (Wonsettler and Webb 1997; Asaoka et al. 2014; Sato et al. 2019).

16.2.5 Distribution Pattern of Superficial Neuromasts on the Head

Presently, our knowledge of the variation in the distribution pattern of superficial neuromasts is not enough to assert a primary and representative distribution pattern in Teleostei, due to the small number of reports showing all of the neuromasts in a whole body. Herein, the pattern in *L. japonicus* (Fig. 16.2) is introduced as a non-derivative condition, since it presents no partial absences in the head canals (which lead to the occurrence of canal neuromast homologues as superficial neuromasts) and its pattern is similar to that of other teleosts, specifically *Acerina cernua* (Percidae: Jakubowski 1963), *Tramitichromis* sp. (Cichlidae: Bird and Webb 2014), *Pholidichthys leucotaenia* (Pholidichthyidae: Springer and Freihofer 1976), *Oplegnathus fasciatus* (Oplegnathidae) (Fig. 16.5a), *Scomberomorus niphonius* (Scombridae: Nakae et al. 2013), and *Cottus bairdi* (Cottidae: Coombs 2001). In *L. japonicus* (Fig. 16.2), ca. 50 superficial neuromasts are present as 7 rows or clusters located on specific positions of the head: around the nostrils (occurring as a cluster), on the cheek (as a transverse row), the preopercular region (cluster), the opercular region (transverse row), the dorsal surface

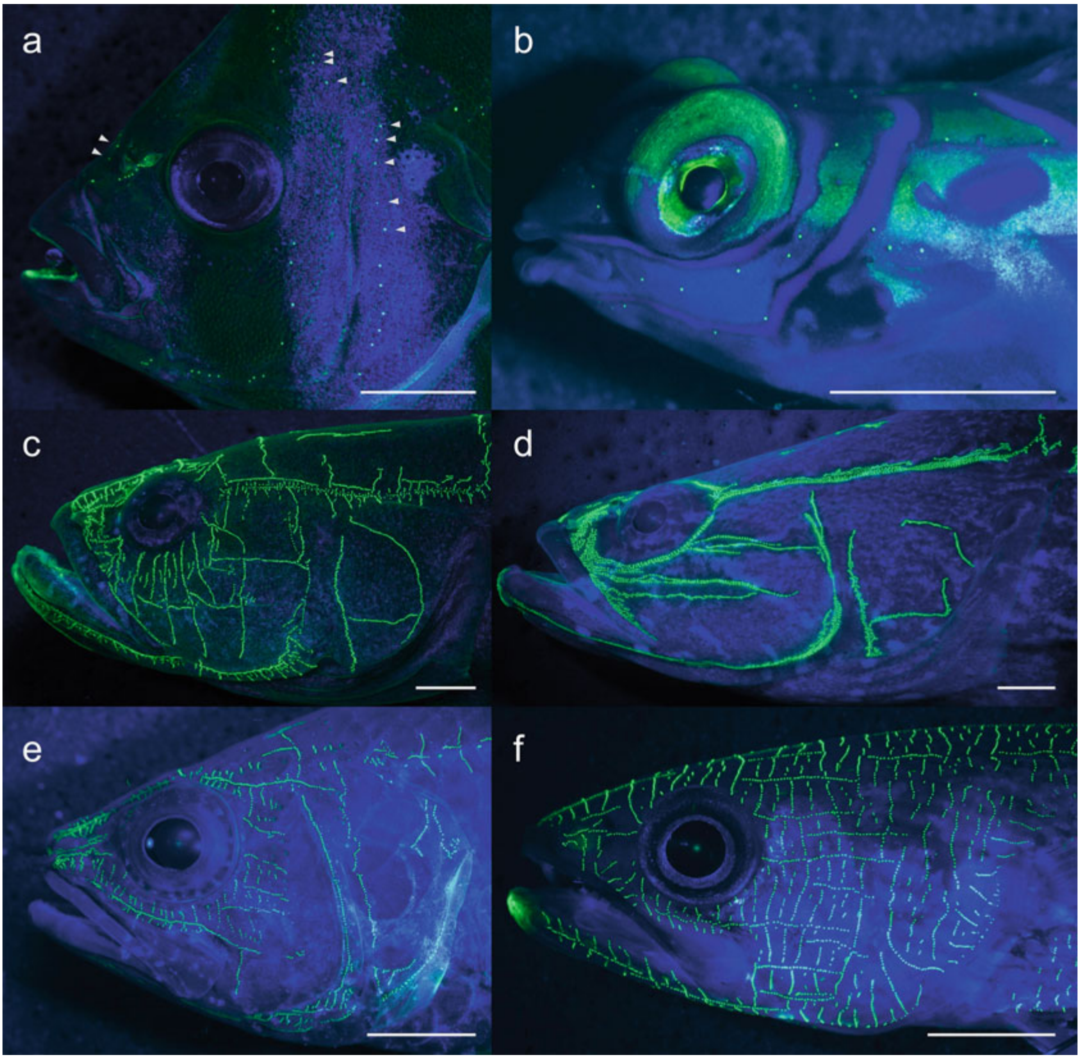

Fig. 16.6 Superficial neuromasts (small dots, indicated by *arrowheads*) stained with DiASP [note: in (**a**, **b**, **e**, **f**), fluorescence of canal neuromasts was largely blocked due to dense melanophores; in (**c**, **d**), canal neuromasts are absent (homologues of the canal neuromasts are present as superficial neuromasts)]. (**a**) *Oplegnathus fasciatus* (Oplegnathidae), (**b**) *Synchiropus splendidus* (Callionymidae), (**c**) *Eleotris fusca* (Eleotridae), (**d**) *Bunaka gyrinoides* (Eleotridae), (**e**) *Fowleria variegata* (Apogonidae), and (**f**) *Pseudamia gelatinosa* (Apogonidae). Scale bar = 5 mm. (**a–e**: The author's observations; **f**: adapted from Sato et al. 2019 with permission from John Wiley & Sons, Inc.)

of the snout (longitudinal row), the parietal region (one longitudinal and two transverse rows), and the lower jaw (longitudinal row).

In several taxa of Teleostei, hundreds to thousands of superficial neuromasts are present on the head, either scattered or arranged in rows (Fig. 16.6c–f). These fishes with a prominent condition of superficial neuromasts have attracted attention and been well documented, in contrast to the non-derivative condition with relatively smaller number of superficial neuromasts (Fig. 16.6a, b). As noted in Sect. 16.2.2, a reduction in head canals frequently leads to the appearance of superficial neuromasts, since the canal neuromast homologues of the lost canals develop on the body surface as superficial neuromasts ["replacement neuromasts" in Coombs et al. 1988]. In Esocidae, the head canals are partly absent in many species, and a general trend toward replacement of the canals by superficial neuromasts is apparent, with the number of superficial (replacement) neuromasts being significantly larger than the number of the canal neuromasts that it should have originally contained (Nelson 1972). Similar cases are found in Cyprinodontiformes (Parenti 1981), Batrachoididae (Clapp 1889; Greene 1899), Gasterosteidae (Wark et al. 2012; Ahnelt et al. 2021), and Gobioidei (Fig. 16.6c, d). Recently, several species of Sternoptychidae, Gonostomatidae, and Stomiidae were revealed to have many superficial neuromast rows on their head and trunk, and this proliferation of superficial neuromasts is possibly ascribed to the canal loss (Marranzino and Webb 2018). In Gobioidei, the inference that a small number of canal neuromasts is replaced by a larger number of superficial neuromasts is supported on the basis of innervation: most of their superficial neuromasts are innervated by the nerve branches which should originally have innervated the canal neuromasts in the reduced canals (Wongrat and Miller 1991; Asaoka et al. 2014).

A proliferation of superficial neuromasts that is regardless of such canal loss have been recognized. In Apogonidae and Kurtidae, numerous superficial neuromasts are arranged in longitudinal and transverse rows on the head (for examples, ca. 2,700 and ca. 58,600 on one side in *Pseudamia gelatinosa* and *Kurtus gulliveri*, respectively), forming characteristic cross-hatch or grid-like patterns (Figs. 16.6e, f and 16.10b) (discussed in Sect. 16.6; Johnson 1993; Bergman 2004; Fraser 2013; Sato et al. 2017, 2019, 2021a, b). Because species of these two families conservatively retain the complete head canals with canal neuromasts, their numerous superficial neuromasts are not the homologues of canal neuromasts. Overall, in Teleostei, proliferation of superficial neuromasts has evolved convergently multiple times, as pointed out by Johnson (1993).

16.2.6 Distribution Pattern of Superficial Neuromasts on the Trunk and Caudal Fin

In the trunk of teleosts, superficial neuromasts are present on the lateral line scales, around the dorsal fin origin, and on the caudal fin (Fig. 16.4c). In *L. japonicus* (Fig. 16.4), each lateral line scale (involving the canal segment) has one superficial neuromast positioned on each of the dorsal and ventral sides of the canal segment and another one is found dorsal to these superficial neuromasts. On the caudal fin, three superficial neuromast rows occur along the caudal fin membranes between fin rays (Sato et al. 2017).

A large number of superficial neuromasts is found on the trunk of several taxa, accompanying the proliferation of those on the head. In several species of Cypriniformes and Characiformes, every trunk scale bears a superficial neuromast row; for example, *Carassius auratus* (Cyprinidae) totals up to ca. 900 superficial neuromasts on one side of the trunk (Schemmel 1967; Puzdrowski 1989; Schmitz et al. 2008; Sumi et al. 2015). In Mugilidae, almost all of the trunk scales have a groove containing a superficial neuromast (total ca. 500 on one side of the trunk in *Mugil cephalus*) (Ishida et al. 2015; Middlemiss et al. 2017). There is a species in which superficial neuromasts are arranged regardless of the arrangement of scales: in *Kurtus gulliveri* (Kurtidae), minute cycloid scales keep the trunk surface evenly smooth, where numerous superficial neuromasts are arranged in a regular grid pattern over the entire trunk surface irrespective of scale arrangement (discussed in Sect. 16.6; Sato et al. 2021a).

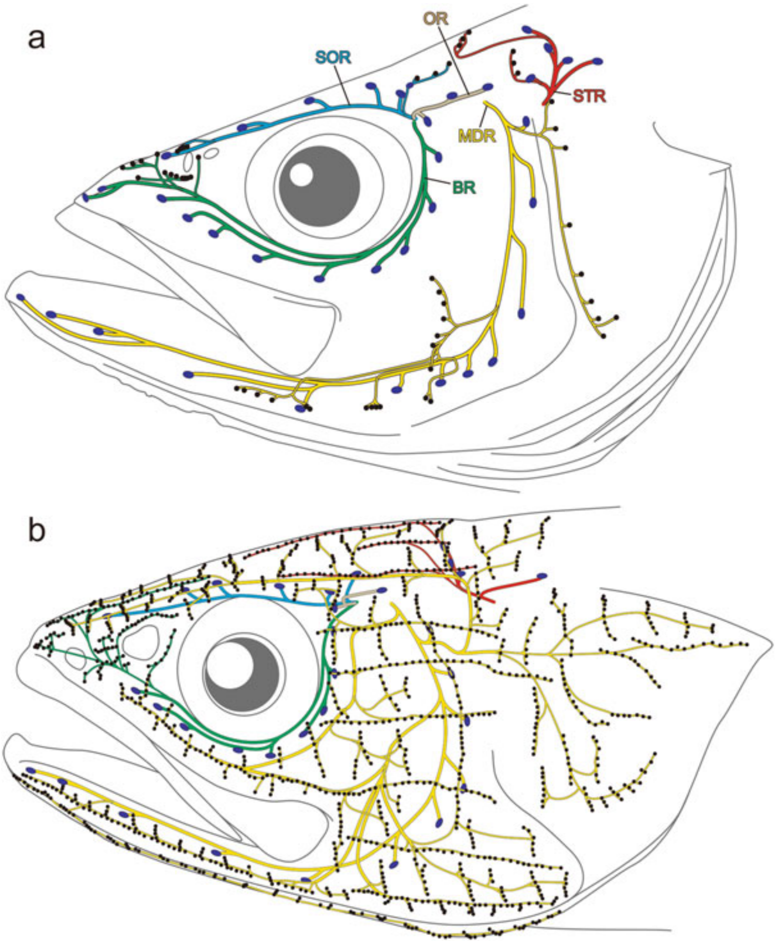

Fig. 16.7 Innervation of the lateral line system on the head in (**a**) *Lateolabrax japonicus* and (**b**) *Gymnapogon japonicus* (Apogonidae). *BR* buccal ramus (*green*), *MDR* mandibular ramus (*yellow*), *OR* otic ramus (*beige*), *SOR* superficial-ophthalmic ramus (*blue*), *STR* supratemporal ramus (*red*). *Large navy* and *small black dots* indicate canal and superficial neuromasts, respectively. (**a**: adapted from Sato et al. 2017 with permission from the Ichthyological Society of Japan; **b**: adapted from Sato et al. 2021b with permission from John Wiley & Sons, Inc.)

16.3 Innervation of the Lateral Line System

The neuromasts in teleosts are innervated by three cranial nerves: the anterior, middle, and posterior lateral line nerves (Puzdrowski 1989; Northcutt et al. 2000). The anterior lateral line nerve, which includes the anterodorsal and anteroventral lateral line ganglions, branches into the superficial-ophthalmic, buccal, mandibular, and otic rami (Fig. 16.7a) (Puzdrowski 1989; Northcutt et al. 2000). The posterior lateral line nerve, including the posterior lateral line ganglion, branches into the supratemporal and lateral rami (Figs. 16.7a and 16.8a) (Puzdrowski 1989; Northcutt et al. 2000). The middle lateral line nerve is a single branch including the middle lateral line nerve ganglion, which merges with the posterior lateral line nerve in its root and innervates a small number of neuromasts on the temporal region (Puzdrowski 1989; Northcutt et al. 2000); this nerve is present in the siluriforms and cypriniforms (and holosts) examined previously (Norris 1925; Lekander 1949; Puzdrowski 1989; Northcutt et al. 2000), but it is not found in more derivative groups of Teleostei (Cole 1898; Cole and Johnston 1901; Garman 1899; Jakubowski 1963; Freihofer 1970; Wongrat and Miller 1991; Nakae and Sasaki 2005, 2006, 2010; Nakae et al. 2006; Asaoka et al. 2014; Sato et al. 2017; Nakae and Hasegawa 2021). Puzdrowski (1989) inferred that the middle lateral line nerve ganglion was

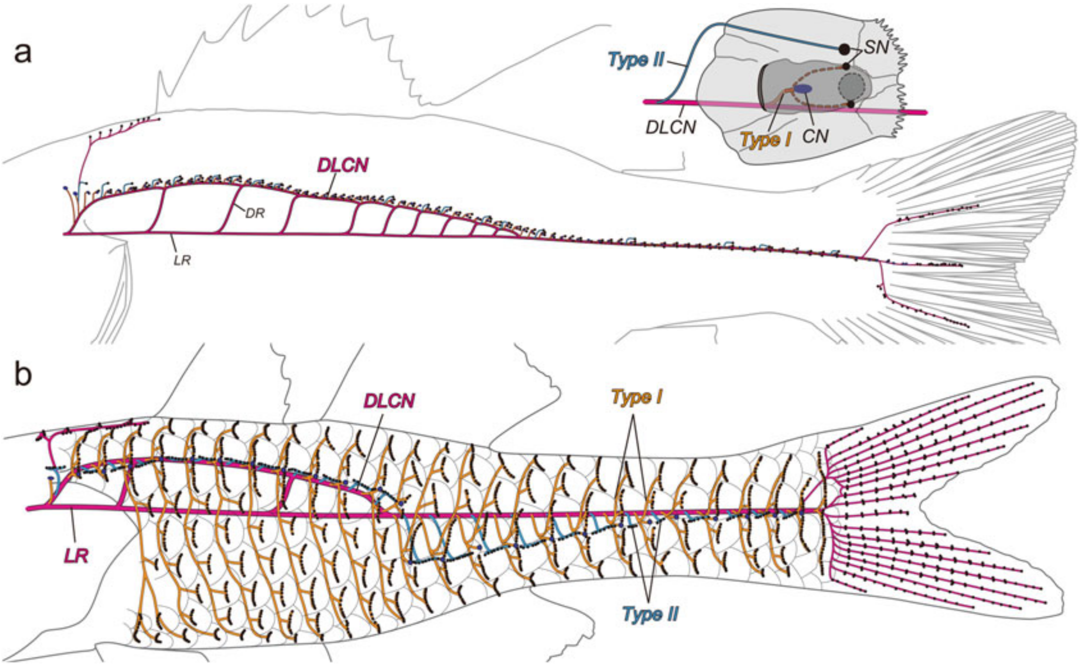

Fig. 16.8 Innervation of the trunk lateral line system (**a**) *Lateolabrax japonicus* and (**b**) *Cercamia eremia* (Apogonidae). *CN* canal neuromast, *DLCN* dorsal longitudinal collector nerve, *DR* dorsal ramule, *LR* lateral ramus (horizontal septum lateral line nerve), *SN* superficial neuromast, *Type I* Type I branch, *Type II* Type II branch. *Navy* and *black small dots* indicate canal neuromasts (or canal neuromast homologues) and superficial neuromasts, respectively. (**a**: adapted from Sato et al. 2017 with permission from the Ichthyological Society of Japan; **b**: adapted from Sato et al. 2019 with permission from John Wiley & Sons, Inc.)

either lost or fused with the posterior lateral line nerve ganglion at some point during the evolution of Euteleostei.

The main trunks of the rami of the lateral line nerves follow approximately identical routes among fishes, although their branching pattern somewhat differs among them to innervate the respective distribution pattern of neuromasts. In *L. japonicus* (Fig. 16.7a) (Sato et al. 2017), the superficial-ophthalmic ramus extends along the supraorbital canal to innervate its canal neuromasts, but also the superficial neuromasts dorsal to the nostril, and a row of those on the parietal region. The buccal ramus courses along the infraorbital canal and innervates its canal neuromasts; it innervates also the superficial neuromasts around the nostrils and on the dorsal surface of the snout. The otic ramus innervates the canal neuromasts of the otic canal, along with the dorsal most canal neuromast in the infraorbital canal. The mandibular ramus runs along the preopercular and mandibular canals, innervating the canal neuromasts in these two canals. This ramus gives off two branches, one innervating the superficial neuromasts on the opercular region and the other innervating those on the cheek, the preopercular region, and the lower jaw. The supratemporal ramus innervates the canal neuromasts of the postotic and supratemporal canals, and the anterior two canal neuromasts of the temporal portion of the trunk canal, and also the superficial neuromast on the parietal region. The lateral ramus (Fig. 16.8a) courses posteriorly along the horizontal septum, its proximal part innervating the posterior two canal neuromasts of the temporal portion of the trunk canal and the superficial neuromasts around the dorsal fin base. In the anterior half of the lateral ramus, ten dorsal ramules arise and collectively form an arched nerve branch [termed “dorsal longitudinal collector nerve" sensu Freihofer 1972] along the arched part of the lateral line scale series. The dorsal longitudinal collector nerve and the lateral ramus innervate the neuromasts of the arched and straight parts of the lateral line scale series, respectively, by detaching two types of nerve branches ("Type I and II" in Sato et al. 2017): the Type I branches each innervate a canal neuromast and its adjacent superficial neuromasts and the Type II branches each innervate a superficial neuromast dorsal to these superficial neuromasts.

In the teleosts examined previously (see Yamanaka et al. 2010), the main trunk of the lateral ramus [termed "horizontal septum lateral line nerve" sensu Freihofer 1972, or simply, the lateral ramus] runs straight along the horizontal septum, with characteristic branching patterns depending on the positional difference of the trunk canal (and neuromasts) among fishes (Fig. 16.5) (Freihofer 1972; Yamanaka et al. 2010; some tetraodontiforms are the exception, see Nakae and Sasaki 2005, 2006, 2010). In fishes with the straight trunk canal, the lateral ramus detaches many short branches each innervating a canal neuromast of lateral line scale (e.g., in Anguillidae; Allis 1902; Yamanaka et al. 2010; Nakae et al. 2021). Otherwise, in Myctophidae and Aulopidae, some ramules arise from the lateral ramus and collectively form a longitudinal nerve branch [termed "latera longitudinal collector nerve" sensu Freihofer 1972] along the horizontal septum by connecting with each other; hence, the nerve innervates neuromasts of the lateral line scales (viz., canal neuromasts within the canal segments and superficial neuromasts on the scales) by detaching short branches (Ray 1950; Yamanaka et al. 2010). In fish with the ventral displaced trunk canal, many ventral branches detach from the lateral ramus, each innervating neuromasts of one or more lateral line scales. For the arched trunk canal, which is common in acanthomorphs, as seen in *L. japonicus*, the dorsal ramules arise from the lateral ramus and collectively form the dorsal longitudinal collector nerve along the anterior (arched) part of the lateral line scale series; the dorsal longitudinal collector nerve and further posterior part of the lateral ramus innervate neuromasts of the arched and straight part of the lateral line scale series, respectively (Freihofer 1972; Yamanaka et al. 2010; Sato et al. 2017). In *Rexea prometheoides* (Gempylidae) with the bifurcated trunk canal, ca. 15 dorsal ramules extend to the dorsal canal, and some of these ramules bifurcate to also innervate the ventral canal (along the horizontal septum) during their respective courses (Yamanaka et al. 2010).

Distinctive branching patterns of the lateral line nerves are found in fishes with a specialized distribution pattern of neuromasts. On the head of Apogonidae with numerous superficial neuromasts and the head canals, the mandibular ramus gives off additional complexly-ramified branches to supply the superficial neuromasts, as well as innervating the canal neuromasts by the main trunk of the ramus, similarly to other percomorphs (Fig. 16.7b) (Sato et al. 2017, 2019, 2021b). In *Cercamia eremia* (Apogonidae), which has a superficial neuromast row in every trunk scale, each of the Type I branches divides into one dorsal and one ventral twig, and these dorsal and ventral twigs innervate several rows of superficial neuromasts, while extending dorsally and ventrally, respectively (Fig. 16.8b) (Sato et al. 2019). In Mugilidae, the lateral ramus detaches ca. 50 branches extending to the lateral surface of the trunk, in addition to giving off one dorsal and one ventral branch which spread to the dorsal and ventral surfaces, respectively; thereby, the lateral ramus innervates neuromasts located on almost all of the trunk scales (Ishida et al. 2015). In *Percopsis transmontana* (Percopsidae), characterized by having superficial neuromast (s) on every trunk scale, the lateral ramus branches in a mesh-like pattern spreading to the entire trunk; from this, a number of short twigs occur, each innervating superficial neuromast (s) on a trunk scale (Freihofer 1972). These derivative innervation patterns suggest that the respective configurations of the system develop according to unique ontogenetic processes. However, actual observations of such ontogenetic process have not yet been accomplished.

16.4 Ontogenetic Basis for the Morphological Diversity in the Lateral Line System

16.4.1 Lateral Line Canals and Neuromasts

A part of the interspecific morphological variation in the lateral line system can be produced by a heterochronic difference in the developmental processes governing the canals and neuromasts. A serial developmental process of lateral line canals has been well studied (see Tarby and Webb 2003; Webb and Shirey 2003): initially, presumptive canal neuromasts (which end up being enclosed in the lateral line canals) occur in the epithelium overlying a dermal bone or scale; next, an ossified canal wall is formed on each side of the presumptive canal neuromasts, in simultaneous with a depression of these neuromasts, thereby a groove containing the presumptive canal neuromasts occurs; lastly, the groove is covered by an epithelial canal roof (with each midpoint between two canal neuromasts remaining as a pore), followed by ossification of the canal roof. Furthermore, the number of branches and pores may increase with fish growth, so the complexity of the canals may gradually increase over a long period of the development of fish (Pastana et al. 2020; Sato et al. 2021b). On this basis, interspecific differences in canal complexity (e.g., presence or absence of the roof and the number of branches and pores) can be owing to differences in the timing of the developmental truncation of the serial canal formation among fishes (Coombs et al. 1988; Webb 1990; Pastana et al. 2020; Sato et al. 2021b): the well-branched canals can be recognized as relatively peramorphic, with canal formation relatively accelerated or continuing over a relatively long term (i.e., juvenile and adult stages); conversely, less-branched and membrane-roofed canals can be recognized as a paedomorphic feature, ascribed to an earlier truncation of the canal formation. The absent and incomplete types are explained as complete and partial truncations of the canal formation, respectively. Although detailed molecular mechanisms of the canal formation are still unknown, at least the presence of neuromasts (or interneuromast cells which are present between the presumptive canal neuromasts: see Ghysen et al. 2014) is related to the introduction of canal formation promoted by osteoblasts and osteoclasts (Wada et al. 2008, 2014).

Heterochrony on the lateral line system affects the overall superficial neuromast distribution pattern, as well as the canal complexity. In Apogonidae (Fig. 16.9), a relatively simple distribution pattern of superficial neuromasts is seen in a paedomorphic species (*Pseudamiops* sp.), which is similar to that seen in a juvenile of its closely related species without the paedomorphic features (*Pseudamia gelatinosa*), representing a case of heterochronic truncation in the development of superficial neuromasts (Sato et al. 2021b).

16.4.2 Innervation Pattern of the Lateral Line System

The courses of the lateral line nerves partially reflect an ontogenetic process of the lateral line system. In an early developmental stage of zebrafish, an embryonic primordium (primI) migrates along the horizontal septum from the head, depositing some founder neuromasts on the body surface lateral to the horizontal septum (Ghysen et al. 2012, 2014). The main trunk of the lateral ramus, which is along the horizontal septum in most teleosts (Yamanaka et al. 2010), is formed on the migration path of the primI (Whitfield 2005; Ghysen et al. 2012, 2014). Then, the founder neuromasts migrate ventrally, while each of them is connected with the lateral ramus by a nerve twig (Whitfield 2005). The twigs seem to be the ventral branches that innervate the neuromasts on the ventrolateral side of the trunk in adult fish. In the case of *Thunnus thynnus* (Scombridae) with arched trunk canal, the founder neuromasts migrate dorsally at that ontogenetic stage (Ghysen et al. 2012), indicating the presence of the dorsal ramules in fishes with

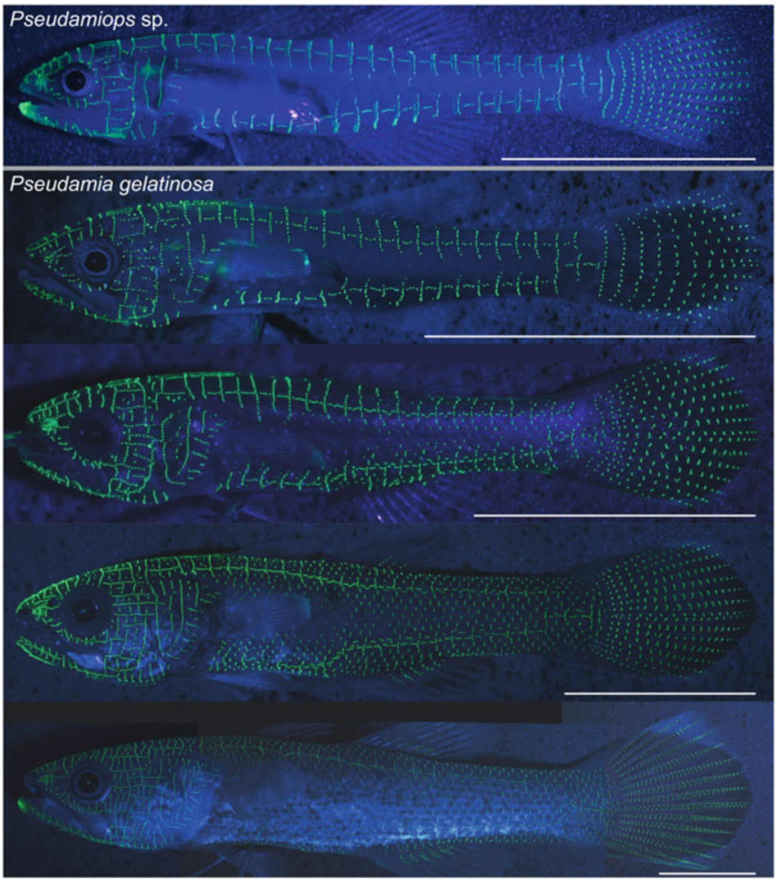

Fig. 16.9 Neuromasts stained with DiASP in a paedomorphic apogonid *Pseudamiops* sp. (23.3 mm SL) and those in non-paedomorphic species *Pseudamia gelatinosa* (both Apogonidae) in increasing sizes: from the uppermost, 17.3, 20.2, 30.5, and 61.0 mm SL. Scale bar = 10 mm. (Adapted from Sato et al. 2019, 2021b with permission from John Wiley & Sons, Inc.)

the arched trunk canal reflects the migration of the founder neuromasts. In zebrafish, each of the migrated founder neuromasts is divided into two or more superficial neuromasts on a scale ("budding process" in Wada et al. 2010, 2013; Ghysen et al. 2014). In this ontogenetic stage, the peripheral end of each ventral branch ramifies, reflecting the division of the associated neuromast (Wada et al. 2013; Wada and Kawakami 2015).

16.5 Functional Significance of the Morphological Diversity in the Lateral Line System

The canal and superficial neuromasts complement each other in regard to detectable frequency band and sensibility, resulting in a system that can detect various motions of water. For oscillatory motions in water, superficial neuromasts generally have sensibility to a lower frequency when compared to that of canal neuromasts, although their detailed properties differ depending on species and even among neuromasts within an individual (Dijkgraaf 1963; Münz 1985, 1989; Chagnaud and Coombs 2013; van Netten and McHenry 2014). Superficial neuromasts, which are directly affected by flows on the body surface, engage in velocity-sensitive responses, whereas canal neuromasts, which can sense motions of associated intracanal fluid, are acceleration-sensitive (van Netten and McHenry 2014). In addition, canal neuromasts can response to oscillatory water motions under a unidirectional flow, whereas superficial neuromasts are saturated by such background flow and consequently insensitive to such oscillatory water motion (Engelmann et al. 2000, 2002). In teleostean fishes, an increase in the number of superficial neuromasts has evolved independently many times (as noted in Sect. 16.2), but it seems this feature tends to be found in species inhabiting environments without turbulent flows, such as ponds, caves, and the deep sea (Marshall 1996; Asaoka et al. 2012; Soares and Niemiller 2013; Marranzino and Webb 2018; Sato et al. 2019, 2021a; Ma et al. 2020). This is consistent with the functionality of superficial neuromasts: since their sensibility to oscillatory water motion is masked by background water flow, it is possible to infer that proliferation of these superficial neuromasts is an adaptation to low-background noise environments.

Denton and Gray (1988, 1989) experimentally showed that canal neuromasts in a canal with membranous (not ossified) canal roof have an increased sensitivity to a particular frequency band (ca. 10 Hz) compared to those without the canal roof. For the branched type, Janssen (2004) proposed the hypothesis that the canals giving off branched tubules play a role as a filter, cutting small disturbances affecting the canal neuromasts. This is based on considerations for the case where two bifurcated tubules (each tubule with two pores) is present in a canal, where a canal neuromast is positioned between the two tubules: if a water disturbance is spatially large enough so that both pores of one tubule have relatively high (or low) pressure compared to the pores of the adjacent tubule, then a flow, passing the neuromast that is positioned between the tubules, is caused due to the pressure-difference between the affected-tubule and the other (non-affected) one; conversely, if the disturbance is spatially so small that it affects just one pore of the tubule, the flow may be primarily between these two pores (within the tubule) and there is little flow passing the neuromast between the tubules.

One of the ultimate causes for the morphological diversity in the trunk lateral line system—in which the components of the system (the trunk canal and neuromasts) primitively present only on a limited body surface (along the horizontal septum) had migrated and sometimes duplicated to a wide area of the trunk—may be that such positional derivation leads to an increase in the spatial resolution in sensing water motion. Klein et al. (2013) examined filter properties of the highly branched trunk canals seen in a species of Stichaeidae, using an artificial lateral line system model which has several tubules, each containing multiple pores. They showed that the artificial lateral line system has the signal-to-noise ratio in a highly turbulent environment, however, a reduction in spatial resolution would be the price to pay for an improvement, thereby suggesting that the canals with multiple-pored tubules are an adaptation to a highly turbulent environment. Accordingly, the multiplication of the trunk canal in Stichaeidae may be a compensation for the reduction in spatial resolution (Klein et al. 2013).

16.6 Taxonomic Groups with Characteristic Lateral Line Systems

16.6.1 Apogonidae

Apogonidae is a large percomorpha family including more than 370 species, they inhabiting shallow coral reefs, sandy bottoms, and seagrass beds, with some groups being seen in deep sea and rivers (Mabuchi et al. 2014). Species of the family are characterized by having many superficial neuromasts, with highly various arrangements among the species (Bergman 2004; Sato et al. 2017, 2019, 2021a). In most apogonids, superficial neuromasts are found on the head, lateral line scales and caudal fin, whereas in five genera, a number of superficial neuromasts occupy the entire surface of the trunk, in addition to the head and caudal fin (viz., *Pseudamia gelatinosa* has ca. 9,600 superficial neuromasts in 61.0 mm standard length; Fig. 16.9) (Sato et al. 2019, 2021b). Considering the molecular phylogeny of Apogonidae and the innervation of the superficial neuromasts, it can conclude that the feature in which superficial neuromasts occupy the entire trunk had evolved independently in at least two lineages, via different morphological derivations in the two groups (Sato et al. 2019, 2021b). Most notably, species of *Pseudamia* have two (dorsal and ventral) lateral line scale series, with an incomplete trunk canal only on the dorsal one; in addition, a superficial neuromast row occurs on all the trunk scales (Sato et al. 2019). This phenotype can be interpreted as a combination of the duplication of the lateral line scale series, incompletely canal formation, and superficial neuromast proliferation. In fact, the dorsal longitudinal collector nerve which is generally on the dorsal part of the trunk is formed also on the ventral part in *P. gelatinosa*, indicating that the developmental process of the trunk lateral line system (see Sect. 16.5) was duplicated to the ventral part of the trunk (Sato et al. 2019). Species of *Pseudamia* are nocturnal and tend to hide, living deep within reef recesses and often in crevices within caves (Randall et al. 1985). Because superficial neuromasts cannot respond to stimulus under a unidirectional background flow (Engelmann et al. 2000, 2002), the proliferation of superficial neuromasts can be inferred as an adaptation to such habitats in which no significant flows frequently occur.

In the family, *Pseudamiops* is characterized by a paedomorphic nature, e.g., small, transparent or translucent body, compared to its sister group *Pseudamia*. A comparison of the lateral line system between the two genera (Fig. 16.9) denotes that lesser-branched canals and a smaller number of superficial neuromasts are present in adult *Pseudamiops* sp. compared to those in the adult of the non-paedomorphic species *Pseudamia gelatinosa*. However, that condition of *Pseudamiops* sp. is quite similar to the juvenile stage of *Pseudamia gelatinosa*, accordingly representing a paedomorphic truncation of the whole lateral line system development (Sato et al. 2021b).

16.6.2 Gobioidei

Gobioidei is a large percomorpha suborder comprising more than 2,000 species organized in eight families, but its phylogenetic position is still under discussion (Nelson 2006; Nelson et al. 2016). In almost all species of Gobioidei, the head and trunk canals are completely or partially absent, while many superficial neuromasts are present (Fig. 16.6c, d) [for example, ca. 4,800 on one side of the body in *Glossogobius olivaceus* (Gobiidae) in 82 mm standard length: Asaoka et al. 2012]. Furthermore, the degree of the canal reduction and the arrangement of superficial neuromasts are various among species or genera, so that these features have been mentioned as diagnostic characteristics for species of Gobioidei in abundant taxonomic studies since the early twentieth century (Sanzo 1911; Aurich 1939; Miller 1978; Miller and Wongrat 1979; Hoese and Gill 1993; Larson 2001; Akihito et al. 2002). Specifically, in species of *Eleotris* (Eleotridae), superficial neuromasts are arranged in several longitudinal and transverse rows spread over the head, with species-specific patterns (Prince 1967; Miller and Wongrat 1979; Miller 1998; Akihito et al. 2002; Pezold and Cage 2002).

In a pioneering work that described the innervation of the lateral line system in Gobioidei, Wongrat and Miller (1991) clarified most of the head superficial neuromast rows are canal neuromast homologues, based on the innervation of the neuromasts in species of Odontobutidae and Eleotridae. Such approach, focusing on the innervation of neuromasts and discussing the homology of neuromasts among species, was followed by Ahnelt and Bohacek (2004) and Asaoka et al. (2011, 2012, 2014) for Gobiidae, Odontobutidae, and Rhyacichthyidae. In an ancestral gobioid *Rhyacichthys aspro* (Rhyacichthyidae), which conservatively retains the complete head and trunk canals, only ca. 30 canal neuromasts are present within the canals, as in other teleosts (Asaoka et al. 2014). On the other hand, species without the head canals possess hundreds of superficial neuromasts, which have originated from the ca. 30 canal neuromasts. This increase in the number of neuromasts is probably achieved by dividing of each canal neuromast homologue into two or more with growth ("budding process" in Wada et al. 2010, 2013). Nickles et al. (2020) showed a SEM image of a superficial neuromast that appears to be in the budding process, in an observation of the ontogenetic process of superficial neuromasts in a species of *Elacatinus* (Gobiidae) (but this neuromast was not asserted to be a canal neuromast homologue).

The presence of many superficial neuromast rows in Gobioidei have also been referred in discussing its sister groups. Recent molecular phylogenetic studies support a close affinity among Apogonidae, Kurtidae, and Gobioidei (Thacker 2009; Thacker and Roje 2009; Thacker et al. 2015; Betancur-R et al. 2013) and the presence of rows has been considered a candidate of synapomorphy among the three taxa, as firstly proposed by Johnson (1993). However, because the innervation pattern of the superficial neuromasts is quite different and no common derivations for supplying the superficial neuromasts are present among the three taxa, the presence of many superficial neuromast rows is pointed as their homoplasy (Sato et al. 2017, 2021a).

16.6.3 Kurtidae

Kurtus gulliveri, one of the only two species of Kurtidae, lives in turbid rivers and estuaries in southern New Guinea and northern Australia. It is known as nurseryfish, because of a unique hook that is presents on the forehead of males for carrying an egg mass (Berra and Neira 2003; Berra 2007; Berra and Wedd 2017). The lateral line system of *K. gulliveri* (and *Kurtus indicus*) is unusual, comprising numerous superficial neuromasts almost all over the body surface including the dorsal, anal, and caudal fins (Fig. 16.10a; Johnson 1993). There are ca. 373,000 superficial neuromasts on one side of the body (in 152 mm standard length specimen), ca. 30% of which are located on the three fins (Sato et al. 2021a). In addition, these superficial neuromasts are arranged in a densely cross-hatch pattern consisting of a number of longitudinal and transverse rows (Fraser 2013; Sato et al. 2021a). SEM observations for the microstructure of each superficial neuromast indicated that the superficial neuromasts of transverse rows each possess the best physiological sensibility to flow parallel to the body axis (i.e., with longitudinal sensory orientation), whereas those in the longitudinal rows each possess the best sensibility to flow perpendicular to the body axis (i.e., transverse sensory orientation) (Fig. 16.10b, c). Therefore, the cross-hatch pattern consisting of these superficial neuromast rows, as a whole, is thought to have similar sensibility for both the longitudinal and transverse directional components of a water movement (Sato et al. 2021a). An almost motionless lifestyle of *K. gulliveri* in a turbid and still water environment may make it the most suitable for the functioning of their specialized lateral line system, since superficial neuromasts cannot correctly detect water movements if under unidirectional background flow (Engelmann et al. 2000). The innervation pattern of numerous superficial neuromasts in *K. gulliveri* is distinctive, differing from all percomorphs known thus far, indicating the presence of superficial neuromasts arranged characteristically is apomorphy of the kurtids (Sato et al. 2021a).

In *K. gulliveri*, the lateral ramus of the posterior lateral line nerve passes laterally to the elaborated swim bladder enveloped by broad ribs (Berra and Neira 2003; Carpenter et al. 2004; Berra 2007), thus Carpenter et al. (2004) hypothesized that the ramus transmits mechanosensory information coming from the swim bladder. Explicitly designed experiments should be performed to further understand the morphological significance of the unique lateral line system, and its relation to the swim bladder.

16.6.4 Pleuronectiformes

The pleuronectiforms show an asymmetric topography of the head canals between the ocular and blind sides, in which both supraorbital canals are present between the eyes on the ocular side (Fig 16.11) (Sasaki et al. 2007; Voronina et al. 2021). This asymmetric topography is apparently owing to the asymmetric change in their cranial bones, accompanied with eye migration. In addition, some canals presenting on the ocular side are absent on the blind side (e.g., a most part of the preopercular canal and the entire mandibular

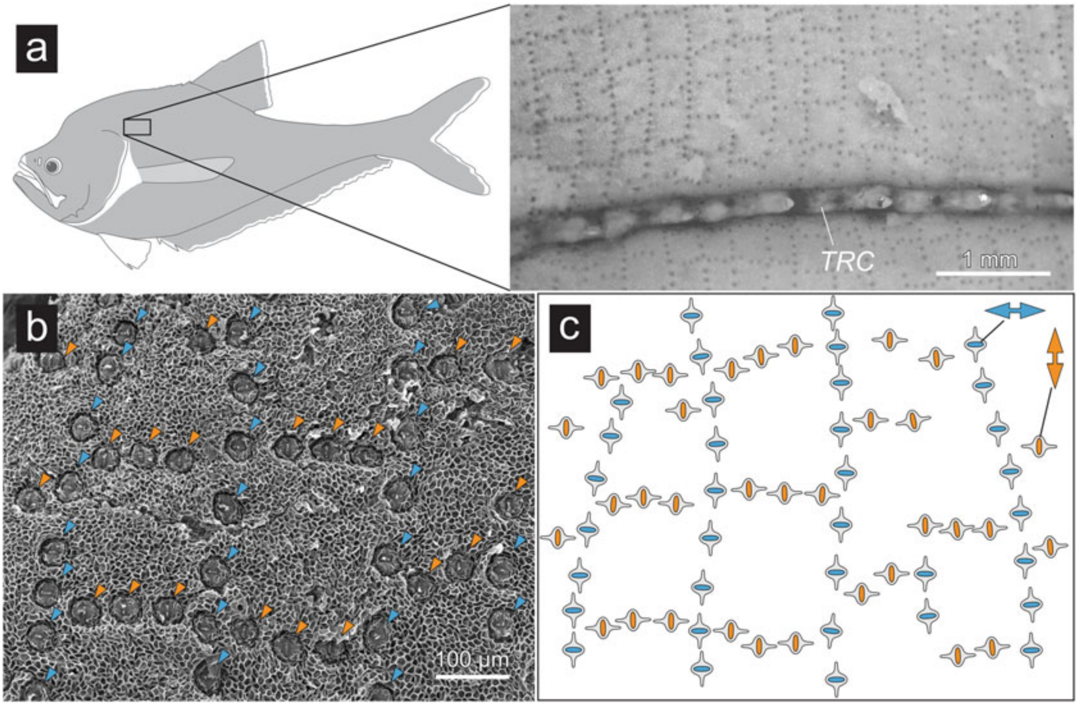

Fig. 16.10 Superficial neuromasts of *Kurtus gulliveri* (Kurtidae). (**a**) Superficial neuromasts (small dots, stained with Cyanine blue) arranged in longitudinal and transverse rows, which are present on the gray area in the illustration of the whole body. (**b**) SEM image of superficial neuromasts on the cheek; orange arrowheads indicate those with transverse sensory strip (i.e., transverse sensory orientation), arranged in longitudinal rows; blue arrowheads indicate those with longitudinal sensory strip (i.e., longitudinal sensory orientation), arranged in transverse rows. (**c**) Diagram of the distribution pattern of superficial neuromasts on the cheek; *double-headed arrows* indicate long axes of sensory strips (i.e., sensory orientation). (Adapted from Sato et al. 2021a in Ichthyology & Herpetology by the American Society of Ichthyologists and Herpetologists, under CC BY 4.0)

canal: Fig. 16.11b) or more branched compared to those of the blind side (see illustrations of Voronina et al. 2021). In *Glyptocephalus zachirus* (Pleuronectidae), the canals on the ocular side are narrow whereas those on the blind side are widened (Voronina et al. 2021), showing a unique asymmetric canal morphology.

When it comes to conservativeness of the head canal topography in teleosts (discussed in Sect. 16.2.1), Cynoglossidae is an exceptional group. Species of *Cynoglossus* (e.g., *Cynoglossus quadrilineatus*) have two unusual additional canals occurring only on the ocular side: one is along the anterior margin of the snout and the other extends from the preopercular canal onto the opercular bone. In addition, most parts of all head canals consist of head scales each having a short canal segment like trunk lateral line scales (Yokogawa et al. 2008; Sato et al. 2018; Voronina et al. 2021), these parts of the head canals being no longer associated with the dermal bones.

The number, size, and distribution pattern of superficial neuromasts are asymmetric in Pleuronectiformes. Especially in Cynoglossidae and Soleidae, many superficial neuromasts arranged in rows are found on the blind side of the head, in opposition to a relatively small number of superficial neuromasts on the ocular side, showing an asymmetric distribution pattern of neuromasts between the body sides (Fig. 16.11a) (Cunningham 1890; Roper 1981; Appelbaum and Schemmel 1983; Harvey et al. 1992; Ma et al. 2016; Sato et al. 2018). Although

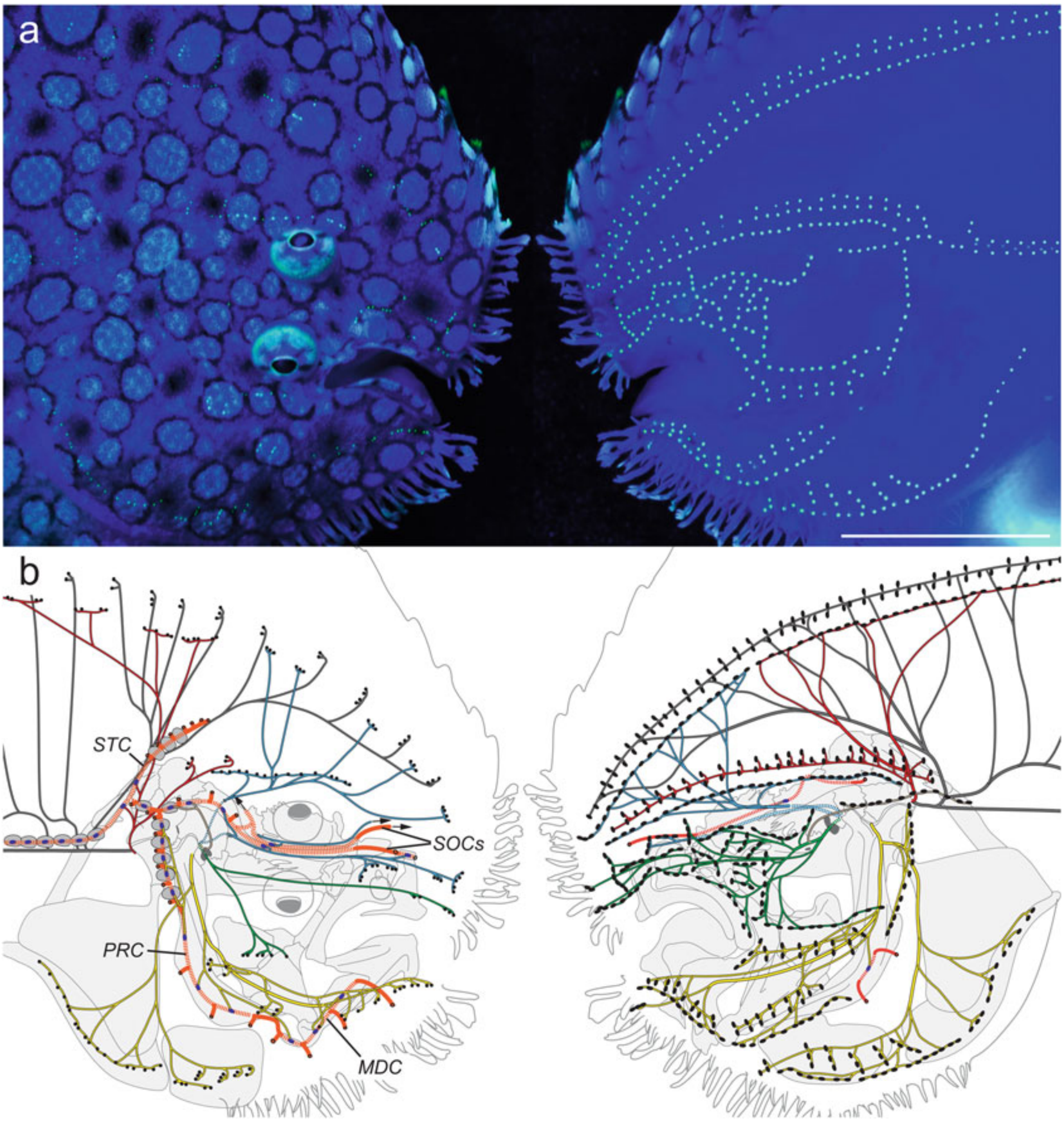

Fig. 16.11 Asymmetric lateral line system on the head of *Pardachirus pavoninus* (Soleidae). (**a**) Superficial neuromasts (small dots) stained with DiASP on the ocular and blind sides. (**b**) Innervation pattern of the neuromasts. *MDC* mandibular canal, *PRC* preopercular canal, *SOCs* supraorbital canals of the ocular and blind sides, *STC* supratemporal canal. Terminology for the nerves is as in Fig. 16.7 (see Sato et al. 2018). *Navy* and *black dots* indicate canal and superficial neuromasts, respectively. *Orange lines* indicate the course of head canals; *broken lines* indicate paths through cranial bones or scales. *Arrows* indicate extension to blind side of the lateral line canals and nerves. Scale bar = 5 mm. (Adapted from Sato et al. 2018 with permission from the Ichthyological Society of Japan)

the identical nerve elements (branches) are present between the ocular and the blind sides, each branch on the blind side is more complexity ramified compared to corresponding branch on the ocular side (Fig. 16.11b) (Sato et al. 2018). On the blind side in Soleidae, each row of superficial neuromasts is located in a channel surrounded by dermal papillae, and the sensory orientation of each superficial neuromast is parallel to the long axis of the associated cannel (Appelbaum and Schemmel 1983; Sato et al. 2018). Therefore, the channels seem to protect the superficial neuromast rows, as well as make water flows to pass through the channels, thus along the sensory orientations of superficial neuromasts.

16.7 Overview of the Morphological Diversity in the Lateral Line System

The lateral line system comprises lateral line canals and neuromasts, and tightly associates with the dermal bones, scales, and sometimes skin surface structures (e.g., "channels" in Soleidaie). Since each of these components varies in its morphology among taxonomic groups, morphological diversity in the whole lateral line system has appeared as an accumulation of interspecific differences in the respective components. Among fishes, a part of the interspecific differences in the canal morphology and neuromast distribution pattern can be explained with heterochrony, given that interspecific variation is recognized in the timing of completion (and truncation) of the ontogenetic process of the system as observed in serial developmental studies. However, unique features that cannot be explained only by heterochrony (e.g., multiple trunk canals) are widely seen in fishes. Since the branching pattern of the lateral line nerves partially reflects its ontogenetic background, other factors contributing to diversification of the system are expected to be found from further comparative morphological studies using fishes with characteristic lateral line systems, as well as by observation of the developmental process in them. The adaptation to habitats and the association to habits (e.g., swimming speed) in respective species have likely contributed to the morphological diversification of the system. Functional distinctions between canal and superficial neuromasts have been discussed using physical models and physiological examinations. However, the number of cases where functional properties of the system and associated ecological significances were experimentally demonstrated is still small compared with the large morphological variations in the system. Overall, there are still many topics to be addressed, from both ultimate and proximate perspectives, by further morphological and functional studies, to fully comprehend the reason for the diversification of the lateral line system.

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17 Recent Distributional Shifts and Hybridization in Marine Fishes of Japan

Hiroshi Takahashi

Abstract

The Japanese Archipelago separates the Sea of Japan from the North Pacific Ocean to the west and east, respectively. The Sea of Japan is a semi-enclosed marginal sea, on which the influence of global warming was remarkable during the twentieth century. The sea surface temperature rose three times faster than that of the world ocean, including the North Pacific Ocean. In response to the warming of the Sea of Japan, rapid northward range shifts have been observed in many marine fishes, some of which have shown increases in the rate of natural hybridization with their close relatives. A notable example is the mass occurrence of natural hybridization observed between two closely related pufferfishes, *Takifugu snyderi* and *Takifugu stictonotus*, between 2012 and 2014. Another example is the recent increase in the number of natural hybrids between two yellowtails, *Seriola quinqueradiata* and *Seriola lalandi*. In both cases, rapid distributional shifts in one of the two species, and the rarity of one parental species in spawning populations, were the likely causes of the increased hybridization. In the former example, past mitochondrial DNA introgression was distinguished from the recent and ongoing hybridization, indicating that hybridization has occurred not only recently, but also occasionally in the past. Although there is evidence of ancient hybridization in many other marine fishes, where past hybridization may have played a role in their diversification, the effects of environmental changes on the temporal dynamics of hybridization remain largely unknown. Continuous monitoring and the application of population genomics to these ongoing hybridizations may provide insight into the relationship between climate change and hybridization dynamics, where the global temperature is now approaching that of the last interglacial period.

Keywords

Climate change · Sea of Japan · Natural hybridization · Hybrid class identification · Tsushima Warm Current

17.1 Introduction

The Japanese Archipelago separates the Sea of Japan from the North Pacific Ocean to the west and east, respectively (Fig. 17.1). The Sea of Japan is a semi-enclosed marginal sea dominated by inflow from the Tsushima Warm Current (TWC), from the East China Sea through the Tsushima Strait (sill depth = 130 m). The TWC flows northward along the western coast of

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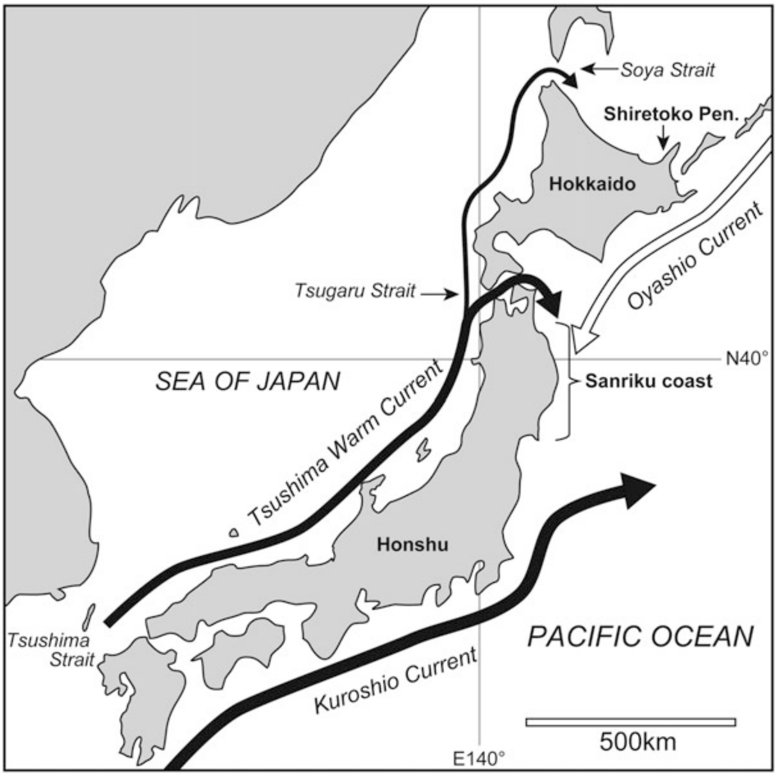
Fig. 17.1 Map of the Sea of Japan and the present current system around the Japanese Archipelago



Honshu Island and supplies a large amount of heat to the Sea of Japan (Kitamura et al. 2001). The majority of the inflowing water flows out to the Pacific Ocean through the Tsugaru Strait (sill depth = 130 m), known as the Tsugaru Warm Current, and the remaining water flows into the Sea of Okhotsk through the Soya Strait (sill depth = 55 m), known as the Soya Warm Current (Onishi and Ohtani 1997). These two branches of the TWC flow clockwise around northern Honshu Island and Hokkaido Island, and reach the Sanriku coast and the Shiretoko Peninsula, respectively. The sea surface temperature gradually decreases along the TWC (e.g., Takizawa 1982; Mugo et al. 2014).

The marine environment of the Sea of Japan has undergone drastic changes due to sea-level changes associated with repeated glaciations during the Quaternary (Oba et al. 1991; Tada 1994). Palaeoceanographic changes in the Sea of Japan during and after the Last Glacial Maximum (LGM) are especially well understood. During the LGM (27–20 ka), the global sea level fell by approximately 120 m, which greatly decreased the inflow of the TWC due to narrowing of the Tsushima Strait. Consequently, the Sea of Japan was almost isolated from the surrounding seas (Oba et al. 1991; Tada et al. 1999). The relative increase of freshwater inflow from the surrounding continent resulted in the development of low-salinity surface water and the seafloor was severely anoxic due to the disappearance of deep-water circulation. After the LGM (ca. 19 ka), the Oyashio Current flowed into the Sea of Japan through the Tsugaru Strait, reestablishing deep-water circulation (Oba et al. 1991). After the last glacial period (after 10 ka; the Holocene), the TWC started to flow into the Sea of Japan through the Tsushima Strait (Oba et al. 1991). Subsequently, the modern oceanographic regime was established during and after the Holocene climatic optimum (ca. 6 ka), when annual mean surface temperatures in the Japanese Archipelago were approximately 2 °C warmer than the present temperatures (Heusser and Morley 1985). Similar environmental changes likely occurred repeatedly since the middle Quaternary (ca. 1.7 Ma) (Kitamura et al. 2001).

Population genetic and phylogeographic studies on coastal and euryhaline fishes of Japan revealed that Quaternary climatic oscillations were important drivers of their diversification. The most characteristic feature observed in some of these fishes, such as threespine sticklebacks (*Gasterosteus*), gobies (*Pterogobius*, *Leucopsarion*, and *Chaenogobius*), and daces (*Pseudaspius*), is the presence of two genetically distinct lineages, corresponding to the Sea of Japan and Pacific Ocean lineages, possibly initiated by the isolation of the former sea during the glacial period (Higuchi and Goto 1996; Akihito et al. 2008; Kokita and Nohara 2011; Hirase and Ikeda 2015; Watanabe et al. 2018). In the Japanese Archipelago, the present-day distribution areas of these two lineages mostly follow the range of the TWC and the Kuroshio Current, respectively. On the other hand, the development of low-salinity surface water in the Sea of Japan during Pleistocene glacial periods might have promoted the dispersal of euryhaline fishes, such as ninespine sticklebacks (*Pungitius*), charrs (*Salvelinus*), and daces (*Pseudaspius*), through the coastal waters (Takahashi et al. 2001, 2016; Yamamoto et al. 2004; Watanabe et al. 2018). The mosaic distribution of widespread and localized mitochondrial DNA (mtDNA) lineages within these species along the coast of Japan suggests that recurring glacial dispersal events and genetic differentiation during the interglacial period played an important role in their diversification. Although the abovementioned studies provided great insights into the role of the Quaternary climatic changes in evolutionary diversification in coastal and euryhaline fishes, such knowledge is still limited for most marine fishes, especially regarding the effects of interglacial global warming on their biodiversity.

The impact of climate change on marine ecosystems is assumed to be greater in the Sea of Japan compared to the Pacific Ocean, because of the former is a semi-enclosed, middle-latitude marginal sea (Nakashiki et al. 2005; Gamo et al. 2014). In fact, the Sea of Japan has been one of the most rapidly warming waterbodies on Earth during the modern warming period: the sea surface temperatures in its southwestern and central parts rose at a rate two or three times faster (+1.31 °C/100 years and +1.72 °C/100 years, respectively) than the average increase in the North Pacific Ocean and world ocean (+0.53 °C/100 years and +0.51 °C/100 years, respectively) (Ministry of Education, Culture, Sports, Science and Technology and Japan Meteorological Agency 2020). In response to the warming of the Sea of Japan, rapid range shifts were observed in many marine fishes toward the downstream area of the TWC (Masuda 2008; Hoshino 2017; Sugisaki and Murakami 2017). For example, the ratio of annual catch of two temperate marine fish groups, pufferfishes (*Takifugu* spp.) and yellowtails (*Seriola* spp.), of Hokkaido, the northernmost main island of Japan, compared to that of the whole country averaged over the past 10 years (2010–2019) was about six times higher than those before 2010 (1995–2009 for pufferfishes and 1956–2009 for yellowtails). Considering that the modern global temperature is likely approaching the warmth of the last interglacial period (128–115 ka) (Bova et al. 2021), we can compare the biological impacts of ongoing climate warming to those of past interglacial climates and vice versa. In addition, ocean warming "hotspots" like the Sea of Japan are thought to serve as critical early indicators of the expected consequences of ongoing climate change (Frusher et al. 2014; Hobday and Pecl 2014).

In this chapter, I will highlight two studies that address the impact of ongoing climate warming on the reproductive interactions and hybridization between closely related marine fish species in Japan. To begin with, I will briefly review examples of climate change-induced hybridization in animal taxa. Then, I will introduce and discuss two of my recent studies, one focused on pufferfishes and one focused on yellowtails (Takahashi et al. 2017, 2021). Finally, I will discuss future research directions, with a focus on applying population genomic approaches to gain insight into the causes and genetic consequences of the ongoing hybridization.

17.2 Distributional Shifts and Hybridization Under Ongoing Climate Change

Recently, rapid distributional shifts in response to ongoing climate change have received increasing attention as one of the major causes of recent hybridization, in addition to other known causes such as human-induced translocation, habitat disturbances, and loss of habitat heterogeneity (Seehausen et al. 2008; Brennan et al. 2014; Chunco 2014; Grabenstein and Taylor 2018). Increased rates of hybridization due to climate change were mainly observed in terrestrial organisms until a few years ago (Chunco 2014). For example, a novel hybrid zone between two closely related flying squirrel species (*Glaucomys* spp.) formed within only 15 years following a 200-km-long northern range shift of the southern species into the range of the northern species (Garroway et al. 2010). In this example, a report of the historical northern range limit of the southern species prior to the range expansion was used to define the historical allopatry of the two parental species and provided evidence for increasing species interactions between them. However, it is generally difficult to determine whether hybridization is increasing, because in most cases adequate baseline information, such as time series data covering the necessary geographic ranges, are not available (Chunco 2014; Potts et al. 2014). For example, genetic data from both museum and contemporary specimens of two closely related species of tiger swallowtail butterflies (*Papilio* spp.) indicated that the hybrid zone between these two species shifted northwards by about 40 km from 1980 to 2012 (Ryan et al. 2018). Despite the rapid distributional shifts, no change in the frequency of hybridization was observed across the entire latitudinal transect. However, in one location, a significant increase in the frequency of early generation hybrids was found, although this increase was related to a decrease in hybrids in the population south of the location (Ryan et al. 2018). This suggests that insufficient sampling may lead to misunderstanding and erroneous conclusions about changes in hybridization frequencies.

Potts et al. (2014) first raised the possibility of an association between the recent increase in hybridization frequency and rapid distributional shifts in response to ongoing climate change in marine fishes. The frequency of natural hybridization between the two sciaenid species *Argyrosomus coronus* and *Argyrosomus inodorus* in samples from two time periods (period 1 = 1994–1996, period 2 = 2008–2009) collected in Namibia was examined. This study describes very rapid warming (+0.8 °C/10 years) in the coastal waters of the Angola-Benguela Frontal Zone over the last three decades, and an associated range shift of the temperature-sensitive coastal species *A. coronus* southward from Angola into Namibia, where *A. inodorus* used to be abundant. The data of a previous study on seven diagnostic allozyme loci (Van Der Bank and Kirchner 1997) were used to identify hybrids caught during period 1, while those of six microsatellite loci were used to identify hybrids caught during period 2. They reported that no hybrid was identified between 16 *A. coronus* and 13 *A. inodorus* individuals during period 1, while five and two hybrids were identified in the 180 *A. coronus*- and 40 *A. inodorus*-like individuals, respectively, during period 2. It should be noted, however, that at least three putative hybrids caught during period 2 were identified as genetically pure *A. coronus*, while the remaining five were first-generation backcrosses (BC1) to *A. coronus*, i.e., they were not F1 hybrids according to their nuclear genotypes. Nevertheless, the assignment success for simulated genotypes of BC1 generated by HYBRIDLAB (Nielsen et al. 2006) was only 50% for six analyzed microsatellite markers. This is in accordance with the results of a simulation study, suggesting that at least 48 diagnostic loci would be necessary to separate BC1 from genetically pure parental individuals, even when the divergence between parental species is high (Vähä and Primmer 2006). In addition, nearly 1%

of BC1 would be misclassified as pure parental species if seven diagnostic codominant markers were used, as was the case for period 1 (Epifanio and Phillipp 1997). Thus, in this case, there is some uncertainty as to whether hybridization is truly increasing.

17.3 Mass Occurrence of Natural Hybrids Between Two Pufferfishes

From around 2012 onward, unidentifiable individuals of pufferfishes morphologically close to *Takifugu snyderi* were found in the coastal waters of eastern Honshu, Japan (Fig. 17.2a). They differed from morphologically typical *T. snyderi* in terms of a slightly yellow anal fin and/or weak spinules on their body surfaces, while *T. snyderi* has a white anal fin and a smooth body surface. The unidentifiable individuals accounted for 55% of the total pufferfish catch (278 individuals) in two bottom-trawl surveys carried out in Ibaraki Prefecture on 20 January 2014. The mass occurrence of unidentifiable pufferfishes created confusion in the fishing industry because unidentifiable individuals must be eliminated from the market by law because of their unknown toxicity (Abe and Tabeta 1994). My colleagues and I researched these pufferfishes in response to various requests from prefectural fisheries experiment stations and fishing industries to clarify this issue.

Pufferfishes belonging to the genus *Takifugu* are prominent examples of recent adaptive radiation of marine fishes (Yamanoue et al. 2009). Both nuclear DNA and whole mitochondrial genome sequencing analyses indicated that they have undergone explosive speciation, giving rise to approximately 20 closely related species during the Quaternary (Yamanoue et al. 2009; Santini et al. 2013). They successfully speciated and radiated in subtropical and temperate waters of Northeast Asia, exhibiting remarkable variety in terms of body size and thermal habitat use compared to other tetraodontid pufferfishes (Yamanoue et al. 2009; Santini et al. 2013). However, the causes of this radiation remain unclear

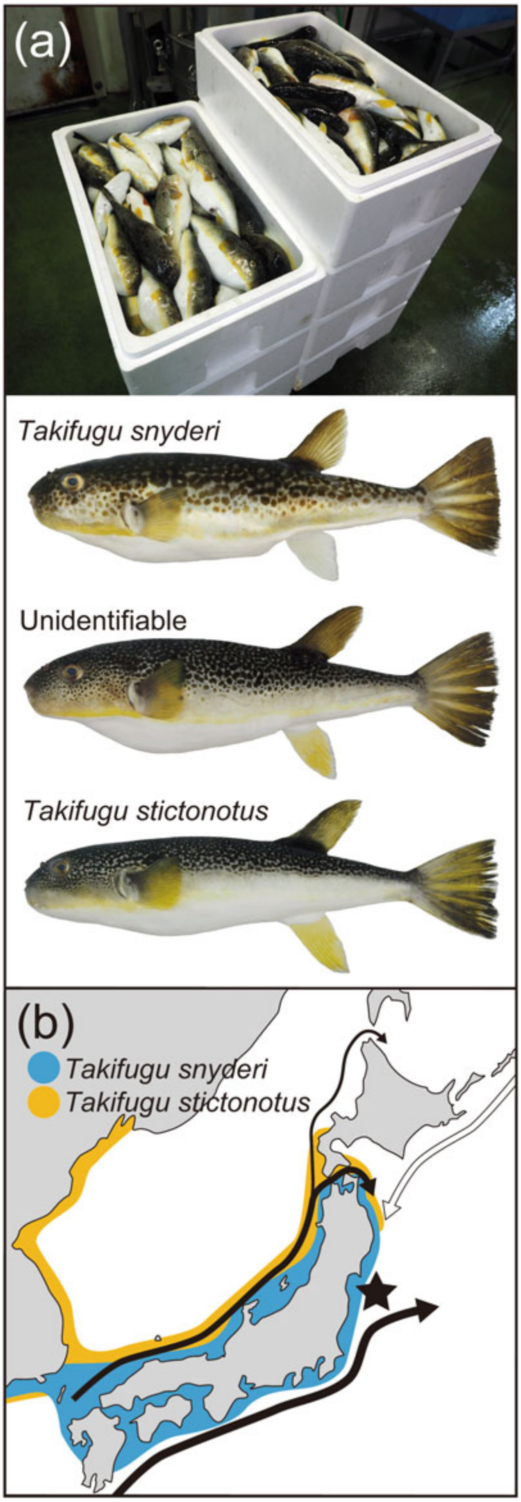


Fig. 17.2 (**a**) A large number of unidentifiable pufferfishes eliminated in a marine product processing

and only a few hypotheses have been suggested (Santini et al. 2013). As most pufferfishes (Tetraodontidae) spawn in tropical/subtropical waters, adaptation to temperate climates could have been a key innovation (Schluter 2000) promoting the diversification of *Takifugu* in cooler climates. For example, *Takifugu porphyreus* is considered to be the most cold-water-adapted species in Tetraodontidae, since it is commonly found in the coastal waters of southern Sakhalin, representing the northernmost distribution range of tetraodontid pufferfishes (Dyldin et al. 2016). On the other hand, Santini et al. (2013) suggested that diversification in this group was driven by Pleistocene glaciation cycles, although no concrete explanation was provided regarding how such climate cycles affected diversification.

Another possible hypothesis is that hybridization played a role in the diversification of *Takifugu*. Young species that have undergone rapid adaptive radiation usually show natural hybridization and potential introgression with other species (Seehausen 2004; Mallet 2005). The role of hybridization in evolutionary diversification as a mechanism promoting novel genetic variation in animal systems has gained support in recent years (Herder et al. 2006; Heliconius Genome Consortium 2012; Lamichhaney et al. 2015). Furthermore, recent studies suggested that introgression via historical and contemporary hybridization is a continuous evolutionary process during adaptive radiation (Mallet et al. 2007; Lamichhaney et al. 2015). Against this background, it is likely that the explosive diversification of *Takifugu* involved natural hybridization as a catalyst of rapid evolutionary change (Arnold et al. 2012). However, the significance of hybridization in their radiation has not been investigated, although a few reports of natural hybridization among species of *Takifugu* seem to imply the importance of hybridization to the diversification of this group (Masuda et al. 1991; Yokogawa and Urayama 2000; Tatsuno et al. 2019).

Returning to the abovementioned unidentifiable pufferfishes, a morphological study revealed that the individuals have intermediate morphological traits between *T. snyderi* and its sister species *Takifugu stictonotus* (see Takahashi et al. 2017). The species are morphologically very similar, but the latter can be distinguished by a lemon-yellow anal fin and spinules on its dorsal and ventral body surfaces (Fig. 17.2a). *Takifugu snyderi* is mainly distributed along the Pacific coast of Honshu, Japan but also occurs in the Sea of Japan along the coast of Honshu and Kyushu (Fig. 17.2b; Abe and Tabeta 1994; Yamada and Yagishita 2013). On the other hand, *T. stictonotus* occurs almost exclusively in the Sea of Japan along the coast affected by the TWC (Fig. 17.2b; Abe and Tabeta 1994; Yamada and Yagishita 2013), although it recently expanded its range toward the downstream region of the TWC and reached the Pacific Ocean off the Sanriku coast beyond the Tsugaru Strait (Itou, personal communication). The coastal waters of Ibaraki and Fukushima prefectures are within the natural range of *T. snyderi* and just outside the range of *T. stictonotus* (Fig. 17.2a). Considering the intermediate morphologies and sister relationships between the two species, these unidentifiable pufferfishes could be hybrids of these species. Although both species are commercially important for coastal fisheries in Japan, unidentifiable individuals must be eliminated from the market as mentioned above. However, these individuals provide a good opportunity to collect quantitative data regarding ongoing hybridization, which are scarce in the marine realm (Muto et al. 2013; Montanari et al. 2014). Such data would allow us to assess the directionality of hybridization and backcrossing, which may provide important clues regarding the causes of rapid diversification of *Takifugu*.

Takahashi et al. (2017) used amplified fragment length polymorphism (AFLP) and mtDNA

Fig. 17.2 (continued) plant. *Takifugu snyderi* (top), an unidentifiable individual (middle), and *T. stictonotus* (bottom) collected off the Pacific coast of eastern Honshu, Japan. (**b**) The natural distribution ranges of *T. snyderi* (blue) and *T. stictonotus* (yellow) around the Japanese Archipelago and the sampling location (Ibaraki and Fukushima prefectures) of the unidentifiable individuals of *Takifugu* (*solid star*) markers to investigate the genetic characteristics of putative hybrids. AFLP allows the characterization of a large number of dominant markers (Vos et al. 1995), and is a very efficient technique for identifying F1 and later-generation hybrids without previous sequence information (Bensch and Åkesson 2005; Albert et al. 2006). On the other hand, sequencing of mtDNA has advantages over other techniques for identifying the female parent species involved in the production of hybrids, as it is maternally inherited (Wirtz 1999; Young et al. 2001). A total of 279 fishes, including morphologically typical *T. snyderi*, *T. stictonotus*, and their putative hybrids, were analyzed. AFLP analysis using 11 selective primer combinations generated a total of 334 fragments, 265 (79.3%) of which were polymorphic. Of these, 34 and 43 were species-specific for *T. snyderi* and *T. stictonotus*, respectively (i.e., 77 diagnostic loci). The fixation index (F_{ST}) between the two species was 0.723, which was highly statistically significant according to the bootstrap resampling method ($p < 0.001$). Based on the simulation and reassignment procedures performed with AFLPOP (Duchesne and Bernatchez 2002), the assignment success was 100% for all of the assumed categories (pure parental species, F1 or F2 hybrids, and BC1 in either direction).

Two Bayesian-based methods were used to identify hybrid individuals, performed using STRUCTURE v2.3.4 (Pritchard et al. 2000; Falush et al. 2007) and NewHybrids v1.1 beta software (Anderson and Thompson 2002; Anderson 2008). The former method assigned posterior probabilities to individuals with recent ancestry in K populations without prior information on individual ancestry. The most probable value of *K* was objectively determined using the method of Evanno et al. (2005); this allowed us to verify the existence of extra ancestral populations (e.g., other species involved in hybridization in our samples). When populations are known to consist of genetically pure individuals of two species and their recent hybrids (as verified through the STRUCTURE analysis), NewHybrids calculates posterior probabilities of individuals belonging to one of the six classes described above. This is essential to determine whether hybridization is ongoing, and to assess the evolutionary and conservational consequences of hybridization.

Numerous early generations of hybrids (131 F1 hybrids and 18 BC1) were identified by analyzing samples collected from the Pacific coast of eastern Honshu, Japan between 2012 and 2014 (Fig. 17.3; Takahashi et al. 2017). Among the 18 backcrosses, 17 were assigned to *T. snyderi* and 1 to *T. stictonotus*. The frequency of F1 hybrids was estimated as 38.5% based on the abovementioned two bottom-trawl surveys. A large number and high percentage of F1 hybrids provided clear evidence of current, ongoing hybridization (Bettles et al. 2005). The frequency of F1 hybrids was much higher than that reported in other pairs of pufferfishes, in which the frequencies of hybrids were estimated to be lower than 0.5% (Masuda et al. 1991; Yokogawa and Urayama 2000). Likewise, this rate is exceptionally high compared to those in other marine fishes for which adequate experimental data are available (Burford et al. 2011; Mirimin et al. 2014; Montanari et al. 2014).

We proposed two explanations for the unprecedented mass occurrence of natural hybrids between the two pufferfishes. One explanation is that F1 hybrids may occupy an intermediate ecological or physiological niche between the two parental species, resulting in a high concentration of F1 hybrids in certain regions. For example, F1 hybrids between European and American eels (*Anguilla anguilla* and *Anguilla rostrata*) account for more than 10% of the total population in Iceland (Albert et al. 2006; Pujolar et al. 2014). In this example, an intermediate migratory behavior of hybrid larvae is thought to be the cause of the high frequency of F1 hybrids in Iceland, located between the distribution areas of yellow eels (the sedentary stage of eels) of the two parental species (Pujolar et al. 2014). However, this explanation is unsatisfactory for the pufferfish example because it only accounts for the higher frequency of F1 hybrids in certain regions, i.e., Ibaraki and Fukushima prefectures, and not for the increases in frequency of F1 hybrids.

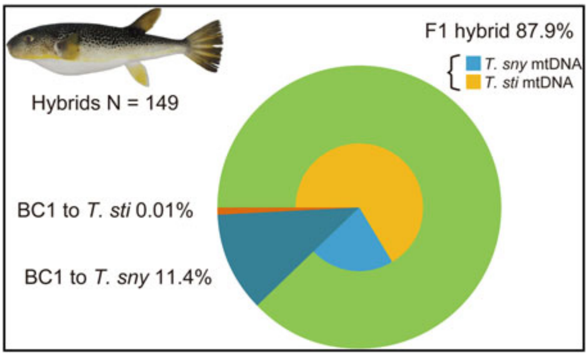


Fig. 17.3 The percentages of hybrid individuals assigned to F1 hybrid, first-generation backcross to *Takifugu snyderi* (BC1 to *T. sny*), and first-generation backcross to *T. stictonotus* (BC1 to *T. sti*) by NewHybrids (Anderson and Thompson 2002; Anderson 2008). The percentages of F1 hybrids with *T. snyderi* and *T. stictonotus* mtDNA lineages (*blue* and *yellow*, respectively) are also indicated

Another explanation is that the mass occurrence of F1 hybrids was driven by recent environmental changes, which would cause rapid distributional shifts of one of the two parental species. As mentioned above, *T. stictonotus* recently expanded its range to the Sanriku coastal region beyond the Tsugaru Strait, probably in response to the rapid warming of the Sea of Japan. In addition, between 1998 and 2012, anomalous temperature events were observed in the fall of 2010 and 2012 along the Sanriku coast, indicating an increased influence of the Tsugaru Warm Current (outflow of the TWC to the North Pacific Ocean through the Tsugaru Strait) in recent years (Wagawa et al. 2015). Since around that time, warm-water fishes, such as Red Sea Bream (*Pagrus major*) and Spanish Mackerel (*Scomberomorus niphonius*), which used to be rare, were caught by coastal fisheries along the Sanriku coast (Murakami, personal communication). Therefore, it is likely that the strengthening of the Tsugaru Warm Current, along with the recent warming of the Sea of Japan, may have facilitated southward invasion of *T. stictonotus* into the coastal waters of Ibaraki and Fukushima prefectures, and consequent hybridization between *T. snyderi* and *T. stictonotus*.

Analysis of mtDNA indicated that the majority of the F1 hybrids (75.6%) were offspring between *T. stictonotus* females and *T. snyderi* males (Fig. 17.3). Although asymmetric hybridization is a widespread phenomenon across a broad range of taxa, empirical support has often been based on a relatively small number of F1 hybrids (Wirtz 1999 and references therein). In comparison, the directionality found here is quantitatively supported by a large number of F1 hybrids (binominal test, $p < 0.01$), thereby providing excellent opportunities to study the causes and consequences of asymmetric hybridization. Although many mechanisms may underlie this phenomenon (Wirtz 1999; see discussion in Takahashi et al. 2017), the rarity of conspecifics is recognized as a frequent cause of hybridization, and it is predicted that hybrid mating occurs more often between females of rarer species and males of more common species (Wirtz 1999; Montanari et al. 2014). As mentioned above, *T. stictonotus* is very rare in the coastal waters of Ibaraki and Fukushima prefectures, where high frequencies of F1 hybrids were observed. This result is in line with the above theory that the southward invasion of *T. stictonotus* into the spawning area of *T. snyderi* caused the hybridization between them.

The mass occurrence of natural hybrids between the two pufferfish species, as well as the rapid distributional shifts of pufferfishes (*Takifugu* spp.), has raised concerns about its negative impact on food safety and biodiversity. In response, the Japanese government promptly set up the “Council on Studying Certification Criteria of Person Performing Pufferfish Processing” (26 April 2019) and issued a notice about the certification criteria which specify that the licensed individuals must pay attention to the occurrence of unidentifiable pufferfishes in Japan, including hybrids, as one of the additional criteria. On the other hand, the vulnerability of *Takifugu* biodiversity to increasing hybridization has yet to be studied. Hybridization can affect biodiversity in various ways, including the disappearance of one parental species, collapse of two parental species into hybrid swarms, introgression of beneficial adaptive genetic variation from one species to another, and the generation of novel hybrid species (Abbott et al. 2013). It has been suggested that investigations of clades showing adaptive radiation are particularly informative about the impact of human disturbance and consequent changes in hybridization frequency on patterns of biodiversity (Brennan et al. 2014). I will discuss this topic in more detail after the next section.

17.4 Increased Hybridization Among Yellowtails

Another example of a recent increase in the frequency of hybridization was observed between two yellowtail species, *Seriola quinqueradiata* and *Seriola lalandi*, both of which are important for marine fisheries and aquaculture in Japan, especially *S. quinqueradiata* (see Takahashi et al. 2021). Around 2011, local fishermen noticed that the catch of unidentifiable individuals that were morphologically intermediate between these two species increased in the Sea of Japan around Yamaguchi Prefecture (Fig. 17.4a). Although both species were subject to extensive multidisciplinary studies due to their importance for marine fisheries and aquaculture in Japan (Shiraishi et al. 2010, 2011; Tian et al. 2012; Martinez-Takeshita et al. 2015; Koyama et al. 2019), to our knowledge there have been no reports of natural hybridization between them.

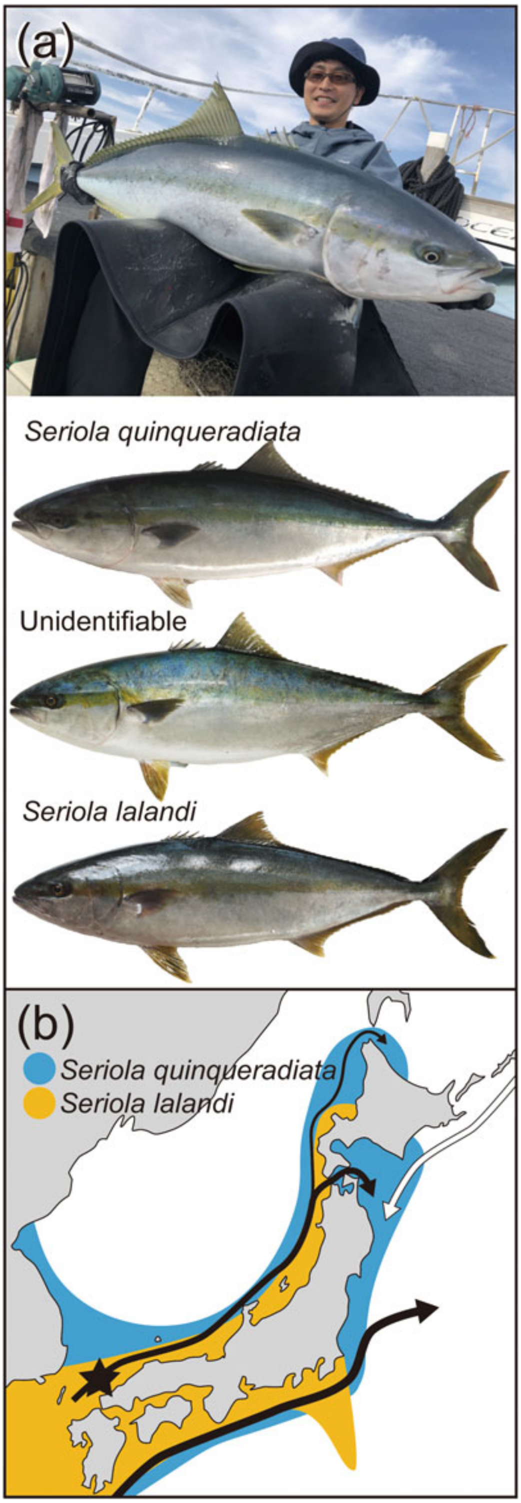


Fig. 17.4 (**a**) An unidentifiable individual of yellowtails (*Seriola* spp.) caught by line fishing. *Seriola quinqueradiata* (top), un unidentifiable individual (middle),

The suspected hybrids became a topic of conversation among recreational anglers because some of them were much larger ($\geq$20 kg) than average *S. quinqueradiata* individuals, which weigh about 15 kg (Fig. 17.4a). Meanwhile, the catch of many suspected hybrids by set netting ($\geq$20 individuals weighing >15 kg) at the same time surprised fisheries managers in the Senzaki wholesale market, Yamaguchi Prefecture, Japan.

Between 2016 and 2017, a total of 31 unidentifiable individuals of *Seriola* were caught by line fishing at two offshore reefs (Shiomaki-sho and Hachirigase reefs) in Yamaguchi Prefecture in cooperation with Mr. Hiroshi Terado, who first noticed the increase of hybrid-like individuals. He distinguished these individuals from morphologically typical individuals of *Seriola*, based primarily on their body shapes and coloration. For comparison, three additional species of *Seriola* native to the Sea of Japan were sampled; 7, 9, and 11 individuals of morphologically typical *S. quinqueradiata*, *S. lalandi*, and Greater Amberjack *Seriola dumerili*, respectively, were caught by line fishing and set netting from the same sea area. The samples were weighed and fin-clipped (right pelvic) for DNA analyses. AFLP and mtDNA markers were used for this study, as well to investigate the genetic characteristics of putative hybrids. The methodology for identifying hybrids and their classes was almost identical to that described above for the pufferfishes. AFLP analysis using 12 selective primer combinations generated a total of 522 fragments, 455 (87.2%) of which were polymorphic. Of these, 36, 44, and 62 were species-specific for *S. quinqueradiata*, *S. lalandi*, and *S. dumerili*, respectively. The F_{ST} among the three species was 0.802 ($p < 0.001$). Based on the simulation and reassignment procedures performed using AFLPOP, the assignment success was 100% for all of the assumed categories (pure parental species, F1 or F2 hybrids, and BC1 in either direction) for each species pair. These results demonstrated that AFLP markers are highly capable of classifying first- and second-generation hybrids of the three species.

Fig. 17.4 (continued) and *S. lalandi* (bottom) collected from the Sea of Japan off Yamaguchi Prefecture, Japan. (**b**) The natural distribution range of *S. quinqueradiata* (*blue*) and *S. lalandi* (*yellow*) around the Japanese Archipelago and the sampling location (Yamaguchi Prefecture) of the unidentifiable individuals of *Seriola* (*solid star*)

STRUCTURE and NewHybrids analyses revealed that 28 of the unidentifiable individuals were hybrids between *S. quinqueradiata* and *S. lalandi* (Fig. 17.5), and three were hybrids between *S. quinqueradiata* and *S. dumerili* (data not shown). This was the first report of natural hybrids of both combinations. Focusing on the former combination, 25 of the 28 hybrids were F1 hybrids, and the remaining three BC1 to *S. lalandi*. The mtDNA lineages of the F1 hybrids revealed that the majority (21 of 25) of individuals were offspring of *S. quinqueradiata* males and *S. lalandi* females, and this disproportion was statistically significant (binominal test, $p < 0.01$).

The presence of early generations of hybrids constitutes evidence of current, ongoing hybridization. Although it is generally challenging to determine whether hybridization is increasing, a few studies determined an increase of hybridization as mentioned above (Potts et al. 2014). However, despite extensive research on the natural populations of these two species (Shiraishi et al. 2010, 2011), no previous study has reported the occurrence of natural hybrids of the two species. Furthermore, as mentioned above, catches of hybrid-like individuals of *Seriola* in the Sea of Japan around Yamaguchi Prefecture have been gradually increasing over the past 10 years. Therefore, it is likely that hybridization between the two species has increased recently.

As mentioned above, the catch distribution of *S. quinqueradiata* has shifted northwards along the coast of the Sea of Japan in recent years, especially since 2011 (Hoshino 2017). However, the rapid northward shift may not be directly linked to increased hybridization, as this species migrates northwards to feed during the inter-spawning period. Nonetheless, the species' northward range extension might result in increased

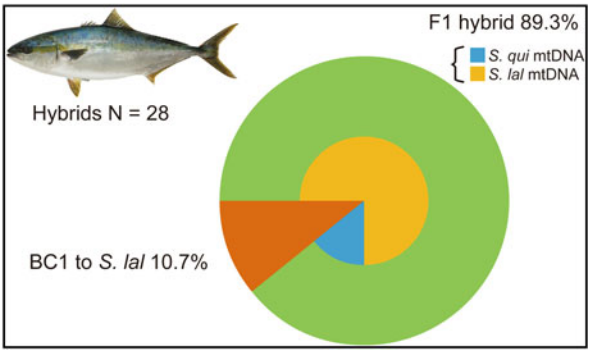


Fig. 17.5 The percentages of hybrid individuals assigned to F1 hybrid between *Seriola quinqueradiata* and *S. lalandi* and first-generation backcross to *S. lalandi* (BC1 to *S. lal*) by NewHybrids (Anderson and Thompson 2002; Anderson 2008). The percentages of F1 hybrids with *S. quinqueradiata* and *S. lalandi* mtDNA lineages (*blue* and *yellow*, respectively) are also indicated

hybridization by causing an imbalance in spawning stock biomass between *S. quinqueradiata* and *S. lalandi*. Tian et al. (2012) predicted that the northward range extension of *S. quinqueradiata*, resulting from the water temperature increase of the Sea of Japan, will have positive effects on the biomass of this species. Furthermore, it was hypothesized that the recent southward expansion of the spawning ground of *S. quinqueradiata* in the East China Sea is a response to the increased density of the spawning population in the northern East China Sea (Sassa et al. 2020). The estimated stock biomass of *S. quinqueradiata* increased nearly threefold over the past 20 years (Kubota et al. 2019), in addition to the fact that the catch of this species is much higher than that of *S. lalandi* in Japan before (e.g., Shiraishi et al. 2010). Although data on the spawning grounds and spawning stock biomass of *S. lalandi* in Japan are lacking (Shiraishi et al. 2010), the rarity of *S. lalandi* in the spawning population might be attributed to the recent rapid distributional shift and population growth of *S. quinqueradiata*. The clear asymmetry in directionality of hybridization observed between the two species is consistent with this theory, because the rarity of conspecifics is recognized as a frequent cause of hybridization, and it is predicted that hybrid mating occurs more often between females of rare species and males of more common ones (Wirtz 1999; Montanari et al. 2014).

17.5 Implications for Further Research

Although neither of the studies discussed here were based on time series data analysis, accurate hybrid and hybrid class identification allowed us to detect the emergence of large-scale hybridization events in the two marine fish groups. Both examples raise the possibility that the rapid warming in the Sea of Japan has a significant effect on the fish diversity of Japan through changes in the reproductive interactions and hybridization between closely related species. To understand the underlying causes and outcomes of recent hybridization, the next step will be to explore the genetic signatures of historical and contemporary hybridization. However, the limited number of loci, as well as the lack of sequence information provided by anonymous AFLP markers, remains a major limitation. With the recent development of new high-throughput DNA sequencing technologies, genomic evidence for ancient hybridization, and of its relevance to the evolutionary diversification of a wide range of animal systems, has accumulated (Heliconius Genome Consortium 2012; Lamichhaney et al. 2015; Meier et al. 2017). However, attempts to link genomic data of ancient hybridization with current, ongoing hybridization through monitoring hybridization dynamics over multiple periods are rare. For example, population genomic analyses of seven tropical eel species (*Anguilla* spp.) revealed that hybridization in this group occurred continuously between 2012 and 2017, rather than fluctuating among time periods (Barth et al. 2020). These results, together with genomic signatures of past introgression across these species, suggest that the combination of cytonuclear incompatibility, hybrid breakdown, and purifying selection has prevented a collapse of these species. Similar approaches will likely be applied to obtain further insight into the above-described pufferfish and yellowtail species.

The presence of backcrosses in both the pufferfish and yellowtail examples implies that some F1 hybrids survive until maturity, and are at least partially fertile under natural conditions (Takahashi et al. 2017, 2021). Furthermore, in the former example, *T. stictonotus* mtDNA introgression was found in 2 of 102 genetically pure individuals of *T. snyderi*, indicating that hybridization occurred not only recently, but also occasionally in the past. Given the increased hybridization caused by human activities, these findings are important because the evolutionary and conservation consequences of hybridization differ in terms of their dependence on the presence or absence of genetic introgression (Allendorf et al. 2001). Anthropogenic hybridization with introgression threatens the genetic integrity of parental species and can precipitate their collapse into hybrid swarms, as observed in several freshwater fish systems (Allendorf et al. 2001). On the other hand, hybridization may help mitigate the effects of climate change on biodiversity by increasing the adaptive potential of species (Becker et al. 2013; Brennan et al. 2014). The extremely small number of observed backcross individuals and absence of F2 hybrids, compared to the large number of F1 hybrids observed, indicates that strong natural or sexual selection against F1 hybrids maintains species integrity in the two examples presented herein, similar to the abovementioned example of tropical eels. On the other hand, the emergence of second- or later-generation hybrids can be expected in the near future, based on the very recent mass occurrence of F1 hybrids in both examples. In either case, the recent emergence of a large number of F1 hybrids might offer a unique opportunity to understand how climate change, especially the interglacial global warming, modulates species interactions and diversity. Continuous monitoring and the application of population genomics to these ongoing hybridizations may provide insight into the relationship between climate change and hybridization dynamics in the age of climate change.

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Part V

Conservation of Fish Diversity in Japan

Coastal Fishes in Sandy Beaches

18

Ryutei Inui

Abstract

Beaches with sand as the main component are called sandy beaches. Approximately three-quarter of the ice-free beaches on the globe are sandy. Sandy beach habitats are largely divided into subtidal (underwater), intertidal, and supratidal zones. The subtidal zone is further divided into the breaker and surf zones, which are the main habitats for fishes inhabiting sandy beaches. Recent advances in biological research pertaining to sandy beaches have revealed many fish species inhabiting sandy beaches. Studies on sandy beach fishes in Japan have been conducted since the 1980s, focusing on the morphology and ecology of juvenile fishes. Subsequently, as studies using large fishing nets were conducted, in addition to juveniles, adult fishes inhibiting sandy beaches were discovered. Moreover, in addition to the resident species of the sandy beaches, fishes that appear at a certain stage of development, visit temporarily for feeding, and visit incidentally from the surrounding habitats have been observed.

Keywords

Exposed beach · Surf zone · Wave · Sediment · Flat fish · Sand borer · Coastal erosion

18.1 What Is a Sandy Beach?

Sedimentary beaches, which are frequently exposed to waves, are mainly composed of gravel and sand. Of these, beaches with sand (grain size, 0.075–2 mm) as the main component are called sandy beaches (Suda 2017). Approximately three-quarter of the ice-free beaches on our planet are sandy beaches (Brown and McLachlan 1990). In Japan, 4773 km (approximately 14%) of the 35,307 km coastline is occupied by sandy beaches, which is a smaller proportion than the global average. In addition, approximately 60% of Japan's sandy beaches are natural beaches with no artificial structures such as seawalls, detached or submerged breakwater, and jetties (Suda 2017). The scale of sandy beaches varies from small ones formed in the bay between capes of rocky coasts and large ones extending over tens of kilometers. In Japan, the distribution of long sandy beaches spread over 20 km is limited to coasts facing the open sea. In Hokkaido, Aomori, Akita, Yamagata, Ibaraki, Chiba, Niigata, Aichi, Tottori, and Fukuoka prefectures, more than half of the coastline facing the open sea is occupied by sandy beaches (Suda 2017).

18.2 Topography of a Sandy Beach

As opposed to rocky or coral reefs, sandy beaches do not have fixed structures; however, the physical interactions between waves and sand

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(morphodynamics) create various landforms. These morphodynamics give rise to diverse sandy beach habitats. The diversity of these habitats is an important foundation for sandy beach ecosystems. On a sandy beach, waves become higher as the waters become shallower and eventually break. The breaking waves continue to move forward and finally hit the shore. According to the characteristics of waves, sandy beaches are classified into the area where the waves break, called the "breaker zone," and the area where the waves continue to move after breaking, called the "surf zone." The area where the waves hit the shore is called the "swash zone." According to the cross-section of the coast, the sandy beaches are classified into the area outside the wave-breaking zone, called "offshore." The critical water depth, which is the water depth at which the effect of waves does not reach the sand on the seabed, is located offshore. The area from the breaker zone to the shoreline at low tide is called the "inshore." The inshore seafloor has a sandy rise called the "coastal bar." The area from the low-tide shoreline to the edge of the shoreline, where the waves come in, is called the "foreshore." The area from the edge of the shoreline to the high-tide shoreline is called the "backshore." In the backshore, sand washed up by waves during high tides and/or storms is accumulated (Brown and McLachlan 1990; Suda 2017).

18.3 Morphodynamic Beaches

"Morphodynamic beaches" are the sandy beaches classified according to their geomorphology. Sandy beaches with a tidal range of <2 m (microtidal beach) (Komar 1998) are classified into three types, namely reflective (Fig. 18.1a), intermediate, and dissipative beaches (Fig. 18.1b) (Wright and Short 1984; Short 1999). In the reflective beach, the slope of the foreshore is steep; thus, the incoming waves from the offshore approach the shore without breaking and hit the foreshore while retaining the wave energy. Therefore, the shoreline of the reflective beach is greatly disturbed by waves, making the accumulation of fine sand difficult. In the dissipative beach, the slope of the foreshore is gentle; thus, the incoming waves lose their energy while breaking repeatedly in the surf zone. Therefore, the waves near the shoreline are calm, and sand is the finest among the three types. The intermediate beaches represent an intermediate state between the reflective and dissipative beaches. The intermediate beach often has a littoral sandbar. Additional transitional states between these three types are observed, and the type of a sandy beach is not fixed and varies with wave conditions. At mesotidal (tidal range, 2–4 m) and macrotidal beaches (tidal range, >4 m) (Komar 1998), tidal effects, in addition to the wave effect, result in complex morphodynamics (Masselink and Short 1993; Short 1999).

18.4 Sandy Beach Habitats

Sandy beach habitats are largely divided into subtidal (underwater), intertidal, and supratidal zones. The subtidal zone includes the breaker and surf zones, which are the main habitats for fishes inhabiting sandy beaches. The breaker and surf zones of sandy beaches are often thought to be home to few organisms because they represent highly disturbed and dynamic environments and harbor no reefs or seagrass beds. However, many organisms, including fishes, inhabit in these zones. When the tidal range is large, tidal flats are formed in the intertidal zone of sandy beaches, even when they face the open sea (Masselink and Short 1993; Short 1999). When the tidal range is narrow, the submarine groundwater discharged from the upper intertidal zone affects the topography of the foreshore (Kuriyama 2006) and serves as a source of nutrients to the sandy beach area (e.g., Adachi etal. 1994; Johannes 1980).

Tidal pools on sandy beaches are called runnels, which are inhabited by many sand-dwelling arthropods (e.g., Mysida and Amphipoda) (Nonomura et al. 2007). These small arthropods are important prey for fishes in the surf zone (Nakane et al. 2010).

Many invertebrates have adapted to the swash zone, which is the area where waves crash onto

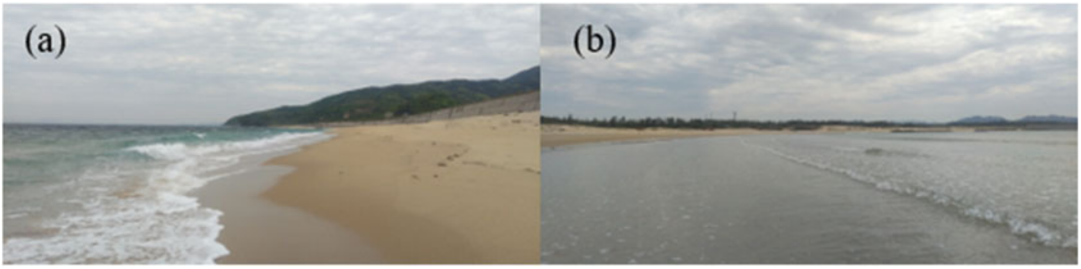

Fig. 18.1 Scenery of the sandy beach. (**a**) Reflective and (**b**) dissipative beaches in Fukuoka Prefecture, Japan

the shore. For instance, small bivalve mollusks, such as *Donax cuneatus* and *Donax semigranosus*, move in the intertidal zone with upwelling waves. Other invertebrates including *Excirolana chiltoni*, *Archaeomysis kokuboi*, and *Haustorioides japanicus* are also found in the swash zone (Kajiwara and Takada 2008; Suda 2017).

Habitats in the supralittoral zone include the backshore and coastal dunes. The backshore, which is covered in dry sand, is also inhabited by various invertebrates such as *Tylos granuliferus* and *Ocypode stimpsoni* of Talitroidea. The drift line at the backshore is the line where the waves reach their maximum height; therefore, a large amount of debris from the sea washed up by the waves is accumulated in this region. Some species of Talitroidea and Hydrophilidae use this debris (Suda 2017). In addition, predators of these organisms, such as tiger beetles, also congregate at drift lines (Sato 2008).

Many species live on coastal dunes. Coastal dunes closer to the sea are inhabited by organisms that can tolerate salinity and desiccation, which is not necessarily the case on the land side.

18.5 Fishes Inhabiting Sandy Beaches

Research pertaining to fishes and other organisms inhabiting sandy beaches is limited compared to that pertaining to life in other coastal environments, such as seagrass beds, rocky reefs, and coral reefs. This may be attributed to the monotony of the sandy beach environment and the harshness of waves in this region (Brown and McLachlan 1990). However, recent advances in biological research on sandy beaches have revealed that many fishes inhabit sandy beaches.

Studies on sandy beach fishes in the world began in the 1940s on the Atlantic coast of North America (Pearse et al. 1942) and in northeastern United States (Warfel and Merriman 1944; Senta and Kinoshita 1998). In the late 1950s and the early 1960s, studies in the Gulf of Mexico (Gunter 1958; McFarland 1963) were conducted. In the 1980s, studies were conducted in South Africa (e.g., Lasiak 1983, 1984, 1986) and western Australia (Robertson and Lenanton 1984). In the 1990s, more detailed studies on the patterns of spatiotemporal variability of fish assemblages and their relationship with the physical environment began in many parts of the world (Romer 1990; Gibson et al. 1993; Santos and Nash 1995; Harris and Cyrus 1996; Clark et al. 1996; Clark 1997; Friedlander and Parrish 1998). Since the late 1990s, studies focusing on microhabitats have been conducted (Harvey 1998; Layman 2000). In recent years, the number of case studies related to sandy beaches in Brazil has increased (e.g., Rodrigues and Vieira 2010, 2013; Rodrigues et al. 2015).

Studies of sandy beach fishes in Japan have mainly been conducted in Kyushu and Shikoku since the 1980s, focusing on the appearance and ecology of juvenile fishes (Senta and Kinoshita 1985; Kinoshita 1993). Subsequently, studies in Tokyo Bay, the Pacific coast of central Honshu were conducted (Arayama et al. 2002). In 2000s, research using large fishing nets began, and both juvenile and adult fishes became the subject of study (Suda et al. 2014a, b). These studies revealed that both juvenile and adult fishes of various species inhabit sandy beaches.

Inoue (2017) comprehensively reviewed the results of studies on fishes inhabiting Japanese sandy beaches. They compared the results of previous collection surveys at nine sandy beaches in Japan (Monbetsu, Hokkaido; Hasaki, Ibaraki Prefecture; outer part of Tokyo Bay, Chiba Prefecture; Uradome, Tottori Prefecture; Doigahama, Yamaguchi Prefecture; Tosa Bay, Kochi Prefecture; Sanri-Matsubara and multiple locations in northern Kyushu, Fukuoka Prefecture; and Fukiagehama, Kagoshima Prefecture) and found that over 350 species belonging to 115 families in 22 orders were collected from these beaches, with each site harboring 37–164 species (Inoue 2017). Five species are listed in Table 18.1 in order of the number of individuals collected at each beach. Fukuoka^{a} shows Sanri-Matsubara by Inoue et al. (2005), and Fukuoka^{b} shows several sites in northern Kyushu by Inui et al. (2010).

Only six chondrichthyan species [e.g., *Mustelus manazo*, *Triakis scyllium*, *Carcharhinus tjutjot*, *Platyrhina tangi*, and *Hemitrygon akajei* (Fig. 18.2a)] were collected from sandy beaches. All the remaining species were osteichthyans. At the family level, Gobiidae was the most abundant, followed by Carangidae, Cottidae, Tetraodontidae, and Mugilidae. *Engraulis japonicus* (Fig. 18.2b) was the only species found on all nine beaches. *Plecoglossus altivelis altivelis*, *Gerres equulus*, *Sillago japonica* (Fig. 18.2c), and *Rhyncopelates oxyrhynchus* were found on all beaches except in Hokkaido, and *Paralichthys olivaceus* (Fig. 18.2d) was found on all beaches except in Ibaraki. Based on the number of individuals, *E. japonicus* was the most abundant species on most beaches, while *P. a. altivelis* was abundant in Kochi and Ibaraki. In addition, *Mugil cephalus cephalus*, *G. equulus*, *S. japonica*, and *Takifugu alboplumbeus* (Fig. 18.2e) were also abundant in many sandy coasts. Large populations of these fishes are widely distributed on sandy beaches, and they likely depend on sandy beaches for a part of their life cycle.

The occurrence of some fishes was affected by geographical differences. For instance, in Hokkaido, the northernmost site, northern coastal fishes including *Gymnocanthus herzensteini*, *Myoxocephalus stelleri*, *Platichthys stellatus*, and *Pleuronectes schrenki* (see Suda et al. 2005) were dominant. In Kagoshima, the southernmost site, southern coastal fishes including *Sardinella aurita*, *Amblygaster leiogaster*, *Caranx ignobilis*, *Caranx papuensis*, and *Caranx sexfasciatus* were dominant.

In addition to geography, the occurrence of many fishes was affected by the surrounding environment, such as inflowing rivers and rocky reefs. For instance, Pseudoblennius percoides and Petroscirtes breviceps, which are mainly found on rocky reefs, were collected from sites in Tottori and Yamaguchi prefectures bordered by rocky reefs on both ends. At sites in Kochi and Fukuoka, where rivers flow into the surrounding area, amphidromous fishes such as P. altivelis and periphyton freshwater fishes such as M. c. cephalus and Chelon lauvergnii were abundant (Kinoshita 1993; Suda et al. 2004; Inoue et al. 2005; Suda et al. 2014a, b). At sites in Chiba and Fukuoka, where inland tidal flats are present in the vicinity, *Acanthogobius flavimanus*, *Favonigobius gymnauchen*, *Gymnogobius heptacanthus*, and *Gymnogobius breunigii*, which are mainly found in estuaries and tidal flats, were abundant (Arayama et al. 2002; Inui et al. 2010).

18.6 Differences in the Use of Sandy Beaches by Fishes

Fishes inhabiting sandy beaches include those that settle on sandy beaches as well as those that appear at a certain stage of development, those that visit temporarily for feeding, and those that usually live in the surrounding environment and visit incidentally. The surf zone of a sandy beach lacks fixed structures such as rocky reefs, coral reefs, and seagrass beds that serve as refuges for fishes. However, sand drift and coastal sandbars may serve as a refuge for small fishes to avoid large predators (Lasiak 1986). Many invertebrates

Table 18.1 Fishes collected from nine beaches in Japan. Five species are summarized in order of abundance at each beach

	Hokkaido	**Ibaraki**	**Chiba**
1	*Hypomesus japonicus*	*Mugil cephalus*	*Salangichthys ishikawae*
2	*Osmerus dentex*	*Salangichthys ishikawae*	*Konosirus punctatus*
3	*Tribolodon brandti maruta*	*Engraulis japonica*	*Pholis* sp.
4	*Clupea pallasii*	*Plecoglossus altivelis altivelis*	Gobiidae sp.
5	*Engraulis japonica*	*Parablennius yatabei*	*Rhinogobius* sp.
	Tottori	**Yamaguchi**	**Kochi**
1	*Lateolabrax japonicus*	*Spratelloides gracilis*	*Plecoglossus altivelis altivelis*
2	*Sillago japonica*	*Takifugu alboplumbeus*	*Konosirus punctatus*
3	*Sardinops melanostictus*	*Sillago japonica*	*Chelon affinis*
4	*Paralichthys olivaceus*	*Engraulis japonica*	*Takifugu alboplumbeus*
5	*Engraulis japonica*	*Gerres equulus*	*Acanthopagrus schlegelii*
	Fukuoka[a]	**Fukuoka**[b]	**Kagoshima**
1	*Lateolabrax latus*	*Gymnogobius breunigii*	*Sillago japonica*
2	*Sillago japonica*	*Takifugu alboplumbeus*	*Hypoatherina bleekeri*
3	*Takifugu alboplumbeus*	*Sillago japonica*	*Mugil cephalus cephalus*
4	*Paraplagusia japonica*	*Acanthogobius lactipes*	*Trachurus japonicus*
5	*Mugil cephalus*	*Favonigobius gymnauchen*	*Engraulis japonica*

[a] Shows Sanri-Matsubara by Inoue et al. (2005)
[b] Shows several sites in Northern Kyushu by Inui et al. (2010)

such as Mysida, Amphipoda, and Copepoda inhabit the surf zone (Brown and McLachlan 1990). These invertebrates are preyed upon by many fishes (e.g., Robertson and Lenanton 1984; Lasiak and McLachlan 1987; DeLancey 1989; Kinoshita 1993). A comprehensive study of the diet of surf zone fishes showed that zooplankton-eating fishes and benthic zooplankton-eating fishes represent a major proportion of surf zone fishes (Inoue et al. 2005). Among the fishes that are thought to be highly dependent on the surf zone, *Sillago japonica*, *Takifugu alboplumbeus*, and *Paraplagusia japonica* (Fig. 18.2f) change their feeding habits with growth (Inoue et al. 2005; Nakane et al. 2010). Based on these results, the surf zone is thought to serve as a place for these species to change their diet (Inoue 2017).

18.7 Relationship Between Sandy Beach Type and Fish Species

Nakane et al. (2013) examined the relationship between sandy beach types and fishes inhabiting them. The authors conducted a survey of three types of sandy beach in Fukiagehama, Kagoshima Prefecture: reflective, intermediate, and dissipative beaches. The highest numbers of species and individuals were found on the dissipative type with a gentle slope, while the lowest number of species was found on reflective type with a steep slope. *Sillago japonica* and *Trachurus japonicus* were collected from the dissipative beach. The species composition of fish assemblages was similar between the dissipative and intermediate beach but varied on the reflective beaches. *Engraulis japonicus*, *Takifugu alboplumbeus*, and *Hypoatherina valenciennei* appeared on all types of beach, whereas *S. japonica* and *T. japonicus* were rare on reflective beaches. This may be because the feeding environment differs across the types of sandy beach.

18.8 Relationship Between Sandy Beach Environment and Fish Communities

Inui et al. (2010) investigated the relationship between the physical environment and fish fauna

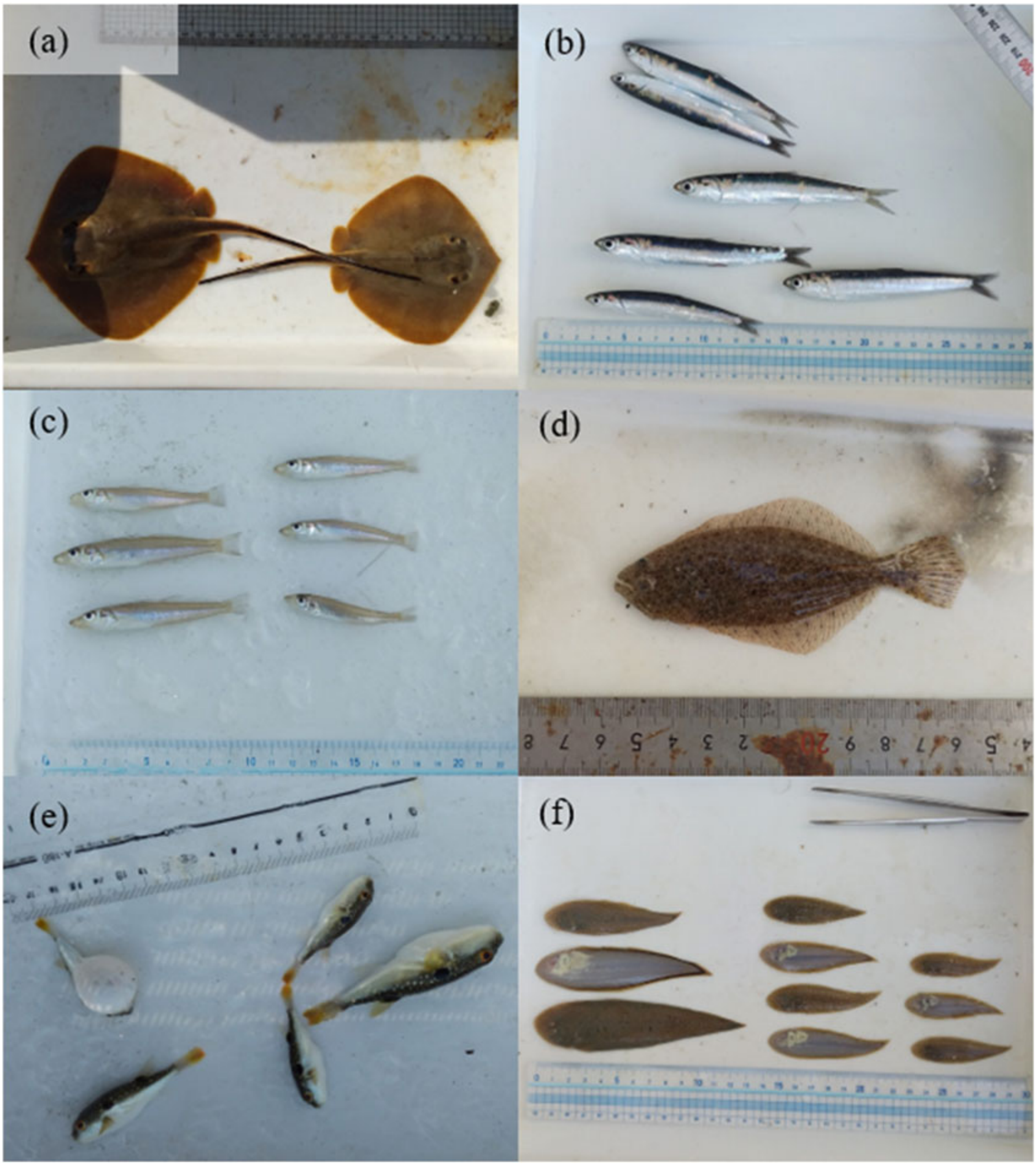

Fig. 18.2 Fishes inhabiting sandy beaches in Japan. (**a**) *Hemitrygon akajei*, (**b**) *Engraulis japonicus*, (**c**) *Sillago japonica*, (**d**) *Paralichthys olivaceus*, (**e**) *Takifugu alboplumbeus*, and (**f**) *Paraplagusia japonica* captured in Fukutsu City, Fukuoka Prefecture, Japan

of 21 sandy beaches in Fukuoka Prefecture. The results of community analysis based on the collection of juvenile fishes showed that the 21 sandy beaches could divided into two major groups: one group dominated by *Takifugu alboplumbeus* and *Gymnogobius breunigii* and the other dominated by *Engraulis japonicus* and *Plecoglossus altivelis altivelis*. The physical environmental factors driving the fish community structure include the slope of the seabed and wave intensity; as such, the number of both species and individuals increases when the slope is gentle and wave intensity is weak. Based on these results, shallow and calm parts of the sandy beaches serve as a nursery ground for juvenile fishes; however, not all fishes occur in these calm parts of the sandy beaches; thus, the physical environmental diversity of the sandy beaches may drive the diversity of fish communities inhabiting them.

18.9 Environmental Problems on Sandy Beaches

In inland bays and estuaries, there are many well-known environmental problems such as the loss of tidal flats and seaweed beds due to land reclamation, deterioration of water quality and bottom sediment due to eutrophication, and mass mortality of organisms due to anoxia. Furthermore, sandy beaches tend to be neglected as the target of environmental conservation in coastal areas because they have fewer noticeable environmental problems and harbor fewer endangered species than inland bays and estuaries.

Nonetheless, environmental problems such as landform changes due to sea level rise, environmental alterations caused by the construction of artificial structures, trampling of beaches and vegetation due to the entry of people and vehicles for recreational activities, pollution by wastewater and garbage, and oil drift are observed worldwide (e.g., Brown and McLachlan 1990; Defeo et al. 2009; Schlacher et al. 2008). In Japan, beach erosion and environmental modification due to beach erosion control measures, loss of continuity between land and sea, and drifting of plastic and oil are the major problems. Coastal erosion is a phenomenon in which waves and currents near the shore erode the beach. Many sandy beaches facing the open sea in Japan continue to be eroded (Uda 1997). The primary cause of beach erosion is a decrease in the amount of sediment supplied by rivers. In addition, the creation of artificial structures and transport of sand from other locations as a result of beach erosion can negatively affect the beach ecosystems (Suda 2017).

18.10 Conservation of the Sandy Beach Ecosystem

As described above, many fishes use sandy beaches as the places of settlement, growth, refuge, and feeding. These include important species for coastal fisheries, such as *Sillago japonica* and *Paralichthys olivaceus* (see Suda 2017). Therefore, it is important to conserve sandy beaches as habitats for fishes, including some important species for fisheries.

However, the number of fish species and individuals inhabiting sandy beaches is not as large as that of fish species and individuals inhabiting rocky reefs, coral reefs, inland bays, and estuaries (including tidal flats and mangroves). Moreover, no notable endangered species inhabit these areas. Therefore, when determining the value of the sandy beach ecosystem, the distribution of species diversity, specifically endangered species, should not be considered a criterion. To date, the significance of the sandy beach ecosystem remains underestimated.

Although sandy beaches serve as important habitats for many fishes, little is known regarding the conservation and management of these ecosystems (Suda 2017). In the future, more information should be complied to guide the conservation and management of sandy beach ecosystems. In addition, many people use sandy beaches for swimming, surfing, fishing, and sightseeing. Therefore, appropriate conservation and management measures for sandy beaches should be designed with consensus among people who use them (Suda 2017).

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Coastal Fishes in Rocky and Coral Reefs 19

Atsunobu Murase

Abstract

Reef communities are based on hard substrata and habitat-producing organisms such as macroalgae and reef builders, which are affected by various physical factors. Japanese reef fishes are diverse in space and time due to the various aspects of reefs and the different ecological environments around Japan. This chapter summarizes regional and temporal variations in fishes inhabiting rocky and coral-reef habitats (i.e., reef fishes) in the Japanese Archipelago, to reveal how global changes affect fishes. The focus is on the transitional zone, which is sensitive to climate change. Recent studies on reef fishes in Japan showed the effects of the warm Kuroshio Current, reef-building corals and long-term sea warming on the establishment of tropical reef fishes in temperate Japan. Furthermore, recent reports on the distribution limits of several cool-temperate fishes indicate the importance of ocean currents and the geomorphology of the coast as limiting factors in the distribution of cool-temperate fishes, while the interactions among fishes of different biogeographic affinities are unclear. In the future, sustainable assessment methods (in terms of cost and effort) are expected to be adopted in ecological studies on reef fishes, to understand and monitor the dynamics of and interactions among reef fishes in Japan.

Keywords

Biogeographic affiliation · Cool-temperate fishes · Global warming · Recreational fishing · Reef fishes · Regional variability · Temporal dynamics · Transitional zone · Tropical fishes

19.1 Introduction

Reef systems are very large habitats (e.g., rocky shores), compared to the soft-bottom systems described elsewhere (Raffaelli and Hawkins 1996). Reef organisms generally live on the surface of the substrata. There are diverse communities of algae, plants, and sessile animals on the substrata, including corals. Sessile organisms living on the hard inorganic substrata make a complex reef system that provides habitat for benthos and nekton (Ecological Society of Japan 2016). The community structures of reef systems vary among regions according to climate (Little et al. 2009). The Japanese Archipelago extends for 3000 km and its coasts are composed of a variety of marine ecoregions (Nishimura 1992; Spalding et al. 2007; Fujikura et al. 2010). The complexity of the reef communities and existence of several marine ecoregions around the archipelago give rise to diverse reef fish

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assemblages in Japan at local and regional scales. Some reef fish families (e.g., Apogonidae, Blenniidae, Chaetodontidae, Labridae, Pomacentridae, Scorpaenidae, and Serranidae) are within the top ten most speciose groups along the coast of southern Japan (Senou et al. 2006; Motomura et al. 2010), and reef-associated fish groups are represented by the most speciose families on the east coast of Kyushu, southern Japan (Murase 2020).

Global warming and its impact on biocommunities are pressing issues in ecological science (Pecl et al. 2017). The poleward shift of tropical species in marine systems due to ocean warming has been the focus of many studies, reflecting changes in community structure. Reef systems may be vulnerable to climate change because macroalgae and reef-building corals, which produce an “organism-based substrate,” are sensitive to temperature change (Precht and Aronson 2004; Abe et al. 2021). Reef fishes depend on these “substrate-providing organisms,” so may be affected by structural changes in macroalgae and coral communities (Beck et al. 2017). This is thought to be particularly important within regions located at the borders of different climate zones (i.e., the southern edge of the temperate zone and northern edge of the tropical/subtropical zone: Horta e Costa et al. 2014; Abe et al. 2021). This chapter focuses on border regions between the temperate and tropical/subtropical zones in Japan and summarizes the geographical and temporal dynamics of reef fish assemblages. The goal was to determine the outlook for Japanese reef fish management. Future directions for ecological studies on Japanese reef fishes are proposed at the end of this chapter.

19.2 Regional Variability

Reef fish communities are affected by physical and biological factors. Reef fish assemblages have been well studied along the southwestern Atlantic coast (Brazil). Studies in Brazil revealed complex functional structure changes (Ferreira et al. 2004) with latitude, as well as a linear gradient of herbivorous fish density (Floeter et al. 2004, 2005). These studies provided a basis for understanding the formation of the present reef fish assemblages according to historical events, and shed light on expected future assemblages (Bender et al. 2013). A recent faunal analysis in Japanese waters revealed that the Kuroshio Current is a key factor driving the present variations in marine fish fauna along the coast of southern Japan (Senou et al. 2006; Motomura et al. 2010). Three points must be emphasized when reviewing studies of reef fish assemblages in Japan. First, the data sets of past studies included fishes associated with all types of habitats. Organismal features (e.g., benthic and nektonic) affect latitudinal patterns of species diversity (Hillebrand 2004). Teleosts are a highly diverse animal group in terms of ecology and species diversity; thus, fish assemblages associated with different habitats (e.g., reef vs. soft bottom) may show different geographical patterns of community structure changes, depending on the specific factors in each habitat (Travers et al. 2010; Murase unpublished data). Second, the data sets of past studies describing only the presence/absence of each species are not based on quantitative data. Assemblage data based on the presence/absence of a certain fish species at a given site are not informative regarding regional changes in the degree of dominance of that species. Quantitative data sampling and analyses are needed to reveal such changes. Finally, biogeographical and/or ecological generalizations (e.g., climatic affiliation and functional guilds) were uncommon in past ichthyofaunal analyses. This type of generalization may allow for global-scale comparisons and index-based general evaluations of regions across years (Elliott et al. 2007; Horta e Costa et al. 2014).

Several studies have been conducted on Japanese reef fishes based on the above aspects (Murase 2013; Arakaki et al. 2014; Okada et al. 2015). These studies were performed in rocky intertidal systems, which have some benefits for biogeographical and ecological studies, such as easy access and amenability to a quantitative analysis approach (Metaxas and Scheibling

1993; Raffaelli and Hawkins 1996). Although no quantitative study of reef fish assemblages on a regional scale in the Japanese Archipelago had been conducted until recently, Arakaki et al. (2014) analyzed rockpool fish assemblages in the warm temperate, subtropical, and tropical zones of southern Japan to clarify latitudinal patterns of community status, such as richness at each taxonomic level (family, genera, and species) and the density of each fish species. Their results showed clear differences in species composition between Kyushu Island (warm temperate zone) and the Ryukyu Islands (tropical zone), which has implications for understanding the effects of local environmental factors (i.e., substrate type). This was the first quantitative/comprehensive analysis of regional differences among different climates in a reef fish community. Moreover, biogeographic generalization of rockpool fish communities revealed the importance of distance from a warm current (Kuroshio Current), as well as latitude in transitional zones (sites located between temperate and subtropical zones). Murase (2013) surveyed the community structure and seasonal variability of a subtropical rockpool fish assemblage in Japan (Yaku-shima Island), and attempted to classify rockpool fish species according to their biogeographic affinity (cool temperate, warm temperate, or tropical). In this manner, the biogeographic compositions of rockpool fish communities were compared among several sites in Japan (coasts of Chiba and Kumamoto prefectures, and Yaku-shima Island). The Yaku-shiman rockpool fish community was clearly distinguished from the other two sites in terms of the predominance of tropical fish species. However, the main factor (latitude or distance from the warm current) driving the biogeographic differences among rockpool fish communities in Japan could not be determined because the latitudes of the three target sites were different. Okada et al. (2015) studied the biogeographic composition of rockpool fish communities at three different sites (two on the Kii Peninsula and an adjacent site within Ise Bay) and compared it with those at sites surveyed by Murase (2013) (six sites compared in total). Their results clearly showed the importance of the warm Kuroshio Current, and distance therefrom, in the predominance of tropical fish species. According to their data, the southernmost point of the Kii Peninsula (exposed to the Kuroshio Current) had more tropical fishes than a latitudinally lower site, but the latter site was well outside the course of the Kuroshio Current (western coast of Kyushu; Arakaki and Tokeshi 2006). These rockpool fish studies show the importance of the Kuroshio Current and latitude in the formation of reef fish communities around the Japanese Archipelago.

19.3 Temporal Dynamics

Temporal changes in community structure can be described at seasonal and annual scales. In the temperate waters of Japan, reef fish assemblages show seasonal variability in terms of species diversity in association with water temperature. Species richness is higher during high-temperature seasons (summer and autumn) and decreases during the low-temperature season (winter), including in subtropical/tropical regions (Kuwamura 1980; Nanami and Nishihira 2002; Nishida et al. 2007; Hirata et al. 2011; Murase 2013). Kuwamura (1987) surveyed decadal changes in the faunal structure of southern Japan in the course of the Kuroshio Current (Tanabe Bay, western coast of Kii Peninsula), by comparing fish assemblage structures between 1974/1975 and 1985/1986. No clear differences were detected between these periods in terms of species composition, but the necessity for future estimates based on the abundance of each fish species was demonstrated. Thereafter, Nakamura et al. (2013) studied the degree of tropical fish dominance, according to the recent development of coral-reef habitats at two reef sites in temperate Japan along the Kuroshio Current (Kochi Prefecture). Their data showed a clear predominance of tropical fish species in terms of species richness and abundance. In addition, the size structure of the tropical fishes suggested overwintering and reproduction at those sites. These results indicate that poleward expansion of reef-building corals and a long-term warming trend (in the order of decades) has promoted the formation of tropical fish communities in temperate Japan. In contrast, an unpredictable extreme cold event could threaten the establishment of tropical fish communities in temperate Japan, due to low temperatures and loss of coral as a food resource for corallivorous fishes (Leriorato and Nakamura 2019). The formation of an algal community negatively affects the recruitment of tropical fish species into temperate waters (Beck et al. 2017).

Temperature is one of the most important factors in the formation of short- and long-term communities. Habitat and resource establishment associated with temperature changes, such as corals in association with a warming trend, promote a fundamental shift in the structure of reef fish communities, as represented by the dominance of tropical fishes. Thus, habitat shifts accompanied by temperature changes should be a focus to elucidate temporal variations in reef fish communities and the management thereof.

19.4 Future Perspectives

Studies on reef fish assemblage structures and dynamics in Japan have focused mainly on the dominance and occurrence rates of tropical fishes, with consideration of the factors affecting those fishes. The findings imply that temporal/spatial temperature distribution and substrate type affect the establishment of tropical reef fish communities in temperate Japanese waters. However, recent studies on the distribution of shallow rocky-reef fishes on the continental coast of a cool-temperate water area (Nakabo 2013; hereafter referred to as “cool-temperate species”) imply that these species have undiscovered distribution limits. Kyushu is located in the southernmost zone of temperate mainland Japan. As the border between the warm temperate and tropical zone, it may be important to the distribution limit of tropical and cool-temperate fishes because of factors associated with the 20 °C isotherm during the coldest month (Briggs 1995). Miyazaki Prefecture is located on the eastern coast of Kyushu, and has oceanographic and geomorphological features that cause differences in the biogeographic composition of the reef fish communities between the northern and southern coasts; a long sandy shore lies at the center of the prefecture and the warm Kuroshio Current runs off the prefecture with a latitudinal temperature gradient (Murase et al. 2017a). These features of the Miyazaki Prefecture coast, which are not present on the western coast of Kyushu, lead to clear distribution limits for some cool-temperate fishes. In particular, Kadogawa Bay is important because it is located in the northern part of the long sandy shore, and the waters from the Seto Inland Sea diminish from north to south until reaching the bay (Murase 2019). Reliable records of the distribution limits of several cool-temperate fishes have been reported (Fig. 19.1). Of these cool-temperate species, only the distribution limit of *Chaenogobius gulosus* has been studied by qualitative and quantitative surveys (Murase et al. 2017a); those of the other species are known only based on specimen records, including photographs. Thus, the ecological importance of these cool-temperate fishes in reef fish communities in the transitional zone, such as Kyushu Island, and factors limiting the distribution and establishment of those species, are obscure. Studies on reef fish assemblage structure and dynamics in the transitional zone of Japan, focusing on cool-temperate and tropical fishes, are needed with consideration of the interactions among fishes in several biogeographic categories.

The ecological importance of regionally/temporally changing contexts has been revealed in global analysis (Bradley et al. 2020). The ecological context in which Japanese reef fish assemblages exist is changing in space and time, as summarized in this chapter. Development of sustainable assessment methods (in terms of cost and effort) is needed to thoroughly assess the regional and temporal dynamics of Japanese reef fish communities. Conventional methods to assess reef fish assemblages, such as visual belt transect survey methods, may be better for species quantification (e.g., Nakamura et al. 2013; Leriorato and Nakamura 2019). However, such methods require taxonomic knowledge of fishes and a SCUBA license, which can be a barrier to conducting long-term monitoring surveys across

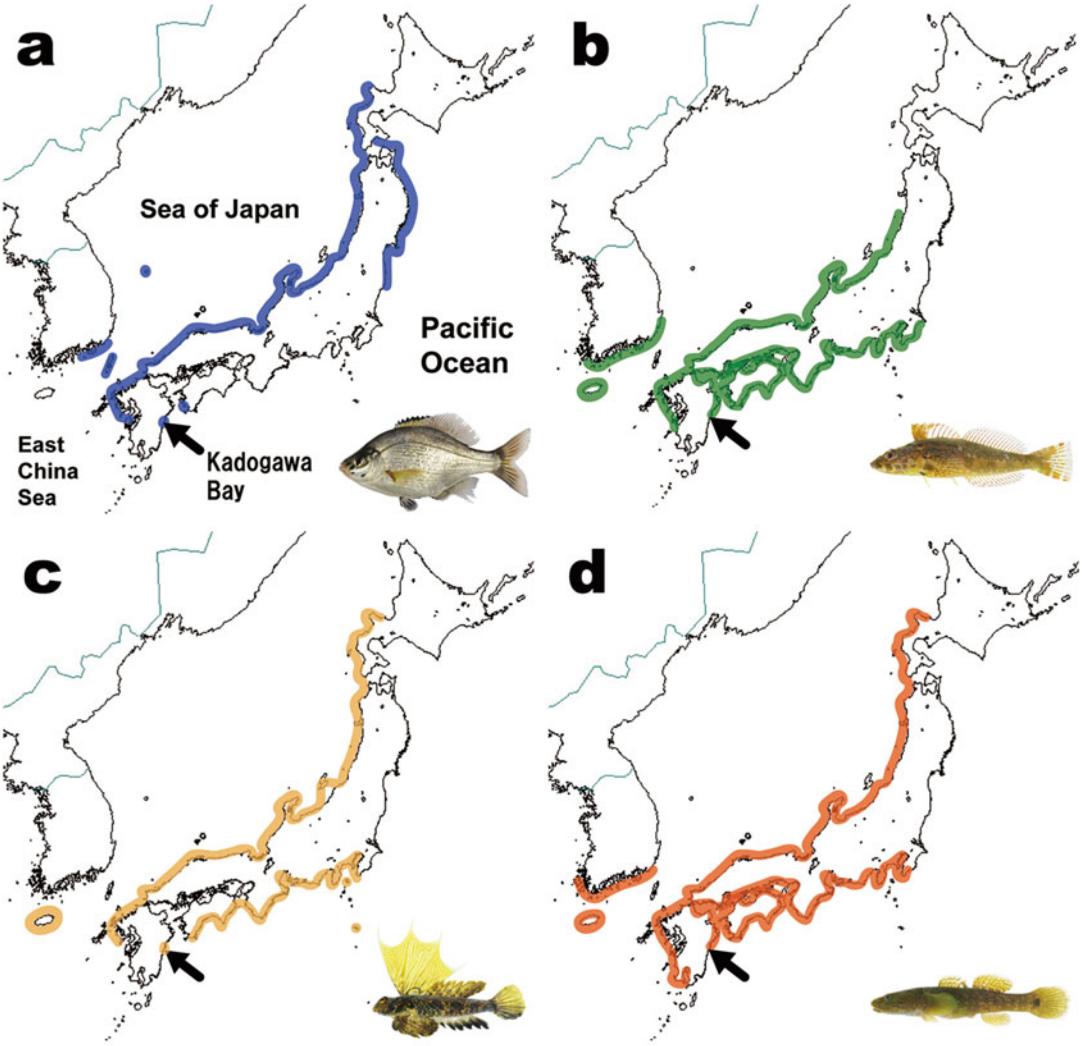

Fig. 19.1 Examples of distribution ranges of some cool-temperate Japanese reef fish species (*colored lines*). (**a**) *Ditrema temminckii* (see Murase et al. 2017b), (**b**) *Pseudoblennius percoides* (see Miki et al. 2017), (**c**) *Neosynchiropus ijimae* (see Ogata et al. 2018), (**d**) *Chaenogobius gulosus* (see Murase et al. 2017a). *Arrow* indicates the position of Kadogawa Bay in the northern part of Miyazaki Prefecture, which is the distribution limit of several cool-temperate fish species along the Pacific coast of Japan. Potentially inaccurate records (i.e., those based on only a few photographs) from the southern part of Miyazaki Prefecture were omitted from (**b**) and (**c**)

several climatic regions. Therefore, simple survey methods should be developed. Intertidal zones (rockpool ecosystems) are among the best areas in which to monitor reef fish assemblages because of the easy access (Raffaelli and Hawkins 1996); the environment in intertidal zones is more stable compared to that outside of pools (Metaxas and Scheibling 1993), and complex trophic webs are established within pools (Mendonça et al. 2018). Moreover, among the organisms in these ecosystems, bottom-associated fishes (Blenniidae and Gobiidae) and crabs are seen in all tidal pool habitats (Gibson and Yoshiyama 1999; Little et al. 2009; Arakaki et al. 2014). Finally, taxonomic data are available in books (e.g., Nakabo 2013; Suzuki et al. 2013; Watanabe 2014) and

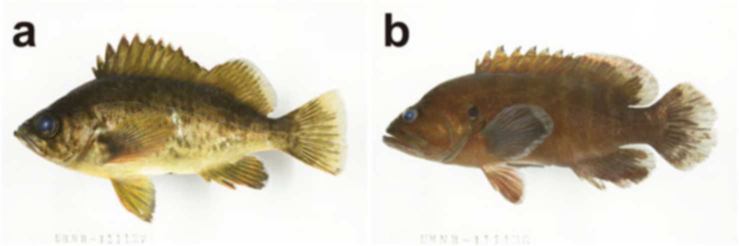

Fig. 19.2 Cool-temperate and tropical reef fishes collected from the transitional zone between the temperate and tropical zones of Japan (Nobeoka City, northern part of Miyazaki Prefecture, eastern Kyushu). (**a**) A cool-temperate reef fish, *Sebastes* cf. *inermis* (Sebastidae); (**b**) a tropical reef fish, *Cephalopholis boenak* (Serranidae). Both reef fishes were captured at a fishing port during a university student field trip (i.e., recreational fishing). (Photographs were taken by the author)

these species can be captured by citizen scientists (Delaney et al. 2008; Suzuki and Sasaki 2010). Murase et al. (2017a) focused on these ecological advantages of rockpools, revealing regional differences in abundance among species of the intertidal goby genus *Chaenogobius*.

Citizen science represents a breakthrough for monitoring reef fishes. Miyazaki and Murase (2020) reported that fishes caught by recreational fishermen reflected the biogeography of the Japanese Archipelago. Furthermore, fishing ports are easy to access by recreational fishermen, and various reef fish species inhabit these ports (Murase et al. 2021; Fig. 19.2). Recreational fishing can yield data (e.g., species presence/absence data, and species abundance by region, season, and year) useful for assessing the temporal dynamics of reef fish assemblages, as well as for determining the biogeographic characteristics of fish species in a given region. Combined with conventional quantitative methods, this sustainable assessment method (in terms of cost and effort) will enhance our understanding and facilitate monitoring of the dynamics of reef fish communities.

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20

Fishes in Seagrass Habitats

Masahiro Horinouchi

Abstract

In total, at least 224 species belonging to 68 families were listed in the seagrass fish assemblage studies treated in this chapter. The most speciose families were Gobiidae, Labridae and Lethrinidae. In several regions around Honshu, the main island of Japan, some fishes including dominants were commonly recorded in seagrass habitats, such occurrence patterns suggesting a certain degree of similarity in seagrass fish assemblage structures, at least along the Seto-Inland Sea and Pacific Ocean coastal regions. Seagrass habitats in Okinawa region supported unique seagrass fish assemblages, most of fishes having not been recorded in studies conducted elsewhere. Similarly, the seagrass habitat in Lake Notoro in the Hokkaido region, supported unique assemblages comprising mainly cold-water fishes, most of them having been seldom or never recorded from areas outside the Tohoku region. Seagrass habitats are one of the most important components of the coastal ecosystem, supporting high overall biodiversity as well as fisheries in coastal areas. However, in recent years, extensive loss of seagrass habitats has occurred in Japan. Seagrass habitat restoration may be a means of compensating for such a loss. Further studies and efforts are urgently needed to explore appropriate designs for seagrass-habitat restoration in damaged coastal areas around Japan.

Keywords

Seagrass fish fauna · Responses to habitat degradation

20.1 Faunal Characteristics of Seagrass Fishes in Japan

Seagrasses (included in the families Zosteraceae, Posidoniaceae, Cymodoceaceae and Hydrocharitaceaee) are higher vascular plants which occur in coastal marine waters, sometimes as dense colonies on sand/mud substrata referred to as seagrass patches, beds or meadows (collectively, seagrass habitats).

Dense seagrass beds provide a highly complex habitat characterized by, for example, abundant foods, shelter against predators and/or strong water movement and a variety of microhabitats, being especially important for small fishes. Therefore, seagrass habitats often support large numbers of fish species and individuals, in addition to serving as a nursery for some species.

Tables 20.1, 20.2 and 20.3 provide lists of fishes recorded in a number of seagrass fish assemblage studies conducted in Japan in and

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Table 20.1 A list of fishes recorded in some studies conducted in the Okinawa region, Japan in and after 2001 which examined the seagrass fish assemblage structures, with their abundance ranks in descending order based on the reported data

	Reference	Nakamura and Sano (2004)		Shibuno et al. (2008)
	Site	Amitori Bay, Iriomote Is.	Urasoko Bay, Ishigaki Is.	Itona coast, Ishigaki Is.
	Sampling month	May, Aug, Nov 2001, Feb 2002	May, Aug, Nov 2001, Feb 2002	Aug, Nov 2004, May, Aug, Nov 2005
	Dominant seagrass species	*Enhalus acoroides*	*Thalassia hemprichii*	*Thalassia hemprichii*
Family	Species	Rank	Rank	Rank
Synodontidae	*Saurida gracilis*	40		
Aulostomidae	*Aulostomus chinensis*	44		
Syngnathidae	*Corythoichthys haematopterus*	44	33	26
Apogonidae	*Sphaeramia nematoptera*	28		
	Cheilodipterus quinquelineatus	16		
	Foa fo	28	7	25
	Ostorhinchus ishigakiensis	3	2	3
Carangidae	*Caranx sexfasciatus*	40		
	Caranx papuensis		33	26
Lutjanidae	*Lutjanus gibbus*	19	13	13
Haemulidae	*Plectorhinchus vittatus*	44	24	
Lethrinidae	*Lethrinus harak*	8	5	10
	Lethrinus atkinsoni	10	4	4
	Lethrinus genivittatus	44		
	Lethrinus nebulosus			17
	Lethrinus obsoletus	16	13	19
	Lethrinus ornatus	35	17	24
	Lethrinus olivaceus			21
	Lethrinus sp.			26
	Unidentified spp.	35	22	
Mullidae	*Mulloidichthys flavolineatus*	21		
	Parupeneus barberinoides	20	8	7
	Parupeneus barberinus	9	15	16
	Parupeneus indicus	35	19	9
	Parupeneus multifasciatus	12	25	11
	Parupeneus pleurostigma			31
	Parupeneus ciliatus	27	33	21
Chaetodontidae	*Chaetodon vagabundus*	44		
Pomacentridae	*Amphiprion ocellaris*	31	22	
	Chrysiptera unimaculata	44		

(continued)

Table 20.1 (continued)

	Reference	Nakamura and Sano (2004)		Shibuno et al. (2008)
	Site	Amitori Bay, Iriomote Is.	Urasoko Bay, Ishigaki Is.	Itona coast, Ishigaki Is.
	Sampling month	May, Aug, Nov 2001, Feb 2002	May, Aug, Nov 2001, Feb 2002	Aug, Nov 2004, May, Aug, Nov 2005
	Dominant seagrass species	*Enhalus acoroides*	*Thalassia hemprichii*	*Thalassia hemprichii*
Family	Species	Rank	Rank	Rank
	Dischistodus prosopotaenia	31	26	
	Pomacentrus chrysurus		31	
	Pomacentrus sp.		33	
Labridae	*Choerodon anchorago*	22		
	Cheilio inermis	11	6	6
	Stethojulis strigiventer	1	3	2
	Halichoeres trimaculatus	40	33	
	Halichoeres argus	23	16	
	Coris batuensis	40	33	31
	Cymolutes torquatus		33	31
	Cheilinus chlorourus	31		
	Oxycheilinus bimaculatus	31		
	Novaculoides macrolepidotus	35	26	31
Scaridae	*Leptoscarus vaigiensis*	13	11	19
	Calotomus spinidens	7	9	5
	Hipposcarus longiceps	44		
	Scarus ghobban	25		
	Scarus spp.			18
	Unidentified spp.	4	12	
Pinguipedidae	*Parapercis cylindrica*	14	33	21
Tripterygiidae	*Enneapterygius philippinus*			26
	Unidentified spp.	35	26	
Blenniidae	*Petroscirtes mitratus*		33	26
	Petroscirtes variabilis	44	26	
Callionymidae	*Anaora tentaculata*	44		
Gobiidae	*Asterropteryx semipunctata*	5	17	14
	Amblygobius phalaena		26	31
	Pleurosicya bilobata	44	31	
	Cryptocentrus caeruleomaculatus	2	20	12
	Tomiyamichthys lanceolatus			14

(continued)

Table 20.1 (continued)

	Reference	Nakamura and Sano (2004)		Shibuno et al. (2008)
	Site	Amitori Bay, Iriomote Is.	Urasoko Bay, Ishigaki Is.	Itona coast, Ishigaki Is.
	Sampling month	May, Aug, Nov 2001, Feb 2002	May, Aug, Nov 2001, Feb 2002	Aug, Nov 2004, May, Aug, Nov 2005
	Dominant seagrass species	*Enhalus acoroides*	*Thalassia hemprichii*	*Thalassia hemprichii*
Family	Species	Rank	Rank	Rank
	Vanderhorstia phaeosticta	15	20	
	Ctenogobiops pomastictus	18		
	Fusigobius neophytus	44		
	Eviota spp.	28		
Siganidae	*Siganus fuscescens*	25	1	1
	Siganus spinus	5	10	8
Acanthuridae	*Acanthurus mata*	44		31
Sphyraenidae	*Sphyraena flavicauda*		33	31
Monacanthidae	*Acreichthys tomentosus*	24		
	Total number of species	55	42	37

Table 20.2 A list of fishes recorded in some studies conducted in the western/central areas or northern Kanto region of the Main Island of Japan in and after 2001 which examined the seagrass fish assemblage structures, with their abundance ranks in descending order based on the reported data

	Region/Area	Seto-Inland Sea	Kinki	Tokai		Kanto
	Reference	Mohri et al. (2013)	Uede et al. (2012)	Sato et al. (2016)		Onuma et al. (2020)
	Site	Ikuno Island, Hiroshima	Tanabe Bay, Wakayama	Lake Hamana, Shizuoka		Hiraiso Harbor, Ibaraki
	Sampling month	Aug 2008 to Jul 2009, monthly	Nov 2004 to Nov 2005, monthly	Sep, Dec 2010, Apr, May, Jun 2011		May, Jun, Jul, Aug 2014
	Dominant seagrass species	*Zostera marina*	*Zostera japonica*	*Zostera marina*		*Zostera marina*
				Perennial phenotype	Annual phenotype	Small fragmented beds
Family	Species	Rank	Rank	Rank	Rank	Rank
Dasyatidae	*Hemitrygon akajei*				25	
Ophichthidae	*Ophichthus altipennis*		37			
Dussumieriidae	*Etrumeus micropus*			43	15	
Spratelloididae	*Spratelloides gracilis*				12	

(continued)

Table 20.2 (continued)

	Region/Area	Seto-Inland Sea	Kinki	Tokai		Kanto
	Reference	Mohri et al. (2013)	Uede et al. (2012)	Sato et al. (2016)		Onuma et al. (2020)
	Site	Ikuno Island, Hiroshima	Tanabe Bay, Wakayama	Lake Hamana, Shizuoka		Hiraiso Harbor, Ibaraki
	Sampling month	Aug 2008 to Jul 2009, monthly	Nov 2004 to Nov 2005, monthly	Sep, Dec 2010, Apr, May, Jun 2011		May, Jun, Jul, Aug 2014
	Dominant seagrass species	*Zostera marina*	*Zostera japonica*	*Zostera marina*		*Zostera marina*
				Perennial phenotype	Annual phenotype	Small fragmented beds
Family	Species	Rank	Rank	Rank	Rank	Rank
Clupeidae	*Sardinella zunasi*	45			25	
	Konosirus punctatus					13
Engraulididae	*Engraulis japonica*	16		31	3	
Plotosidae	*Plotosus japonicus*	4	7	36		
Osmeridae	*Hypomesus nipponensis*					23
Plecoglossidae	*Plecoglossus altivelis altivelis*	23		6		
Aulorhynchidae	*Aulichthys japonicus*	15				
Fistulariidae	*Fistularia commersonii*					23
Syngnathidae	*Urocampus nanus*	35	20	43		
	Syngnathus schlegeli	11		19	18	8
	Hippichthys penicillus		24			
	Hippocampus mohnikei			43		
	Hippocampus coronatus	32		43	17	
Mugilidae	*Mugil cephalus cephalus*	24				5
	Planiliza macrolepis	45				
	Chelon lauvergnii			4	8	
	Chelon sp.		22			
Atherinidae	*Doboatherina bleekeri*		14	36		
Hemiramphidae	*Hyporhamphus sajori*	35	37		20	
Sebastidae	*Sebastiscus marmoratus*	38	19			
	Sebastes schlegelii				16	
	Sebastes cheni	2		7	9	
	Sebastes inermis	12		13	12	
	Sebastes ventricosus	8		2	25	
	Sebastes oblongus	27				

(continued)

Table 20.2 (continued)

	Region/Area	Seto-Inland Sea	Kinki	Tokai		Kanto
	Reference	Mohri et al. (2013)	Uede et al. (2012)	Sato et al. (2016)		Onuma et al. (2020)
	Site	Ikuno Island, Hiroshima	Tanabe Bay, Wakayama	Lake Hamana, Shizuoka		Hiraiso Harbor, Ibaraki
	Sampling month	Aug 2008 to Jul 2009, monthly	Nov 2004 to Nov 2005, monthly	Sep, Dec 2010, Apr, May, Jun 2011		May, Jun, Jul, Aug 2014
	Dominant seagrass species	*Zostera marina*	*Zostera japonica*	*Zostera marina*		*Zostera marina*
				Perennial phenotype	Annual phenotype	Small fragmented beds
Family	Species	Rank	Rank	Rank	Rank	Rank
	Sebastes hubbsi	45				
	Sebastes longispinis	45				
	Sebastes sp.					6
Tetrarogidae	*Paracentropogon rubripinnis*	19		5		
Synanceiidae	*Inimicus japonicus*	45				
Platycephalidae	*Cociella crocodila*			39	25	
	Inegocia japonica				25	
Lateolabracidae	*Lateolabrax japonicus*	39	9	9	2	3
Scombropidae	*Scombrops boops*			25	18	
Carangidae	*Trachurus japonicus*	42		23	12	
	Scomberoides lysan				20	
Leiognathidae	*Nuchequula nuchalis*			13	6	
Lutjanidae	*Lutjanus* sp.		30			
Gerreidae	*Gerres equulus*		1	33	11	
Sparidae	*Rhabdosargus sarba*		5	1	1	
	Acanthopagrus latus		7			
	Acanthopagrus schlegelii	5	11			7
	Pagrus major	32				
Lethrinidae	*Lethrinus genivittatus*			13		
	Unidentified sp.		37			
Sillaginidae	*Sillago japonica*	9	30	28		23
Mullidae	*Upeneus tragula*		30	31		
Latridae	*Goniistius zonatus*			39		
Embiotocidae	*Ditrema jordani*	28				
	Ditrema viride	30				
	Ditrema temminckii temminckii					4
	Ditrema temminckii pacificum	7		16		

(continued)

Table 20.2 (continued)

	Region/Area	Seto-Inland Sea	Kinki	Tokai		Kanto
	Reference	Mohri et al. (2013)	Uede et al. (2012)	Sato et al. (2016)		Onuma et al. (2020)
	Site	Ikuno Island, Hiroshima	Tanabe Bay, Wakayama	Lake Hamana, Shizuoka		Hiraiso Harbor, Ibaraki
	Sampling month	Aug 2008 to Jul 2009, monthly	Nov 2004 to Nov 2005, monthly	Sep, Dec 2010, Apr, May, Jun 2011		May, Jun, Jul, Aug 2014
	Dominant seagrass species	*Zostera marina*	*Zostera japonica*	*Zostera marina*		*Zostera marina*
				Perennial phenotype	Annual phenotype	Small fragmented beds
Family	Species	Rank	Rank	Rank	Rank	Rank
Teraponidae	*Rhynchopelates oxyrhynchus*		10	23		
Girellidae	*Girella punctata*	42	24	12		
	Girella sp.					2
Labridae	*Stethojulis interrupta terina*			39		
	Parajulis poecileptera	40				
	Halichoeres tenuispinis	42				
	Unidentified sp.		37			
Scaridae	Unidentified sp.		30			
Hexagrammidae	*Hexagrammos agrammus*	21	27			
	Hexagrammos otakii	22	30			
Cottidae	*Pseudoblennius cottoides*	10		16		9
	Pseudoblennius marmoratus		27			
	Pseudoblennius percoides			43		19
	Pseudoblennius sp.1		30			
	Pseudoblennius sp.2		17			
Stichaeidae	*Zoarchias glaber*					14
Pholidae	*Pholis crassispina*					23
	Pholis nebulosa	45		3	7	14
Blenniidae	*Omobranchus elegans*					19
	Petroscirtes breviceps	20		18		
Callionymidae	*Callionymus beniteguri*	31				
	Repomucenus ornatipinnis	34				
	Unidentified sp.		20			
	Unidentified spp.	37				

(continued)

Table 20.2 (continued)

	Region/Area	Seto-Inland Sea	Kinki	Tokai		Kanto
	Reference	Mohri et al. (2013)	Uede et al. (2012)	Sato et al. (2016)		Onuma et al. (2020)
	Site	Ikuno Island, Hiroshima	Tanabe Bay, Wakayama	Lake Hamana, Shizuoka		Hiraiso Harbor, Ibaraki
	Sampling month	Aug 2008 to Jul 2009, monthly	Nov 2004 to Nov 2005, monthly	Sep, Dec 2010, Apr, May, Jun 2011		May, Jun, Jul, Aug 2014
	Dominant seagrass species	*Zostera marina*	*Zostera japonica*	*Zostera marina*		*Zostera marina*
				Perennial phenotype	Annual phenotype	Small fragmented beds
Family	Species	Rank	Rank	Rank	Rank	Rank
Gobiidae	*Luciogobius guttatus*	45				
	Acanthogobius flavimanus		2	33	5	11
	Tridentiger trigonocephalus	17	13	26		
	Tridentiger sp.		17			
	Heteroplopomus barbatus		30			
	Rhinogobius sp.					16
	Mahidolia mystacina		37			
	Acentrogobius pflaumii	6	3			
	Acentrogobius sp.			22		
	Favonigobius gymnauchen	3	4	10	10	12
	Gymnogobius petschiliensis					23
	Gymnogobius opperiens				20	
	Gymnogobius urotaenia				20	23
	Gymnogobius heptacanthus	13		26	4	
	Gymnogobius breunigii			36	25	
	Chaenogobius annularis	45				1
	Chaenogobius sp.		12			
	Unidentified sp.1		6			
Siganidae	*Siganus fuscescens*		37	8		
	Siganus sp.		26			
Sphyraenidae	*Sphyraena obtusata*					16
	Sphyraena japonica					19

(continued)

Table 20.2 (continued)

	Region/Area	Seto-Inland Sea	Kinki	Tokai		Kanto
	Reference	Mohri et al. (2013)	Uede et al. (2012)	Sato et al. (2016)		Onuma et al. (2020)
	Site	Ikuno Island, Hiroshima	Tanabe Bay, Wakayama	Lake Hamana, Shizuoka		Hiraiso Harbor, Ibaraki
	Sampling month	Aug 2008 to Jul 2009, monthly	Nov 2004 to Nov 2005, monthly	Sep, Dec 2010, Apr, May, Jun 2011		May, Jun, Jul, Aug 2014
	Dominant seagrass species	*Zostera marina*	*Zostera japonica*	*Zostera marina*		*Zostera marina*
				Perennial phenotype	Annual phenotype	Small fragmented beds
Family	Species	Rank	Rank	Rank	Rank	Rank
	Sphyraena sp.		37			
Pleuronectidae	*Pseudopleuronectes yokohamae*				25	23
	Pleuronichthys cornutus	45				
Cynoglossidae	*Paraplagusia japonica*			43		
Triacanthidae	*Triacanthus biaculeatus*			39		
Monacanthidae	*Rudarius ercodes*	1	15	11		
	Thamnaconus modestus	26				
	Stephanolepis cirrhifer	40		33		
Ostraciidae	*Lactoria cornuta*			43		
Tetraodontidae	*Canthigaster rivulata*			28		
	Takifugu pardalis	18	16	30	25	19
	Takifugu vermicularis			43		
	Takifugu flavipterus	28		19	20	16
	Takifugu alboplumbeus	14		21		
	Takifugu sp.1		22			
	Takifugu sp.2					10
	Arothron sp.		27			
	Total number of species	52	43	50	32	29
				60		

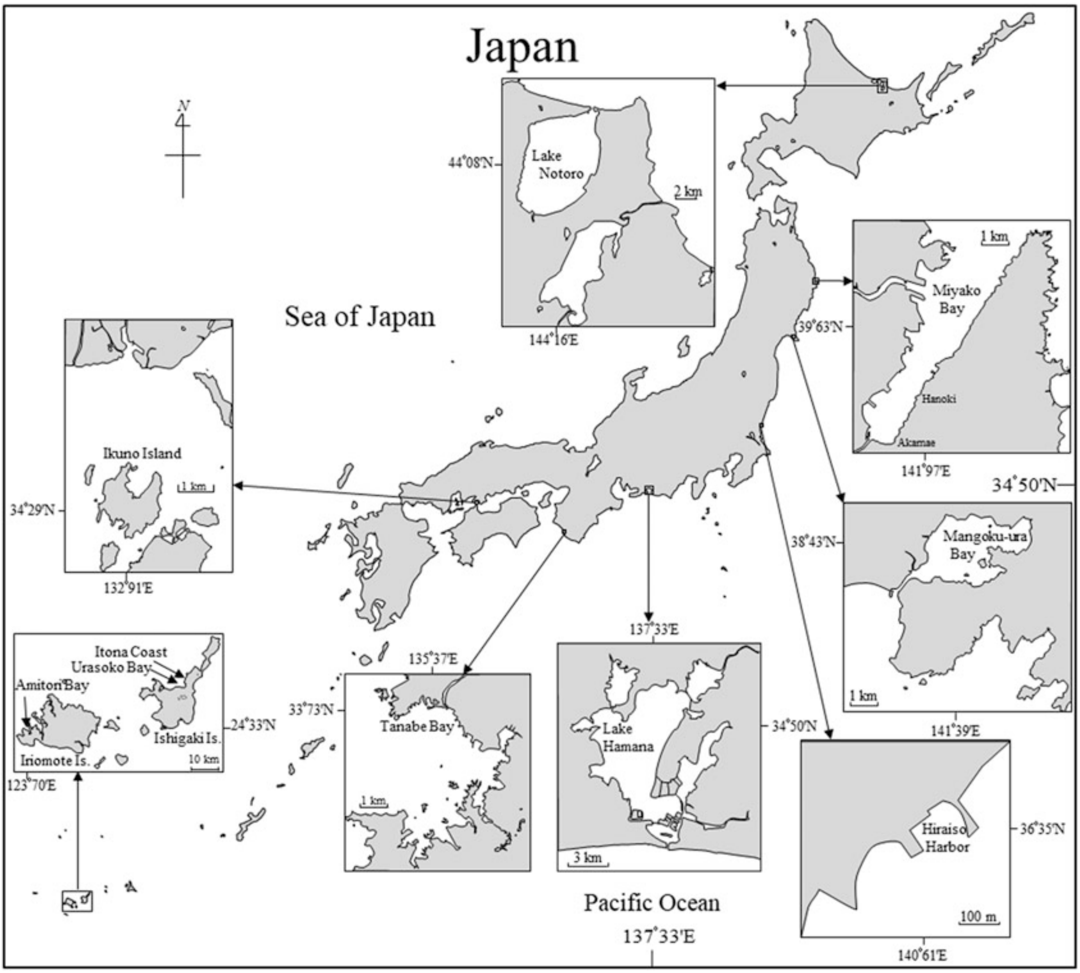

Fig. 20.1 A map of sites where studies listed in Tables 20.1, 20.2 and 20.3 were conducted

after 2001, and published in peer-reviewed journals (for the location of the study sites, see Fig. 20.1). Studies with single census only have been omitted because such seldom include sufficiently accurate information on assemblage structures. For this reason, therefore, the seagrass fish fauna in some areas around Japan, such as the coast of the Sea of Japan, Kyushu and Shikoku regions are not included in these lists.

In total, at least 224 species belonging to 68 families are included on these lists, most individuals being of small body size, including juveniles of relatively large species such as *Rhabdosargus sarba* or *Siganus fuscescens* (body size information for recorded species included in some publications cited in Tables 20.1, 20.2 and 20.3, though some lacked such information). The most speciose families were Gobiidae (34 species), Labridae (14 species) and Lethrinidae (10 species), with the most dominant fishes in the various seagrass habitats (arbitrarily defined as the 3 most abundant species in each) representing 32 species in 21 families (see Tables 20.1, 20.2 and 20.3). Of these families, Gobiidae were most numerous (8 species), followed by Cottidae (3 species), and Sebastidae and Pholidae (2 species each).

Table 20.3 A list of fishes recorded in some studies conducted in the Tohoku or Hokkaido regions of Japan in and after 2001 which examined the seagrass fish assemblage structures, with their abundance ranks in descending order based on the reported data

	Region/area	Tohoku						Hokkaido	
	Reference	Shoji and Morimoto (2016)			Noda et al. (2017)			Tanaka et al. (2018)	
	Site	Mangoku-Ura Bay, Miyagi			Hanoki/Akamae, Miyako Bay, Iwate			Lake Notoro, Hokkaido	
	Sampling month	*Jun 2009, Jul 2010	**Aug 2011	***Aug 2012, Jul 2013, Jun 2014	*Jun 2010	**Jun 2011	***Jun 2012	May, Aug, Nov 2013	
	Dominant seagrass species	*Zostera marina*			*Zostera marina*			*Zostera marina* and *Z. caespitosa*	
			Seriously disturbed			Seriously disturbed		Daytime	Nighttime
Family	Species	Rank	Rank	Rank	Rank	Rank	Rank	Rank	Rank
Clupeidae	*Konosirus punctatus*		11						
Engraulididae	*Engraulis japonica*								12
Cyprinidae	*Pseudaspius hakonensis*				11	6	19		
	Tribolodon hakonensis			27				3	3
Osmeridae	*Hypomesus japonicus*					19	17		
	Hypomesus nipponensis						19		
	Hypomesus spp.							1	1
Plecoglossidae	*Plecoglossus altivelis altivelis*					9	19		
Salmonidae	*Oncorhynchus keta*				9	5		2	
Gadidae	*Eleginus gracilis*								2
Hypoptychidae	*Hypoptychus dybowskii*							3	4
Aulorhynchidae	*Aulichthys japonicus*	18		19					
Syngnathidae	*Syngnathus schlegeli*		4	9	10	8	4		
	Hippocampus mohnikei			27					
Mugilidae	*Mugil cephalus cephalus*	4		9					
	Chelon lauvergnii							12	
Sebastidae	*Sebastes schlegelii*							12	6
	Sebastes cheni	3		11					
	Sebastes inermis			15					
	Sebastes ventricosus	13		22					

(continued)

Table 20.3 (continued)

	Region/area	Tohoku						Hokkaido	
	Reference	Shoji and Morimoto (2016)			Noda et al. (2017)			Tanaka et al. (2018)	
	Site	Mangoku-Ura Bay, Miyagi			Hanoki/Akamae, Miyako Bay, Iwate			Lake Notoro, Hokkaido	
	Sampling month	*Jun 2009, Jul 2010	**Aug 2011	***Aug 2012, Jul 2013, Jun 2014	*Jun 2010	**Jun 2011	***Jun 2012	May, Aug, Nov 2013	
	Dominant seagrass species	*Zostera marina*			*Zostera marina*			*Zostera marina* and *Z. caespitosa*	
			Seriously disturbed			Seriously disturbed		Daytime	Nighttime
Family	Species	Rank	Rank	Rank	Rank	Rank	Rank	Rank	Rank
Lateolabracidae	*Lateolabrax japonicus*			19					
Scombropidae	*Scombrops gilberti*						19		
Sparidae	*Acanthopagrus schlegelii*		7	27					
Sillaginidae	*Sillago japonica*					19			
Embiotocidae	*Ditrema jordani*			6					
	Ditrema viride	2		8					
	Ditrema spp.				13				
Hexagrammidae	*Pleurogrammus azonus*						19		
	Hexagrammos agrammus	12	11	27	13				
	Hexagrammos otakii	14	10	16	13	13	15		
Hemitripteridae	*Hemitripterus villosus*					18	14		
	Blepsias cirrhosus				5	9	12		15
Cottidae	*Gymnocanthus herzensteini*						1		
	Myoxocephalus brandtii						19	10	6
	Myoxocephalus stelleri	15		13	7	7	2		
	Ocynectes modestus				13				
	Pseudoblennius cottoides	7		5	3	2	8		
	Pseudoblennius marmoratus			25					

Agonidae	*Pallasina barbata*					19	19	10	12
Liparidae	*Liparis tanakae*						19		
Stichaeidae	*Ernogrammus hexagrammus*	10		14					
	Opisthocentrus ocellatus				4		13	12	
	Opisthocentrus tenuis				2	9	10		
	Pholidapus dybowskii							8	12
	Neozoarces steindachneri								10
Pholidae	*Pholis crassispina*	9	8	2	6	4	5		
	Pholis nebulosa	6		4	8	16	9		
	Pholis picta								15
Ammodytidae	*Ammodytes japonicus*					9			
Blenniidae	*Omobranchus elegans*		11						
Callionymidae	*Callionymus valenciennei*			25					
	Callionymus beniteguri		6						
Gobiidae	*Acanthogobius flavimanus*	8	8	3	12	3	7		
	Tridentiger trigonocephalus	11	5	22		17	15		
	Tridentiger bifasciatus	15		21					
	Tridentiger obscurus			27					
	Acentrogobius virgatulus	1	1	16					
	Acentrogobius spp.					15	17		
	Favonigobius gymnauchen	5	3	18		19	6		
	Gymnogobius heptacanthus				1	1	3		
	Gymnogobius mororanus			1				6	10
	Gymnogobius breunigii	18						5	9
	Chaenogobius annularis			12					

(continued)

Table 20.3 (continued)

	Region/area	Tohoku						Hokkaido	
	Reference	Shoji and Morimoto (2016)			Noda et al. (2017)			Tanaka et al. (2018)	
	Site	Mangoku-Ura Bay, Miyagi			Hanoki/Akamae, Miyako Bay, Iwate			Lake Notoro, Hokkaido	
	Sampling month	*Jun 2009, Jul 2010	**Aug 2011	***Aug 2012, Jul 2013, Jun 2014	*Jun 2010	**Jun 2011	***Jun 2012	May, Aug, Nov 2013	
	Dominant seagrass species	*Zostera marina*			*Zostera marina*			*Zostera marina* and *Z. caespitosa*	
			Seriously disturbed			Seriously disturbed		Daytime	Nighttime
Family	Species	Rank	Rank	Rank	Rank	Rank	Rank	Rank	Rank
	Chaenogobius gulosus			7					
	Unidentified sp.2								15
Paralichthyidae	*Paralichthys olivaceus*				13		19		
Pleuronectidae	*Platichthys stellatus*								15
	Pseudopleuronectes obscurus							7	5
	Pseudopleuronectes schrenki							9	8
	Pseudopleuronectes yokohamae	15		24		13	11		
Tetraodontidae	*Takifugu alboplumbeus*		2						
	Unidentified sp.							12	
	Total number of species	19	13	31	17	22	27	15	18
								22	

The asterisk symbols i.e., *, ** and *** denote the periods before, just after, and after the Great East Japan Earthquake occurred on 11 March 2011, respectively

20.1.1 Okinawa Region

Studies conducted in the subtropical Nansei Islands, Okinawa region, reported distinctly unique seagrass fish assemblages, with greater diversity (Table 20.1). In total, 69 species representing 22 families occurred in the studied seagrass habitats, most of them (except *Siganus fuscescens* and *Lethrinus genivittatus*) having not been recorded in studies conducted elsewhere (see Tables 20.2 and 20.3). The species diversity of some families, such as Lethirinidae, Mullidae, Labridae or Scaridae was apparently higher compared with other regions.

20.1.2 Honshu, the Main Island of Japan

Some fishes, including *Acanthogobius flavimanus*, *Pholis nebulosa*, *Lateolabrax japonicus* or *Pseudoblennius cottoides*, regarded as dominants in some seagrass habitats, as well as relatively less abundant fishes, such as *Syngnathus schlegeli*, *Tridentiger trigonocephalus*, and *Hexagrammos agrammus*, were commonly recorded in seagrass habitats in several regions around Honshu, the main island of Japan (see Tables 20.2 and 20.3). Such occurrence patterns suggest a certain degree of similarity in seagrass fish assemblage structures, at least along the Seto-Inland Sea and Pacific Ocean coastal regions. On the other hand, some fishes, including both dominant and relatively less abundant species, which were specific to a particular region(s). *Myoxocephalus stelleri*, *Gymnocanthus herzensteini*, *Opisthocentrus tenuis*, *Pholis crassipina*, *Gymnogobius mororanus*, *Pseudaspius hakonensis*, and *Oncorhynchus keta* were restricted to northern areas, i.e., Tohoku and/or northern Kanto regions (the last-named species also occurs in Lake Notoro, Hokkaido region). Conversely, several fishes, including *Rudarius ercodes*, *Gerres equulus*, and *Rhabdosargus sarba*, were recorded across central to western areas of Honshu. Both of these latter species groups, therefore, add certain regional characteristics of Japan's seagrass fish assemblages.

20.1.3 Hokkaido Region

The seagrass habitat in Lake Notoro situated in the Hokkaido subarctic region, supported unique assemblages comprising mainly cold-water fishes (Table 20.3). The dominant species, *Hypomesus* spp., *Eleginus gracilis* and *Hypoptychus dybowskii* have not yet been recorded in seagrass habitats in other areas. Similarly, most of the other Lake Notoro inhabitants, such as *Oncorhynchus keta*, *Pseudopleuronectes obscurus*, *Pseudopleuronectes schrenki*, and *Platichthys stellatus*, have been seldom or at no time recorded from areas outside the Tohoku region.

The exclusion of seagrass fish assemblage studies from other regions of Japan (e.g., the coast of the Sea of Japan, Kyushu and Shikoku regions) in this review, for reasons noted above, reinforces the need for further studies on such assemblages, employing appropriate census designs, so as to clarify the overall characteristics of seagrass fish assemblages within the Japanese Archipelago.

20.2 Responses of a Seagrass Fish Assemblage to Habitat Degradation

20.2.1 Seagrass Fish Categories Based on Their Occurrence/Distribution Patterns

Seagrass-associated fishes can be divided into several categories and subcategories (see Kikuchi 1974; Horinouchi 2007).

1. Permanent residents: fishes, generally of small body size, occurring in a seagrass habitat nearly all year round include seagrass habitat specialists (e.g., small filefish *Rudarius ercodes*) and habitat generalist which occur

also in other nearby habitats (e.g., some benthic gobies in the genus *Acentrogobius*).

2. Seasonal residents: fishes occurring in a seagrass habitat during a specific season (s) including juveniles of some species (utilizing the seagrass habitat as a nursery) (e.g., Pink Ear Emperor *Lethrinus lentjan*, Humpback Red Snapper *Lutjanus gibbus*).
3. Transients: fishes migrating temporarily into a seagrass habitat for foraging and/or use of such a habitat as a "path/corridor" between habitats, such as coral/mangrove areas (e.g., Yellowtail Barracuda *Sphyraena flavicauda*).
4. Occasional migrants: fishes occurring in a seagrass habitat by chance during migration.

Of these categories, adults of seasonal residents and transients also occur in other habitats, some of them being regularly targeted by local fisheries (e.g., emperors/snappers/barracudas). Therefore, seagrass habitats are one of the most important components of the coastal ecosystem, supporting high overall biodiversity in coastal areas as well as coastal fisheries.

20.2.2 Transition of Fish Assemblage Structures with Progress of Seagrass Habitat Degradation

In recent years, because of anthropogenic and/or natural disturbances extensive loss of seagrass habitats has occurred worldwide (e.g., Short et al. 2014). The loss process sometimes includes habitat fragmentation, which results in significant changes in fish assemblage structures (see Fig. 20.2). In cases of habitat fragmentation remaining at a low level, seagrass fish diversity and/or abundance of some species may sometimes increase due to factors including higher microhabitat variety/availability of microhabitats (e.g., edge microhabitat). These may contribute to not only coastal biodiversity but also local fisheries resources. While the effects of seagrass habitat fragmentation have not yet been studied in Japan, Horinouchi et al. (2009) examined fish assemblage structures in fragmented and continuous seagrass habitats in Trang, Thailand, finding fish diversity in the former habitats with some species more abundant, including those targeted by local fisheries, such as *Lethrinus lentjan* and *Stolepholus* sp. (reported as *Stolepholus indicus*). Those findings suggested that a similar scenario may well be applicable to seagrass habitats in Japan.

However, where disturbance continues over a long period of time or is of a severe nature, habitat fragmentation may be excessive (or very fast), resulting in extreme or total loss of seagrasses and a change in the fish assemblage structures. The removal of residents strongly reliant on seagrass habitat impacts negatively on fish diversity/abundance in the immediate area as well as the overall coastal region, with consequences for local fisheries (see Fig. 20.2). Nakamura (2010) examined the effects of such seagrass removal, apparently due to a typhoon, on fish assemblage structures at Iriomote Island, Okinawa, by comparing the fish assemblage structure in the seagrass-removed habitat with that in the undisturbed seagrass habitat. A significant decrease in overall seagrass fish species richness and abundance as well as abundance of some residents, including juveniles of commercially important coral reef fishes, was recognized. This indicated that increasing seagrass habitat loss will cause serious reductions in seagrass-associated fishes and fishery resources (Nakamura 2010). Severe disturbance of seagrass habitats also occurred concurrent with the Great East Japan Earthquake and resultant tsunami on 11 March 2011. Shoji and Morimoto (2016) and Noda et al. (2017) examined changes in seagrass fish assemblage structures before and after the event in Mangoku-ura Bay and Miyako Bay, respectively (see also Table 20.2). Comparison with the study by Nakamura (2010) were not always straightforward, likely due to the influence of several other factors including changes in anthropogenic disturbance intensity and/or environmental factors. Without going into details here, the fish assemblage structures were drastically changed after the severe disturbance caused by this event (for details, see cited references and Table 20.2).

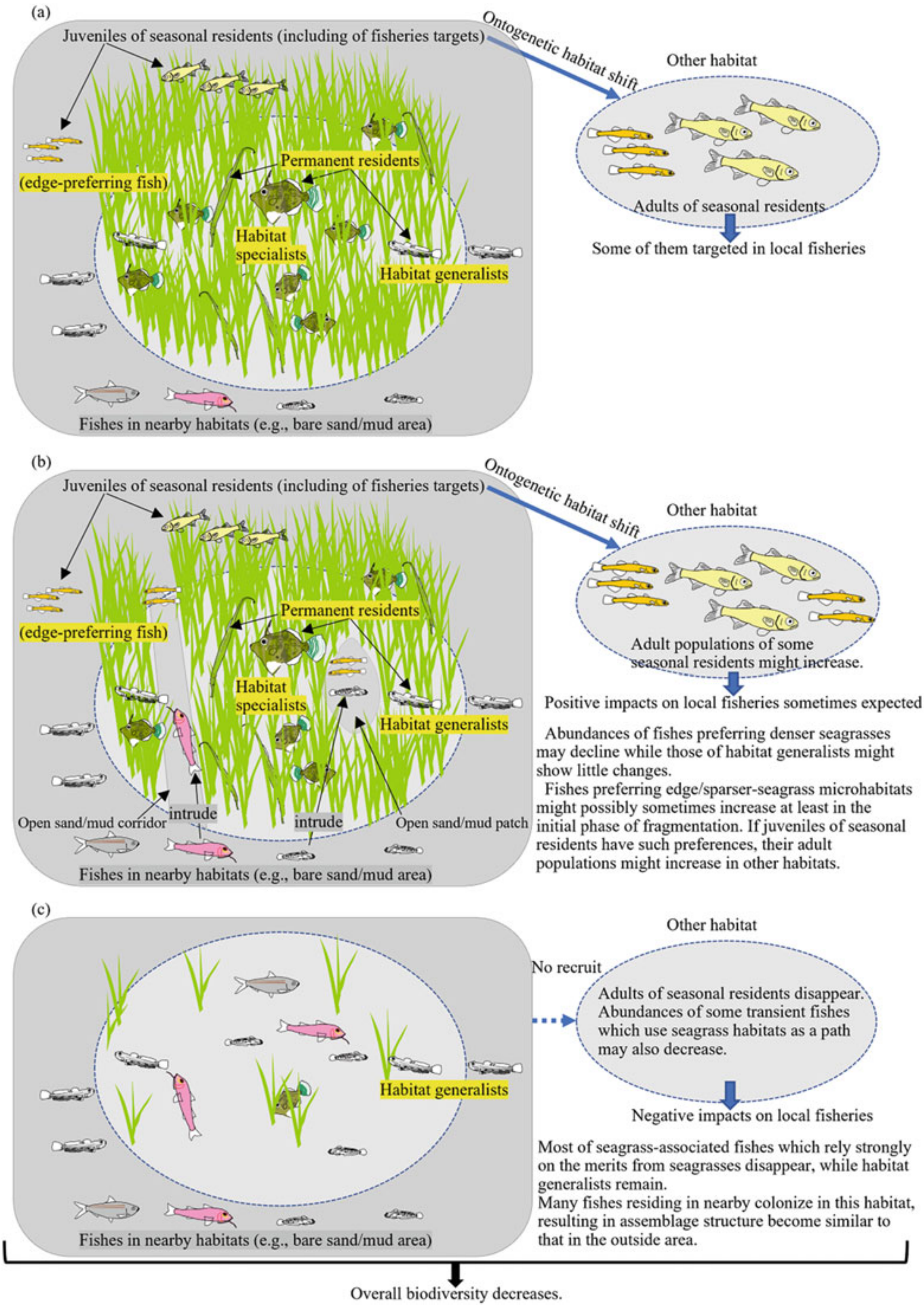

Fig. 20.2 A scheme of expected process of transition of a seagrass fish assemblage structure with progress of habitat fragmentation. (**a**) Continuous seagrass habitat; (**b**) Slightly/moderately fragmented seagrass habitat; (**c**) Severely disturbed seagrass habitat. In case anthropogenetic/natural disturbances are quite severe, the phase (**b**) should often be skipped

20.2.3 Brief Implications on Seagrass Habitat Restoration

In cases of extreme loss of seagrass habitats from an area, seagrass-planting (i.e., seagrass habitat restoration) may be a means of compensating for such a loss. In fact, because of increasing concerns over seagrass habitat loss, not a few trials of seagrass-habitat restoration have been conducted in various locations around Japan (see e.g., Terawaki et al. 2005; Van Katwijk et al. 2016; Hori and Sato 2019). To date, however, fish assemblage structures in restored seagrass habitats in Japan have been seldom described in detail in peer-reviewed papers, although feedback from such studies is essential for establishing appropriate designs and strategies for seagrass-habitat restoration, which must surely lead to the recovery of ecosystem services (e.g., Orth et al. 2020). Admittedly, such a goal must require considerable inputs of time and energy. The "appropriate design" would likely differ among locations, due to differences in fish fauna and other fauna (and flora), plus environmental and social factors, resulting in area specific responses to restoration. Despite this, further studies and efforts are urgently needed to explore appropriate designs for seagrass-habitat restoration in damaged coastal areas around Japan.

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21 Coastal Fishes in Mangroves

Kusuto Nanjo

Abstract

Mangrove forests found in intertidal areas of estuaries in southern Japan, especially in the Ryukyu Islands, provide suitable habitats for a wide variety of fishes, including those of Carangidae, Gerridae, Lutjanidae, Apogonidae, Pomacentridae, and Gobiidae. Fish species richness being greater than that in temperate estuaries, the diversity of fishes in mangrove habitats is closely related to habitat complexity structured by mangrove roots, which provides shelter from predation and abundant food for fishes. According to analyses of fish food habits, a wide variety of food items are taken by mangrove fishes, food availability determining the distribution of several fish species. The sheltering function of mangrove roots has also been demonstrated by unique field experiments, using artificial units mimicking mangrove roots. With increasing root density, fish abundance increased and predation mortality rates for small fishes decreased. Additionally, such habitat functions have a flow-on effect on coral reef fish populations, due to some reef fishes, such as Lutjanidae, utilizing mangrove habitats as nurseries. Because the critical decline and degradation of mangroves worldwide have led to significant lowering of fish diversities in mangrove ecosystems, significant efforts must be made to conserve mangrove ecosystems.

Keywords

Mangrove · Estuary · Food availability · Shelter · Habitat complexity · Nursery · Ecosystem function · Conservation

21.1 What Are Mangroves?

Mangroves are salt-tolerant trees and shrubs, flourishing in the intertidal areas of sheltered shores, estuaries, lagoons, and mudflats in tropical and subtropical regions. They occur globally in the Indo-West Pacific, Asia, Polynesia, the eastern Pacific, and in the west and east Atlantic (FAO 2007). In Japan, mangrove forests are mainly found in estuaries in Okinawa and Kagoshima prefectures, the majority occurring in the Ryukyu Islands (Fig. 21.1). Common mangrove species are *Rhizophora stylosa*, *Bruguiera gymnorhiza*, *Kandelia obovata*, *Avicennia marina*, *Lumnitzera racemose,* and *Sonneratia alba*, although a total of 11 mangrove species have been recorded in Japan (FAO 2007).

Mangroves are uniquely adapted to marine and estuarine (i.e., salt-water) conditions, with high tidal interference, high salinity fluctuations, and muddy anaerobic substrates. Their unique root

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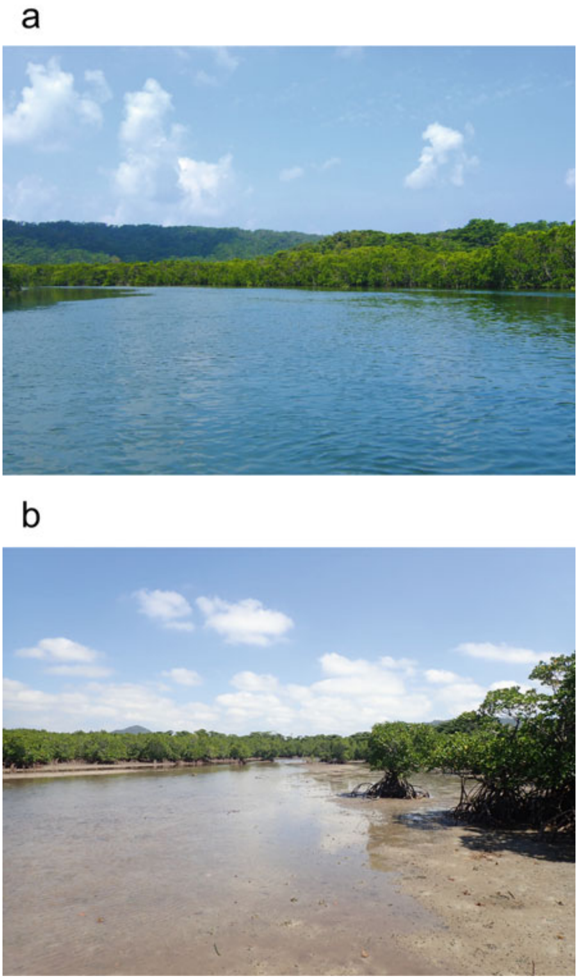

Fig. 21.1 Mangrove estuaries in the Ryukyu Islands, southern Japan, (**a**) at high tide, (**b**) at low tide

system, incorporating "aerial roots," provides gas transport in anaerobic sediments and supports the trunks in soft muddy sediments. The shape and structure of the aerial roots differ among species, including "prop roots" in *Rhizophora stylosa*, and "pneumatophores," being stick-like in *Avicennia marina* and knee-shaped in *Bruguiera gymnorhiza* (Fig. 21.2). The root systems also exclude salt from mangroves during water uptake, while some species possess salt glands on their leaves for salt secretion.

21.2 Fishes Occurring in Mangrove Habitats

A wide variety of fishes occur in mangrove estuaries, fish species richness being usually an order of magnitude greater than that in temperate estuaries. For example, Tachihara et al. (2003), who studied the fish fauna in four mangrove estuaries on Okinawa, Miyako, Ishigaki, and Iriomote islands, reported a total of 155 species (47 families) collected. More than 100 species have been reported from the Urauchi River, Iriomote Island, from creeks within an area of 0.5 km^2 with extensive mangrove forests (Nanjo et al. 2010, 2014a). The dominant taxa were Carangidae, Gerridae, Lutjanidae, Apogonidae, Pomacentridae, and Gobiidae, including common species such as Brassy Trevally *Caranx papuensis*, Deep-bodied Mojarra *Gerres erythrourus*, Mangrove Red Snapper *Lutjanus argentimaculatus*, Blacktail Snapper *Lutjanus fulvus*, Amboina Cardinalfish *Fibramia amboinensis*, Brackish Damsel *Pomacentrus*

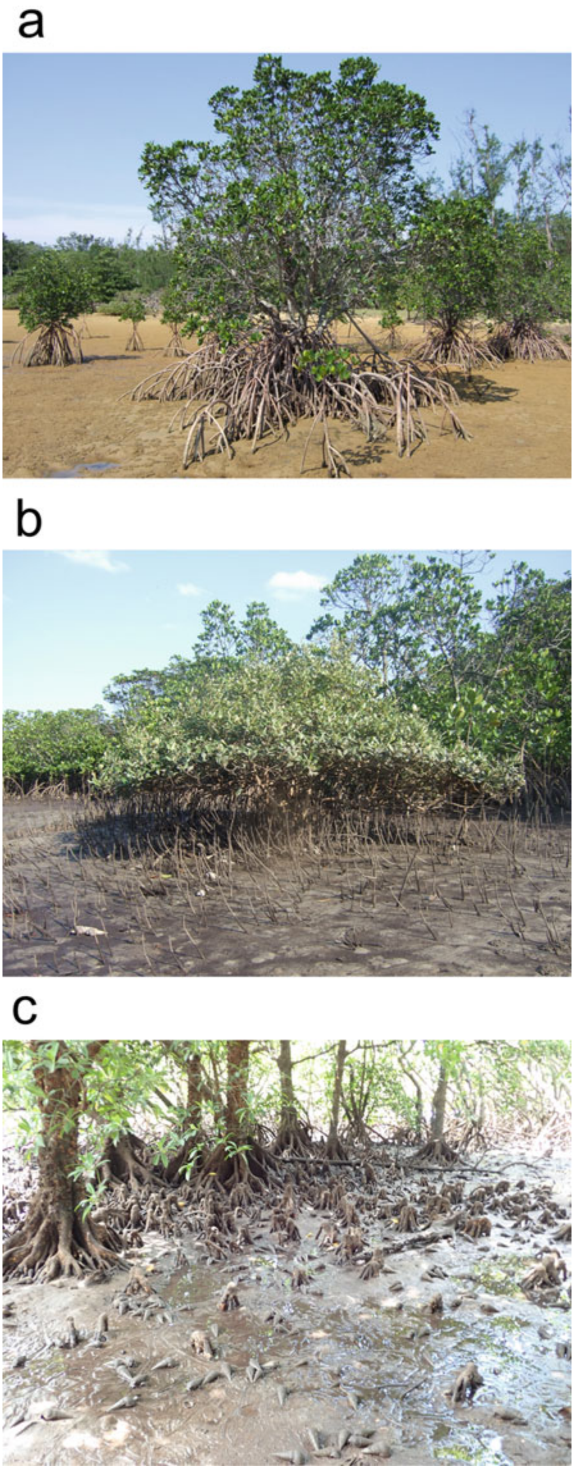

Fig. 21.2 Root structures of mangroves, (**a**) prop roots of *Rhizophora stylosa*, (**b**) pneumatophores of *Avicennia marina*, (**c**) pneumatophores of *Bruguiera gymnorhiza*

taeniometopon, and Sand Goby *Favonigobius reichei* (Fig. 21.3). A unique species is Barrede Mudskipper *Periophthalmus argentilineatus* (Periophthalmidae) (Fig. 21.3), occupying exposed sand/mud areas within mangrove forests at low tide, as does *Periophthalmus modestus* on temperate tidal flats. Unlike tropical coral reef fishes with highly colorful bodies, many mangrove fishes have a silvery-white body, not unlike temperate estuarine fishes.

Fishes occurring in mangrove habitats are classified into several categories, i.e., marine, estuarine, diadromous, and freshwater species, based on estuarine use patterns through their life histories, such being associated with spawning location, feeding and/or refuge, and migratory movements between estuaries and other ecosystems (Potter et al. 2015). In Japan, mangrove fishes comprise mostly marine and estuarine species, diadromous and freshwater species being relatively few.

Marine species spawn at sea, entering estuaries in large numbers at a later stage (typically juvenile) in their life cycle (marine estuarine-opportunist/dependent) or accidentally in low numbers (marine straggler). For example, several lutjanid fishes, such as Mangrove Red Snapper *L. argentimaculatus*, Blacktail Snapper *L. fulvus,* and Dory Snapper *L. fulviflamma*, utilize mangrove estuaries as juveniles and move to marine habitats with growth (marine estuarine-opportunist) (Nakamura et al. 2008; Kimirei et al. 2013), whereas some coral reef fishes, such as Threadfin Butterflyfish *Chaetodon auriga* and Longfin Bannerfish *Heniochus acuminatus*, sometimes occur sporadically in mangrove estuaries (marine straggler) (Nanjo et al. 2014a).

On the other hand, estuarine species complete their entire life cycle within the estuarine environment (solely estuarine) or have larval stages completed outside the estuary before returning to estuaries for growth and reproduction (estuarine migrants). The halfbeak, Duncker's River Garfish *Zenarchopterus dunckeri* and Amboina Cardinalfish fish *Fibramia amboinensis*, for instance, may spend its entire life cycle within an estuary (solely estuarine) (Kanai et al. 2014; Shirai et al. 2018), whereas larvae of *F. amboinensis* have been found on the sandy beach near a river mouth, subsequently entering the estuary (Maeda and Tachihara 2014). Although marine species have been dominant within mangrove fish assemblages in other countries (Blaber 2000), estuarine species have often been abundant in mangrove estuaries in Japan (Nanjo et al. 2014a; Inoue et al. 2016).

21.3 Factors Affecting Fish Diversity in Mangrove Habitats

Fish diversity in mangrove habitats is closely related to habitat complexity structured by mangrove vegetation, such as prop roots, pneumatophores, trunks, and fallen branches (Blaber 2000). It is generally believed that greater habitat complexity provides shelter from predation, increased microhabitat availability, and abundant food. The complex structure of mangrove roots enhances sedimentation rates, trapping leaf litter, and also harbors epiphytic algae on the root surface, thereby enabling colonization by large numbers of small invertebrates, such as crabs, shrimps and gastropods. For example, many kinds of crabs, including soldier crabs, sentinel crabs, and sesarmid crabs, inhabit mangrove habitats (Kawaida et al. 2017). Consequently, fishes are able to feed on a variety of food items in mangrove habitats. Zoobenthivorous fishes, such as lutjanids, gerrids, apogonids, and haemulids, prey mainly upon gammaridean amphipods, crabs, shrimps, and polychaetes, whereas herbivorous fishes, such as pomacentrids, feed on macroalgae and filamentous algae (Nanjo et al. 2008). Piscivorous fishes, including Great Barracuda *Sphyraena barracuda* and Clouded Lizardfish *Saurida nebulosa* prey upon small fishes, whereas zooplanktivores (e.g., ptereleotrids) and detritivores (e.g., mugilids) feed mostly on copepods and detritus, respectively (Nanjo et al. 2008). Uniquely, some species such as Duncker's River Garfish *Zenarchopterus dunckeri* and Banded Srcherfish *Toxotes jaculatrix* prey mostly on terrestrial insects (Nanjo et al. 2008; Kanai et al. 2017). Such diverse and abundant food items may affect

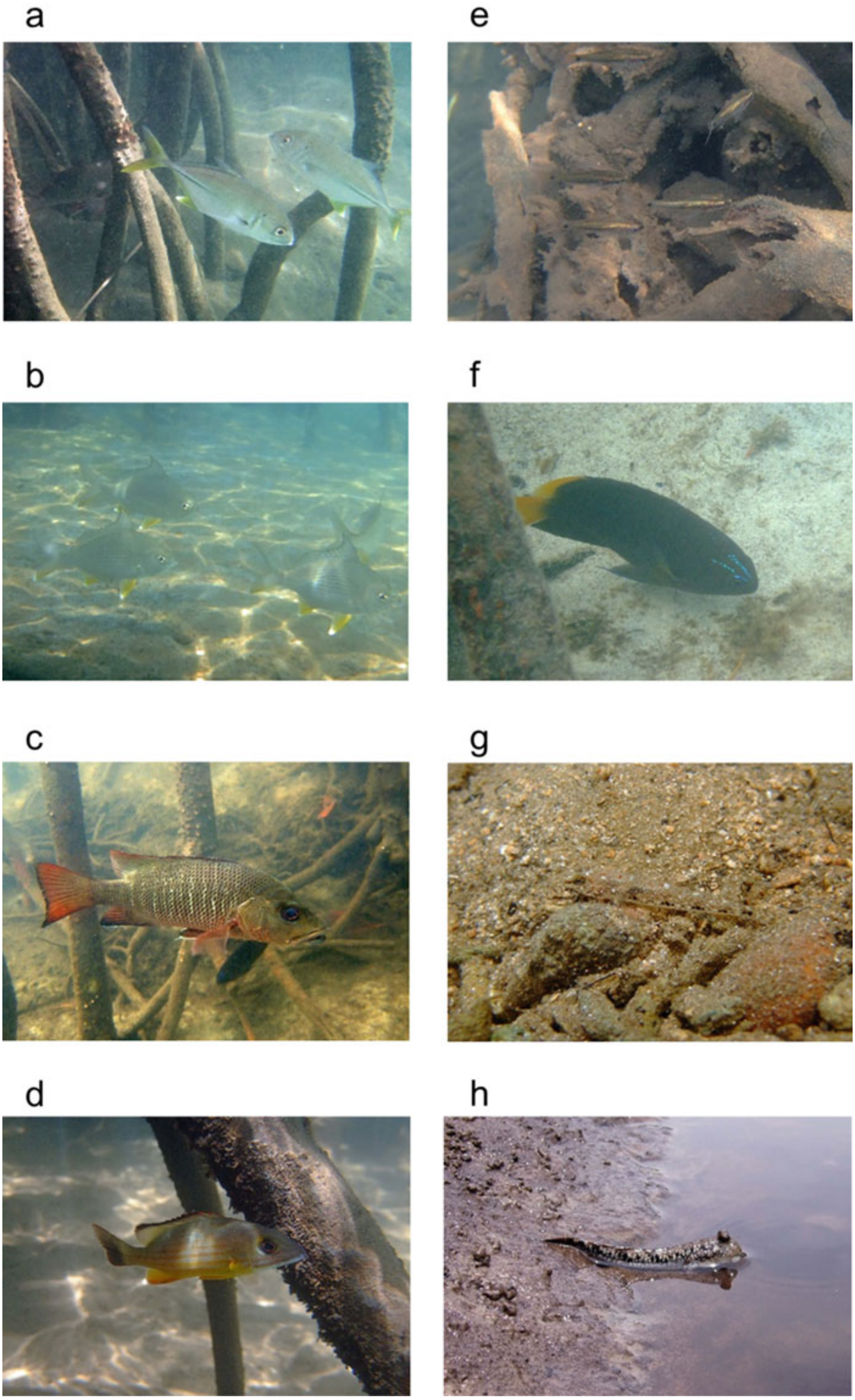

Fig. 21.3 Common fishes in mangrove estuaries in Japan, (**a**) Brassy Trevally *Caranx papuensis*, (**b**) Deep-bodied Mojarra *Gerres erythrourus*, (**c**) Mangrove Red Snapper *Lutjanus argentimaculatus*, (**d**) Blacktail Snapper *Lutjanus fulvus*, (**e**) Amboina Cardinalfish *Fibramia amboinensis*, (**f**) Brackish Damsel *Pomacentrus taeniometopon*, (**g**) Sand Goby *Favonigobius reichei*, (**h**) Barred Mudskipper *Periophthalmus argentilineatus*

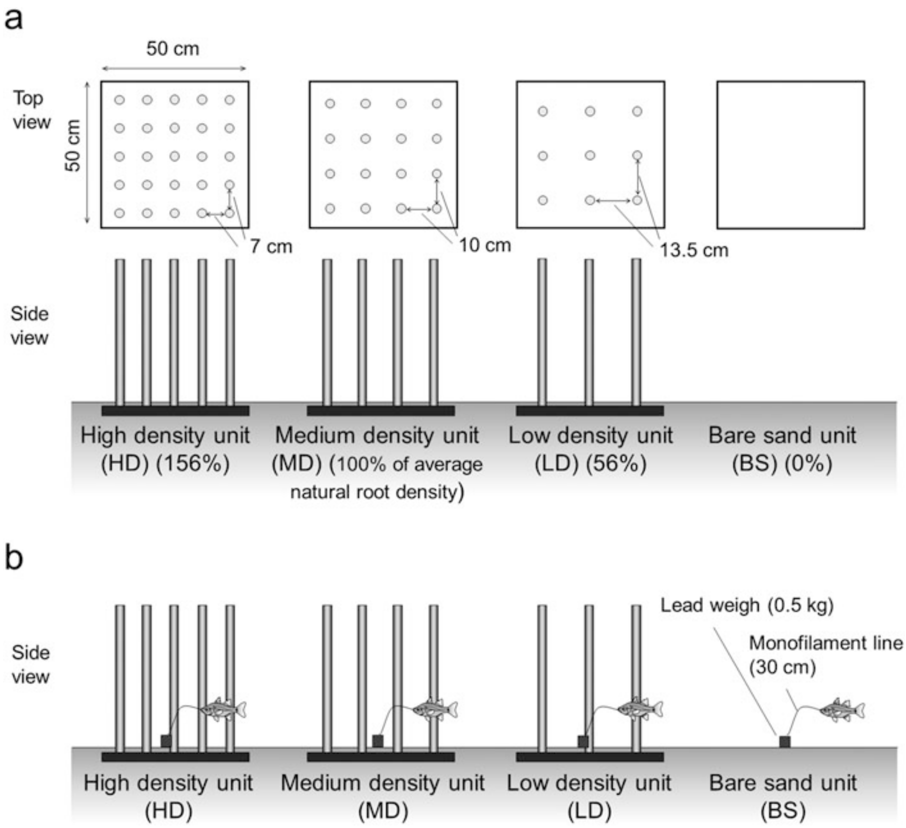

Fig. 21.4 (**a**) Designs of experimental unit treatments, (**b**) tethering experiment (modified from Nanjo et al. 2014b)

fish diversity and distribution. In fact, zoobenthivorous and herbivorous fishes inhabit mangrove root areas with more abundant food resources compared to unvegetated sandy areas with relatively few food resources, suggesting that greater food availability explained the greater fish species richness in mangrove habitats (Nanjo et al. 2014a).

The habitat structure of mangrove root systems may also provide potential refuges for small fishes, by reducing visibility for and limiting movements of large predators. This hypothesis has been inferred indirectly from fish distribution patterns, higher densities of small fishes, and lower densities of large predatory fishes in mangrove habitats (Robertson and Blaber 1992). However, recent studies have demonstrated such sheltering effects by unique field experiments, using artificial units mimicking mangrove root structures (Fig. 21.4). When artificial units with different levels of root densities were established in natural mangrove estuaries (Fig. 21.5), fishes responded strongly to the root structure complexity of the units, fish species richness and abundance being consistently higher in the units with roots than in those without roots (Fig. 21.6). With increasing root density, fish abundance increased considerably, and predation mortality rates, tested by tethering experiments (Fig. 21.6), decreased for small fishes which depended upon root structure in their anti-predator tactics (Nanjo et al. 2014b). On the other hand, some species use different anti-predator tactics, fleeing quickly (e.g., Deep-bodied Mojarra) or having cryptic body coloration similar to the substratum (e.g., Sand Goby) (Nanjo et al. 2011). Nevertheless, the sheltering effects against predators provided by root structure may be the significant factor explaining greater fish species richness/abundance in mangrove habitats.

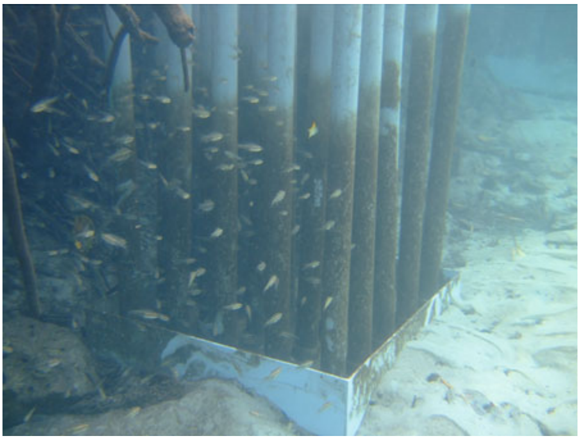

Fig. 21.5 An artificial experimental unit comprising a concrete base and PVC pipes, established in a mangrove estuary

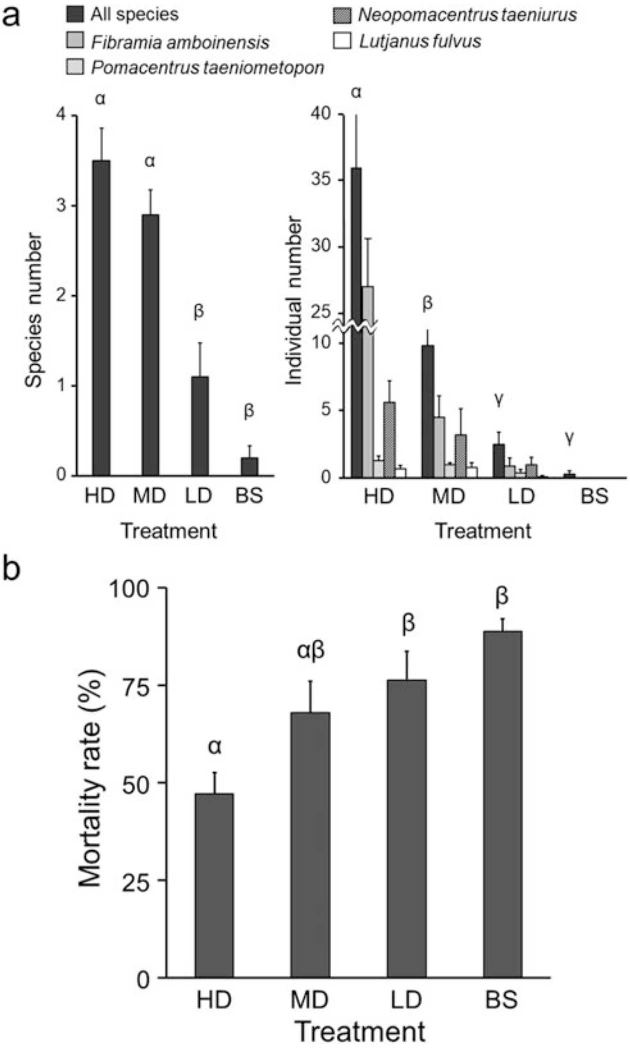

Fig. 21.6 (**a**) Mean total species and individual numbers, and mean individual numbers of four dominant mangrove estuary species (Amboina Cardinalfish *Fibramia amboinensis*, Blacktail Snapper *Lutjanus fulvus*, Freshwater Demoiselle *Neopomacentrus taeniurus,* and Brackish Damsel *Pomacentrus taeniometopon*) per replicate, occurring in artificial units ($n = 10$) of each treatment. (**b**) Mean predation mortality rates of *Fibramia amboinensis* per replicate ($n = 12$) in each treatment. Bars indicate standard error. *HD* high density unit, *MD* medium density unit, *LD* low density unit, *BS* bare sand unit. Statistical differences for all species data indicated by α, β, γ, and δ (post-hoc Games-Howell test, $p < 0.01$) (modified from Nanjo et al. 2014b)

Such habitat functions provided by mangrove roots, greater food availability and sheltering effects, may not be in conflict since the relative importance of each is species-specific. Furthermore, other factors, such as water temperature, salinity, turbidity, and water depth, can potentially affect fish distributions on broader scales (Blaber 2000). Further studies are needed to clarify biotic/abiotic factors and their interactive effects on fish diversity in mangrove habitats.

21.4 Connection Between Mangrove Habitats and Coral Reefs as Fish Habitats

Some species of coral reef fishes, typically belonging to Lutjanidae, Haemulidae, and Siganidae, utilize mangrove habitats as juveniles, subsequently migrating to coral reefs with growth. For example, muscle tissue in large juveniles of Blacktail Snapper *Lutjanus fulvus* in coral reefs had a carbon isotopic signature characteristic of a mangrove-based food web, suggesting migration of those individuals from mangrove habitats (Nakamura et al. 2008). Analyses of otolith microchemistry could also provide evidence of ontogenetic migration in lutjanid fishes. Adults of Dory Snapper *L. fulviflamma*, inhabiting offshore reefs, showed a depleted $\delta^{13}C$ signature in the juvenile otolith zone compared to that in the adult otolith zone, suggesting that almost all adults had passed through mangrove habitats as juveniles (Kimirei et al. 2013). For coral reef fishes of this type, mangrove habitats function as nurseries, the greater contribution per unit area to adult populations by juvenile habitats than other habitats (Beck et al. 2001) being essential for maintaining the populations along a mangrove-coral reef continuum. In the Caribbean region, the abundance of such nursery species of lutjanids and haemulids was much lower in coral reefs of islands lacking mangroves than of islands with mangroves (Nagelkerken et al. 2002), the adult populations in the latter increasing with increased areas of mangrove forests (Serafy et al. 2015). However, such nursery species have not always been abundant in fish assemblages in coastal ecosystems of southern Japan (Shibuno et al. 2008).

21.5 Mangrove Habitat Threats and Conservation

Mangroves have faced critical degradation and decline worldwide, at a rate of 0.66–2.1% per year (Valiela et al. 2001; FAO 2007), 3–5 times higher than the average rate of loss of land forests. An estimated 20% (3.6 million hectares) of mangroves were lost between 1980 and 2005 (FAO 2007), in the worst instance, ca. 50% of mangrove forests having been lost in Thailand prior to 1990 (Aksomkoae 1993). Mangrove forest loss has been due to conversion to other uses, including infrastructure, aquaculture (mainly shrimp farming), rice and salt production. Such land-use changes have resulted in ca. 62% of global mangrove losses since 2000 (Goldberg et al. 2020).

The loss of mangroves equates to loss of their habitat function, resulting in significant loss of fish diversity in mangrove ecosystems. Fish species richness and abundance have significantly decreased in mangrove-cleared areas compared to mangrove areas in several countries (Shinnaka et al. 2007; Mwandya et al. 2009), including Japan (Tatematsu et al. 2013). Pantallano et al. (2018) also found lower fish diversity and abundance in rivers without mangroves compared to those in mangrove-rich rivers in Okinawa and Ishigaki islands. Such negative effects have an impact not only on mangrove fishes, but also offshore fish populations, such as coral reef fishes, some of which are highly dependent upon mangrove habitats as nurseries (Mumby et al. 2004). The reasons for declining fish populations may be the decline in food resources and shelter provided by mangroves, many fishes, including juveniles, being unable to live in mangrove-cleared habitats.

Mangrove ecosystems provide several ecosystem functions for ecological sustainability (e.g., nutrient and organic matter cycling, and sediment control), environmental security (natural barriers against tsunami and floods, and reducing the impact of global warming by absorbing CO_2), and economic prosperity (supporting a not insignificant proportion of the global fish catch and providing wild seeds for aquaculture), as well as supporting diverse flora and fauna, including globally threatened species (Barbier et al. 2011). Therefore, mangrove forests should be conserved and managed in an effective manner. Marine protected areas have already been established in

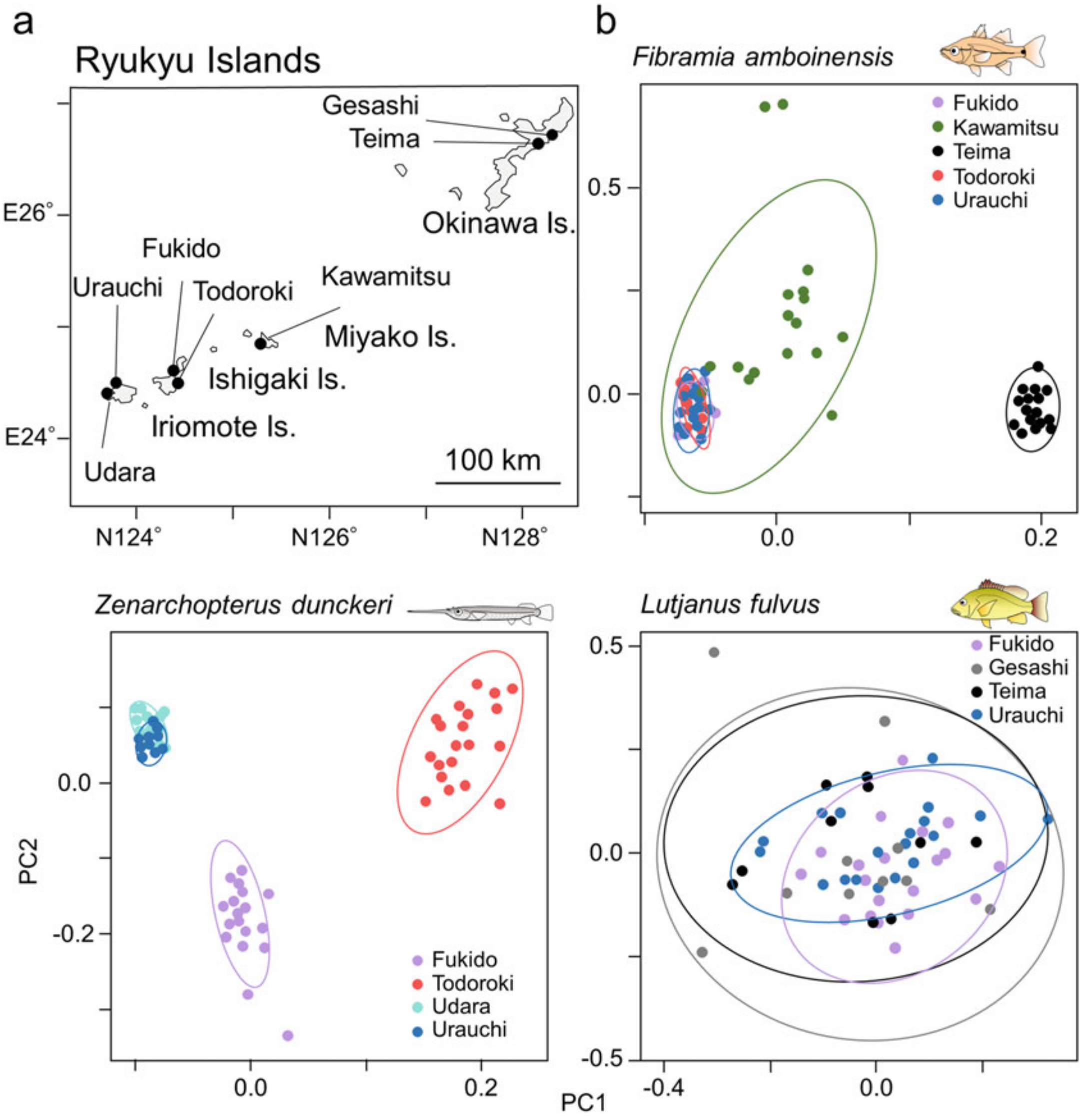

Fig. 21.7 (**a**) Map showing mangrove estuaries in the Ryukyu Islands, Japan. Black dots indicate sampling stations. (**b**) Plots of principal component analyses of genetic structures for Amboina Cardinalfish *Fibramia amboinensis*, Duncker's River Garfish *Zenarchopterus dunckeri*, and Blacktail Snapper *Lutjanus fulvus*. Plots represent samples; circles indicate confidence ellipsis of populations (modified from Hosoya et al. 2019)

several countries in order to conserve coastal ecosystems, with ca. 36% of global mangrove areas covered (Spalding et al. 2014). However, the effectiveness of mangrove conservation within the protected areas is highly variable, due to poorly designed schemes or lack of enforcement, and thus fails to prevent mangrove degradation and loss in some regions (Spalding et al. 2010). In Japan, many areas of mangrove forests have been included in National Parks and/or natural monuments.

For effective conservation of fish diversity in mangrove habitats, the habitat use patterns of mangrove fishes throughout their life histories must be considered. To maintain fish populations, estuaries with unrestricted connections to marine areas are essential for most marine species, but not for estuarine resident species, due to little or no larval input from marine areas and/or other estuaries. However, the latter species may be affected directly by estuarine habitat degradation throughout their life history stages, resulting in increased risk of localized extinction. Recently, Hosoya et al. (2019), who examined the genetic structure of mangrove fishes in the Ryukyu Islands by using random PCR-based genotyping-by-sequencing technology, reported that two resident fish species, Duncker's River Garfish *Zenarchopterus dunckeri* and Amboina Cardinalfish *Fibramia amboinensis*, showed different genetic structures among islands within an archipelago, whereas the marine species, Blacktail Snapper *Lutjanus fulvus* constituted a genetically homogeneous population with directional recent gene flow (Fig. 21.7).

Accordingly, an estuary dominated by estuarine resident fishes may be subject to conservation and management on a small spatial scale (i.e., for each estuary or island). On the other hand, for marine migrant fishes, maintaining connectivity between marine and estuarine areas, and avoiding crucial events in their recruitment season may be important, requiring a broader spatial scale. Such conservation efforts should be conducted globally with an optimal-spatial scale for the targeted regions, to maintain both species and genetic diversity of mangrove fishes.

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Coastal Fishes in Tidal Flats and Salt Marshes

22

Akihiko Koyama

Abstract

Tidal flats and salt marshes which are formed in the estuarine intertidal zones are important habitats for fishes worldwide. In this chapter, I outline the current status of tidal flats and salt marshes and their ecological roles for fishes, and review the conservation actions for intertidal fishes, focusing on the area of Japan. In the recent years, the economic value of these estuarine intertidal habitats and their conservation in Japan has been emphasized. However, due to urban development after 1945, intertidal environments such as tidal flats and salt marshes have disappeared significantly. Consequently, many species of fishes that mainly inhabit intertidal zones have become threatened. Compared to studies on fishes in tidal flats, few studies have focused on fishes in salt marshes in Japan. The intertidal habitats were seldom restored for the purpose of fish conservation in Japan, even though several studies have shown that these actions are effective. In the future, to conserve intertidal fishes, we should address the following four topics: (1) accumulation of ecological traits of these fishes, (2) restoration of large intertidal habitats, (3) adaptive management based on the results of long-term monitoring of mitigated/restored areas, and (4) identification of priority conservation areas managing fish diversity.

Keywords

Adaptive management · Biodiversity conservation · Estuary · Gobiidae · Intertidal flat · Indicator species · Salt marsh · Wando

22.1 Introduction

In general, salt marshes refer to vegetation areas in upper intertidal zones (Foster et al. 2013), and tidal flats refer to sedimentary areas between salt marshes and subtidal zones (Gao 2019). Murray et al. (2019) estimated that there are at least 127,921 km^2 of intertidal flats with gravelly, sandy, or muddy sediments in the world, and Mcowen et al. (2017) mapped the distribution of 5,495,089 ha of salt marshes around the world. The need for conservation of these intertidal habitats is emphasized because of their fruitful ecosystem services; however, these habitats have decreased and deteriorated due to anthropogenic impacts, including reclamation, land use changes, overfishing, water pollution, alien species invasion, and climate change (Sato 2010; Barbier et al. 2011; Foster et al. 2013; Murray et al. 2019).

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Estuarine habitats, including tidal flats and salt marshes, are utilized by fishes for a variety of purposes and are an important environment that supports fish diversity (Potter et al. 2015; Whitfield 2017). Ichthyofauna in intertidal habitats differs between high and low tides; in particular, salt marshes are formed in the upper intertidal zones, which is why fish can enter these habitats only for a short time (Whitfield 2017). Nevertheless, tidal flats and salt marshes are more productive than subtidal zones and are important nursery and feeding grounds for fishes (França et al. 2009; Mendonça et al. 2019). Small fishes and juveniles utilize these intertidal habitats to avoid predation by large fishes and crustaceans (Veiga et al. 2006). Moreover, adults of several fish species spawn in intertidal habitats, even though these intertidal habitats are exposed to air for a certain period of time every day (Dando 1984).

Therefore, the conservation of tidal flats and salt marshes is an important issue for managing fish diversity and sustainable resources. This chapter explains the current status of intertidal habitats in Japan and the threats to fishes inhabiting these habitats. Furthermore, the chapter reviews research on the mitigation and restoration of intertidal habitats for fish conservation in Japan, and finally, presents the studies on selection of prioritized conservation areas. The aim of this chapter is to consider what is required in the future for the conservation of fish diversity in intertidal habitats in Japan.

22.2 Current Status of Tidal Flats and Salt Marshes in Japan

In Japan, areas inhabitable by people are small in size; consequently, the lowlands adjacent to estuaries have historically used and developed (Kusuda and Yamamoto 2008). Before 1945, 82,621 ha of tidal flats existed in Japan, but this number had decreased to 49,380 ha by 1996 (Ministry of the Environment 1980, 1994, 1998) (Fig. 22.1). The major cause of declining tidal flats during the period from before 1945 to the 1970s is land reclamation, being the cause of 93.2% of the total tidal flat decline (Ministry of the Environment 1980). Since the 1950s, advances in concrete technology have led to an increase in intensive river management projects, such as embankments, weirs, estuarine barrages, and training walls, as well as coastal protection projects against coastal erosion and tidal waves (Takahasi and Uitto 2004). It has been speculated that salt marshes are in a crisis situation because of the concrete revetment of Japanese rivers and coastlines (Kimura and Kimura 1999; Horinouchi et al. 2008; Yuhara et al. 2016), but the degree of salt marsh loss has not been investigated.

In the recent years, large intertidal habitats have not been modified, but small-scale modifications have been carried out with the goal of river improvement for disaster prevention (Koyama et al. 2019b). Worldwide, intertidal habitats are valued as green infrastructures with wave attenuation functions (Foster et al. 2013); however, in Japan, they are, in some instances, a source of concern as they can increase the risk of disaster. For example, in Japan's first-class rivers, expanded intertidal habitats prevent river flow and increase the risk of flooding. Consequently, sandbars and supratidal zones, including salt marshes, are dredged to reduce this risk (Nakajima et al. 2008; Nagahama et al. 2015).

Marine species diversity in Japanese waters is among the highest in the world (Fujikura et al. 2010), and the ecosystem services of these tidal flats and salt marshes are indispensable for sustainable development. Ministry of the Environment (2014) estimated that the current ecosystem services of tidal flats in Japan have an economic value of JPY 12.42 million/hectare/year, and the entire tidal flat has a value of JPY 610 billion/year. Recent research suggested the possibility that the actual economic value of these areas is more than five times higher than this estimate (Okada et al. 2020). Japan has the 35th largest area of intertidal tidal flats in the world (Murray et al. 2019), and the benefits of their ecosystem services are globally important. Unfortunately, the economic value of ecosystem services related to salt marshes has not been evaluated in Japan. Many studies have documented the importance of salt marshes for biodiversity (e.g., Kimura and

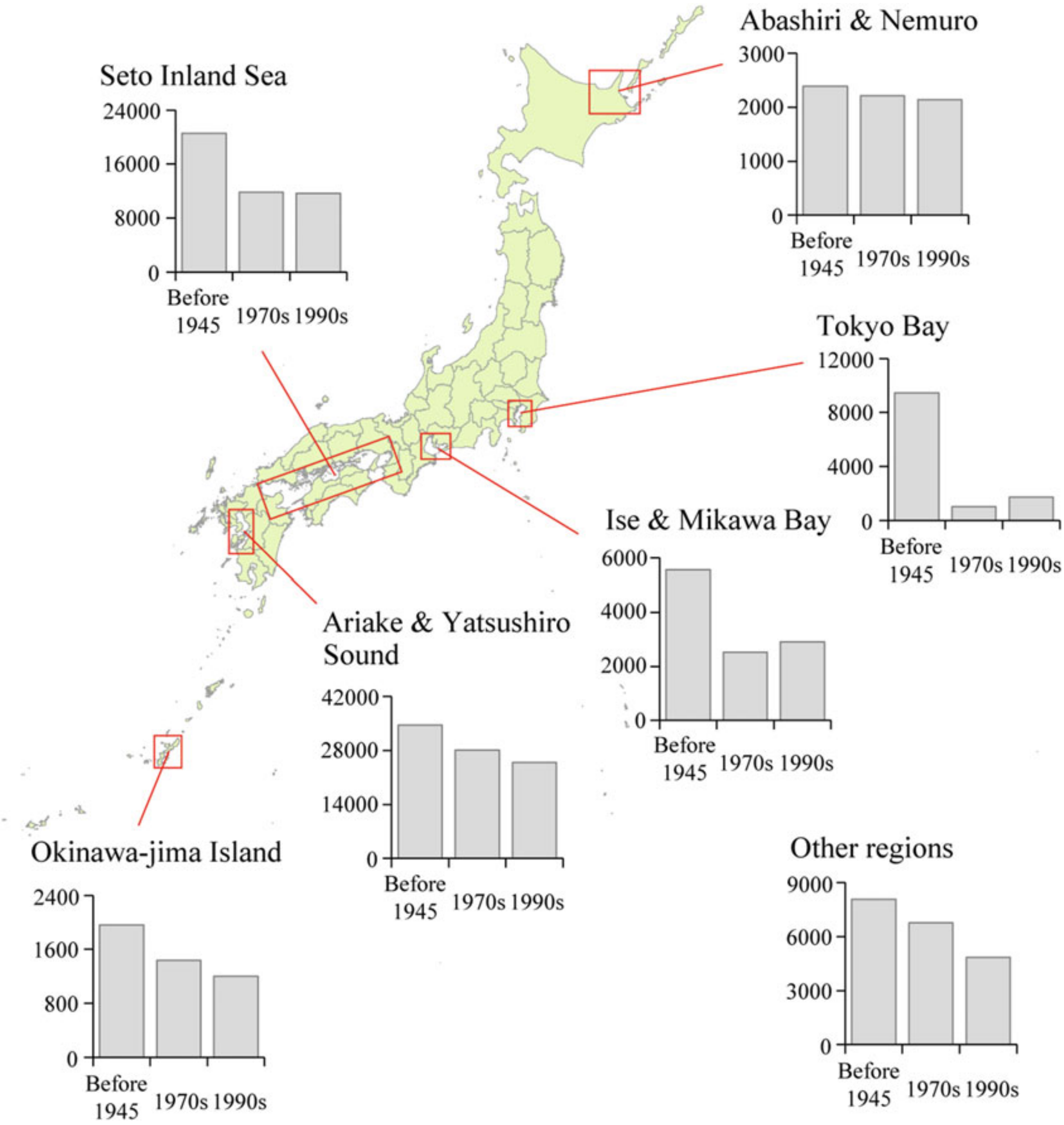

Fig. 22.1 Spatial distribution and decrease in the areas of tidal flats of Japan from before 1945 to the 1990s. The vertical axis of the graphs indicates the area of the tidal flats (ha). The areas in the period before 1945 and 1970s were obtained from the Ministry of the Environment (1980), and those in the 1990s were obtained from the Ministry of the Environment (1994, 1998)

Kimura 1999; Yuhara et al. 2016; Kaneko et al. 2019a), and their distribution, area, and economic value should be evaluated in the future.

In Japan, small intertidal habitats in rivers play an important role in supporting estuarine biodiversity. Japan is composed of small, mountainous islands. Generally, Japanese rivers are short and steep, and the tidal areas within these rivers are short. As a result, tidal flats and salt marshes develop on the coasts around rivers that flow into the inner bay, whereas in the inner parts of rivers, these habitat areas are relatively small (Kimura and Kimura 1999). Nevertheless, a wide variety of estuarine shellfishes and fishes inhabit tidal flats and salt marshes of these rivers, and their species composition depends on the gradient of physicochemical factors, such as salinity, relative elevation to tidal datum, and sediment grain size (Kobayashi 2000; Yamashita et al. 2002; Yuhara et al. 2016; Koyama et al. 2019a). Moreover, these riverine intertidal habitats are subdivided according to microenvironments, such as hard substrates, decayed wood, and burrows of benthic invertebrates (Kimura and Kimura 1999; Inui et al. 2018).

Figure 22.2 shows the four types of intertidal habitats in the temperate estuaries of Japan. Gravel tidal flats (Fig. 22.2a) tend to form in riverine areas, that is, the upper estuaries (Inui and Koyama 2014; Koyama et al. 2019a). Fine sediments tend to be deposited in the lower estuaries, where the river widens and flow velocity decreases. Thus, sand and mud flats are relatively larger than gravel flats (Fig. 22.2b, c). Various salt-tolerant plants are found in the upper intertidal marshes; in temperate rivers and estuarine lakes, salt marshes are mainly composed of reed *Phragmites australis* (see Kon et al. 2020). As explained earlier, most estuaries in the rivers of Japan have been artificially modified, leaving little of the natural intertidal habitat landscape. For example, in the river shown in Fig. 22.2b, sand flats are still widely present, but the upper intertidal zone (that is, salt marshes) has almost disappeared because of the construction of roads.

22.3 Ecological Role of Intertidal Habitats for Fishes

Several studies have shown that Japanese tidal flats in temperate and subtropical zones play an important ecological role as habitats for resident and transient fishes. A total of 26 species of fishes were collected from the temperate mouth of the Tama-gawa River in Tokyo Bay (Kanou et al. 2000), and approximately ten species were collected from tidal pools on the flats in this area (Uchida et al. 2008; Kanou et al. 2018). Kunishima and Tachihara (2020) collected 28 and 49 species of fishes from the subtropical estuarine tidal pools in the Shioya and Sashiki tidal flats on Okinawa-jima Island, respectively. Several species of goby, such as *Pseudogobius* and *Mugilogobius* species, appear in tidal pools of temperate and subtropical zones in all seasons (Okazaki et al. 2012; Kunishima and Tachihara 2020), whereas *Acanthogobius* species utilize tidal flats during only their growth season, after which they migrate to their spawning grounds (Okazaki et al. 2012; Kunishima et al. 2019). Fish communities differ among tidal flats even in the same ecological region, suggesting that habitat heterogeneity and/or anthropogenic impacts in each tidal flat affect the composition of fish communities (Kanou et al. 2000; Kunishima and Tachihara 2020). The prey for fishes is very diverse around the tidal flats, and the feeding groups of fish larvae and juveniles can be classified into six groups: fish feeders, detritus feeders, zooplankton feeders, small benthic and epiphytic crustacean feeders, polychaete feeders, and mollusks feeders (Kanou et al. 2004).

Small species of estuarine fishes utilize tidal flats as spawning grounds. Mudskippers, such as *Boleophthalmus pectinirostris* and *Periophthalmus modestus*, burrow the tidal flats to make their spawning nests (Takita and Ishimatsu 2015). Moreover, benthic invertebrates support the reproduction of these fishes. For example, *Trachidermus fasciatus* and *Tridentiger* species use shells of oysters and fun-mussels scattered on tidal flats as spawning substrates (Tsukahara 1952; Dôtu 1957). *Eutaeniichthys gilli* and several *Gymnogobius* species spawn inside burrows of mud shrimps and ghost shrimps that inhabit tidal flats covered with fine sediment (Dôtu 1955; Koyama et al. 2017; Henmi et al. 2018). The males of these fishes care for their eggs to prevent silting and poorly oxygenating the eggs (Dando 1984).

However, few studies have focused on fishes in salt marshes of Japan, and their survey areas are limited to Lake Shinji and Lake Hinuma which are temperate estuarine lakes (Kon et al. 2020). The composition of fish species around the salt marshes and their creeks in both of these lakes mostly includes species of Gobiidae (Horinouchi

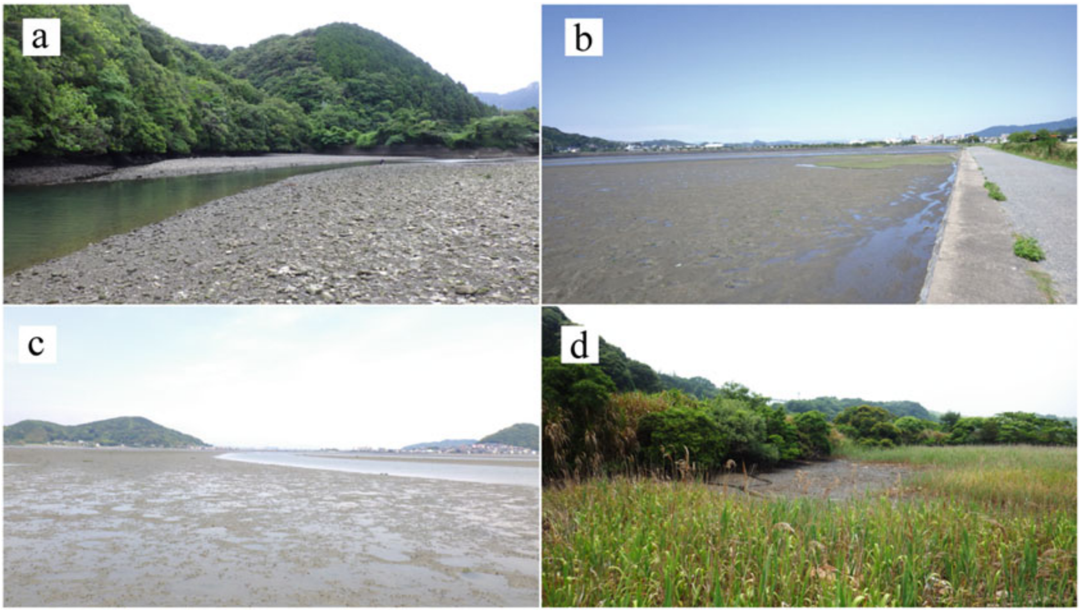

Fig. 22.2 Landscapes of temperate intertidal habitats in Japan, (**a**) gravel tidal flats, (**b**) sand tidal flats, (**c**) mud flats, and (**d**) salt marshes. (The photographs were taken during low tide in early summer)

et al. 2008; Kaneko et al. 2019a). Biotic and abiotic factors, such as dissolved oxygen, water depth, silt and clay content, and prey differ between the upper marshes and the edge of the salt marshes in Lake Hinuma, and these factors affect the fish communities in each area (Kaneko et al. 2019a). In particular, the upper marsh is relatively shallower than the lower marsh and functions as a fish refuge; for example, *Oryzias latipes* hides here to avoid predation (Kaneko et al. 2019b). In both Lake Shinji and Lake Hinuma, fishes mainly feed on mysids, copepods, and gammaridean amphipods around the salt marshes (Horinouchi et al. 2008; Kaneko et al. 2016).

22.4 Threats for Fishes in Tidal Flats and Saltmarshes

Ecological information of 201 species of fishes threatened and near threatened was described by the Red Data Book of Japan (Ministry of the Environment 2015), and more than half of these species utilize estuaries temporarily or permanently depending on their life history. The number of fish species that inhabit tidal flats and/or salt marshes in the book is 22 (Table 22.1). However, although not specified in this book, several fishes, such as *Anguilla japonica* and *Trachidermus fasciatus*, utilize intertidal habitats (Sato 2010; Takeshita and Onikura 2011). Thus, it should be noted that a higher number of endangered fish species than the 22 species shown in the table need tidal flats and salt marshes to complete their life cycles.

One of the major threats for these fishes is the direct modification of intertidal habitats as a consequence of their destruction or changes in sediment conditions (Table 22.1). For example, in Isahaya Bay in Ariake Sound, mud flats of 29 km^2 were lost in 1997 because of a reclamation project (Sato 2010), and the local populations of *Boleophthalmus pectinirostris* and *T. fasciatus* in this area have become extinct (Takegaki et al. 2005; Takeshita and Onikura 2011). Populations of *Sillago parvisquamis* in Tokyo Bay and Ise Bay may have become locally extinct because of the decreasing tidal flats which this species inhabited (Shigeta and Usuki 2011).

Table 22.1 Threats for 22 species inhabiting tidal flats and salt marshes. The information including species names and categories was obtained from the Ministry of the Environment (2015)

Category	Species name	Habitat			Threats
		Tidal flats	Salt marshes	Others	
CR	*Sillago parvisquamis*	+			HLM, SI (ns)
	Scartelaos histophorus	+			HLM, WSP, Of, SI (ns), SI (es)
EN	*Boleophthalmus pectinirostris*	+			HLM, WSP, Of
	Taenioides cirratus[a]	+			HLM
	Gymnogobius cylindricus	+			HLM, WSP, Of[b]
VU	*Oryzias sakaizumii*		+	+	HLM, WSP, Of, SI (es)
	Oryzias latipes		+	+	HLM, WSP, Of, SI (es)
	Apocryptodon punctatus	+			HLM, WSP
	Brachyamblyopus anotus	+			HLM
	Odontamblyopus lacepedii	+		+	HLM, WSP, Of
	Taenioides limicola	+			HLM
	Gymnogobius macrognathos	+		+	HLM
	Gymnogobius uchidai	+		+	HLM, WSP
	Acanthogobius hasta	+		+	HLM, Of
	Acanthogobius insularis	+		+	HLM, WSP
	Pseudogobius masago	+	+		HLM
	Acentrogobius viridipunctatus	+			HLM, WSP
NT	*Periophthalmus modestus*	+	+		HLM
	Eutaeniichthys gilli[c]	+		+	HLM, WSP
	Silhouettea dotui	+		+	HLM
	Tridentiger nudicervicus	+		+	HLM, WSP
	Tridentiger barbatus	+			HLM

CR critically endangered, *EN* endangered, *VU* vulnerable, *NT* near threatened, *HLM* habitat loss and/or modification, *WSP* water and/or sediment pollution, *Of* overfishing, *SI (ns)* species interactions with native species, *SI (es)* species interactions with exotic species

[a] *Taenioides cirratus* includes at least four cryptic species in Japan (Kurita and Yoshino 2012)

[b] Overfishing of mud shrimp whose burrows are utilized as a habitat for *Gymnogobius cylindricus*

[c] *Eutaeniichthys gilli* includes at least two cryptic species in Japan (Mukai et al. 2003)

Odontamblyopus lacepedii and *Acanthogobius hasta* may be negatively impacted by the changes in sediment conditions, which occurred as a consequence of the development of fishery grounds for commercial clams (Ministry of the Environment 2015).

Construction of estuarine barrages not only directly destroys the upper estuary, but also hinders the migration of diadromous fishes (Russell et al. 1998). These fishes are highly diverse on small islands, including Japan (McDowall 2010), and in Japan, habitat fragmentation by estuarine barrages and dams has a negative impact on these fishes (Ministry of the Environment 2015). Moreover, these artificial barriers may block the supply of sediment from upstream to estuaries, thereby indirectly altering the intertidal habitats used by endangered gobies (Inui and Koyama 2014).

Not only abiotic but also biotic factors are influenced by anthropogenic impacts, which indirectly threaten fishes. For example, Takeshita and Onikura (2011) reported that the density of oyster shells that can be used by *T. fasciatus* for spawning was reduced because the oysters at the spawning grounds of this sculpin were transferred to fishery farms by fishermen. In Japan, *Scartelaos histophorus* is distributed only in several mud flats on Okinawa-jima Island, but one of the mud flats has decreased due to the overgrowth of artificially introduced mangroves (Hosoya 2014; Hiranaka et al. 2019). Furthermore, as this species is a semi-terrestrial goby, predation pressure by waterfowl may result in the decrease in the population of this species (Ministry of the Environment 2015).

Overfishing and pollution of water and sediment also have a negative influence on fishes in intertidal habitats (Table 22.1), but these influences have not been quantitatively assessed to date. It has been empirically recognized that the populations of these endangered and near threatened fishes have decreased, but unfortunately, few studies have quantitatively assessed these populations. One of the reasons is that most of the fishes that are residents of the intertidal habitats are small gobies and are not used commercially. Another reason is that vast mud flats are difficult to traverse during low tides, which makes it impossible to adequately assess the population size of fishes in these areas (e.g., Takegaki et al. 2005).

Knowledge of ecological traits is necessary for determining the role of a species in an ecosystem and its tolerance to environmental changes, including anthropogenic impacts (Galán-Acedo et al. 2019). Since 2000, ecological traits of threatened fishes inhabiting intertidal habitats in Japan, including life history (Saimaru et al. 2018; Kunishima et al. 2019, 2021), genetic pattern (Kanemori et al. 2006; Mukai and Sugimoto 2006), distribution (Inui et al. 2014; Murase et al. 2017), habitat (Maeda et al. 2011; Kunishima et al. 2014; Henmi et al. 2014; Koyama et al. 2016; Inui et al. 2018), prey (Kanou et al. 2004), and reproduction (Inui et al. 2011; Hasegawa and Shoji 2017; Koyama et al. 2017; Henmi et al. 2018) have been identified. Some ecological traits are still lacking, and further investigation is needed to address this gap.

22.5 Conservation

22.5.1 Mitigation and Restoration

Since the Basic Environment Law and the Law for the Promotion of Natural Restoration were enacted in 1993 and 2003, respectively, conservation actions for estuarine organisms inhabiting intertidal zones and mitigation and restoration of these habitats have been attempted in various regions of Japan (Kusuda and Yamamoto 2008; Kuwae 2016). A total of 157.4 ha of artificial tidal flats existed in the 1990s in Japan (Ministry of the Environment 1998). In many cases, artificial sand flats have been constructed for resource management of commercial clams, and few artificial tidal flats have been constructed for fish conservation (Kuwae 2016). In other words, mud flat restoration has rarely been carried out because these habitats are not suitable for commercial clam cultivation. The effectiveness of these artificial habitats has mainly been evaluated using benthic invertebrates (Kuwae 2016). Therefore, in Japan, very few studies have evaluated the effects of artificial intertidal habitats on fishes. In this section, I review Japanese articles on mitigation, restoration, and small-scale conservation activities aimed at fish conservation.

22.5.1.1 Intertidal Flats

Mitigation and restoration of mud flats aimed at conserving *Scartelaos histophorus* is one of the few cases that target a fish species. Since 1990, in Nakagusuku Bay, Okinawa Prefecture, construction of artificial tidal flats, prohibition of coastal development during its breeding season, and release of artificially hatched juveniles have been carried with the aim of conserving this species (Hosoya 2014). Because of these conservation actions, an increase in the population of this species was observed in the northern part of the bay from 1995 to 2000. However, the population has been declining since 2003 (Hiranaka et al. 2019). Furusawa et al. (2009) estimated the habitable areas of this species in an artificial tidal flat constructed in the northern part of the bay based on the physicochemical environment, mud thickness, grain size, and concentration of NH_4-N. Their prediction model showed that the habitable area in the artificial tidal flat was limited because of mismatches in sediment thickness and/or grain size. Furthermore, the authors emphasized the reduction in habitat by introduced mangroves. In this area, mangroves were exterminated on approximately 10 ha from fiscal year 2016–2017 with the aim of expanding the habitat of *S. histophorus* (see Hiranaka et al.

2019). Monitoring of *S. histophorus* is ongoing in Nakagusuku Bay.

For the conservation of *Periophthalmus modestus*, an artificial tidal flat with a length of 460 m and a width of 12.5 m (i.e., approximately 0.6 ha) was constructed in 1992 in the drainage channel of the Edo-gawa River which flows through Tokyo Bay. Moreover, the revetment of the artificial tidal flats was covered with muddy sediment, and reeds were transplanted there. All individuals of *P. modestus* in the area were captured before the construction of the artificial tidal flat and released afterwards. Monitoring surveys from 1991 to 2001 evaluated the density of *P. modestus* spawning nests and showed that after 1996, the density in the artificial tidal flat increased to the same level as that in natural tidal flats (Sakurai et al. 2000, 2002). Furthermore, erosion of mud-covered revetments was observed within 2 years of construction. Sakurai et al. (2002) considered that the fine sediment that flowed out due to erosion contributed to the maintenance of the spawning ground of this species.

In the period from 2002 to 2004, 1.0 ha of tidal flat, 1.2 ha of sandy beach, and 4.6 ha of shallow subtidal areas were constructed next to the Keihin Canal in Tokyo Bay. The mitigation was aimed at securing green spaces, enhancing urban disaster prevention, reinforcing water amenities, and improving the water environment (Takeyama et al. 2013). The artificial sandy beach and tidal flat were expanded by adding sediment in 2007 and 2011, respectively. Monitoring of physicochemical environments showed that the fine sediment of the artificial tidal flat decreased from 2002 to 2004 (Takeyama et al. 2018). The monitoring of fishes and benthic macroinvertebrates from 2012 to 2013 recorded about 13 fish species, including the endangered species *Pseudogobius masago*, at the tidal pools and small channels of the artificial tidal flat (Takeyama et al. 2013). In particular, *P. masago*, which was only observed in tidal pools, was collected throughout the year. *Acanthogobius flavimanus* was found in the tide pools and the shallow water zone, but during the growth season, the individuals in the former were significantly smaller than those in later areas. These findings showed that the artificial tidal flat functions as a nursery for several species of goby.

In the Ibi-gawa River, which flows into Ise Bay, a restoration project was planned in 1990 in the section 0–5 km upstream from the river mouth. From 1994 to 1995, a cumulative total of 25,000 m^3 of sediment was installed 1.3–2.5 km from the river mouth (Suzuki et al. 2003). As part of this project, artificial tidal flats were constructed using natural power sources, including wind and waves. Monitoring surveys conducted in 1995, 1997, 1998, and 2000 showed that tidal flat topography was intricately changed for about 3 years after construction (Suzuki et al. 2003). The effectiveness of the tidal flats was evaluated by monitoring benthic invertebrates and fishes, mainly goby species and *Kareius bicoloratus*, in the period from 1994 to 2000. As a result, more than ten species of fishes were recorded, and the authors revealed that the biomass of *K. bicoloratus* was the highest, especially in February each year. Further restoration of tidal flats and salt marshes has been actively conducted at the mouth of the Ibi-gawa River since 2003 (Asano et al. 2012).

22.5.1.2 Wando Pools

In Japan, stagnant water areas along riverbanks that are partially connected to the main stream are often called “wando” (Fig. 22.3). In 2001, a sandbar including a wando located 4 km upstream of the Kita-gawa River mouth, which flows through Miyazaki Prefecture, was dredged in order to reduce the risk of flooding. To mitigate the dredging, the sandbar upstream of the old wand was excavated at a length of 600 m and a frontage of 50 m, and an artificial wando pool was constructed. Nakajima et al. (2008) conducted fish and benthic invertebrate surveys from 2001 to 2006 and identified 72 species of fishes in this area. Moreover, the number of fish species collected in the artificial wando during the survey period was similar to that collected in the old wando from 1998 to 2000; therefore, the authors suggested that the artificial wando was successfully used as a fish habitat similar to the old wando. Although fishes were mainly collected in the subtidal zones of the artificial wando, the

authors considered that the tidal flats and seagrass beds that formed in the area after the construction of the artificial wando might contribute to increased fish diversity.

In the Naka-gawa River, which flows through Tokushima Prefecture, at wando of approximately 2.8 ha, located 2 km upstream from the river mouth, was modified by approximately 24% from 2013 to 2014 by the countermeasure project for earthquakes and tsunamis. As several endangered microbenthic species inhabited this wando, including gobies that preferred muddy intertidal zones, two artificial intertidal habitats, namely mud flats and salt marshes, were constructed by excavating the dried riverbeds in the wando in 2013. From 2013 to 2017, Koyama et al. (2019b) monitored the two artificial habitats and assessed the mitigation using brachyuran crabs and gobies as indicator species. In the year after the construction of the two artificial habitats, flooding with an average daily flow of approximately 5000 m^3/s occurred, resulting in the development of coarse sediment conditions in the wando, including the mitigation areas. Based on adaptive management for environmental modification by floods, dredged sediment from a neighboring river mouth was used to reconstruct a muddy intertidal habitat in the mitigation area. Furthermore, reeds were transplanted to one of the two artificial habitats. The authors identified more than 25 goby species in the wando, including eight threatened and near threatened species listed in the Ministry of the Environment (2015). They showed that at the lower intertidal and subtidal zones in the mitigation areas, it took more than 4 years for the goby fauna to develop to a similar extent to that before modification.

These two mitigation projects in the Kita-gawa River and the Naka-gawa River revealed high fish diversity in the estuarine wando, indicating that the wandos are important water areas for estuarine fish conservation in Japan. The authors of each study also emphasized that the planning of mitigation actions should consider the effects of flooding in order to maintain artificial riverine intertidal habitats. Nakajima et al. (2008) emphasized the need for continuous reinforcement to maintain artificial habitats. Koyama et al. (2019b) proposed the construction of restoration habitats at multiple locations to reduce the risk of habitat loss due to flooding.

22.5.1.3 Spawning Grounds

In the Ongagawa River, which flows through the Sea of Japan in Fukuoka Prefecture, a new fishway was constructed in 2013 to mitigate the inhibition of fish migration and the loss of upper estuaries because of the estuarine barrage, which has been in operation since the 1980s (Fig. 22.4a–c). Unlike the previous concrete fishway, the new fishway is meandering with a gentle slope of 1/200 and an extension of 300 m. Boulders and cobbles of various sizes were placed in the fishway to vary the diversity of flow velocity and water depth. Koyama et al. (2018) surveyed the new fishway every month for 1 year from June 2013 and found that a total of six species of gobies use boulders and cobbles in the fishway as spawning substrates. Furthermore, using salinity loggers, they revealed that a salinity gradient was formed in the new fishway in longitudinal direction. In particular, *Leucopsarion petersii*, which is a threatened anadromous species in Japan (Ministry of the Environment 2015), spawned in the places where salinity was detected for a period of only a few hours during 2 weeks (Fig. 22.4d). Another study revealed that this species spawned in similar salinity environments (Hasegawa and Shoji 2017). Therefore, Koyama et al. (2018) suggested that the newly constructed fishway plays a role in the spawning of several goby species, including *L. petersii*, in low-salinity habitats. Today, the Ongagawa River Fishway Park is attracting attention not only as a habitat for fishes but also as a place for environmental education (Ministry of Land, Infrastructure, Transport and Tourism 2019).

Scientists and citizens manage spawning grounds for threatened fishes by improving spawning substrates through small-scale conservation activities without public work. For the conservation of *Trachidermus fasciatus*, 40 bamboo poles were set as artificial spawning substrates on two tidal flats on the west coast of the Ariake Sound in 2000 (Takeshita and Onikura 2009). In 2002, because of the complete disappearance of the oyster shells, the bamboo poles were utilized by the target species for spawning, and the utilization rates of the artificial substrates ranged from 13% to 45% between 2002 and 2008 (Takeshita and Onikura 2011). At the mouth of the Muromi-gawa River, which flows into Hakata Bay in Fukuoka Prefecture, spawning grounds of *L. petersii* have been conserved since 1984 because this species is commercially important. Iyooka et al. (2013) modeled suitable spawning habitats for this species using several physical environmental factors and showed that riverbeds with a low rate of sand and small thickness of fine sediment are highly suitable for its spawning. In 2012, the authors removed fine sediment from the riverbeds using hoes or shovels at four locations in the Muromi-gawa River mouth to expose boulders and cobbles, which are the spawning substrates for this species. As a result, spawning of this species was observed in these conservation areas, after which the conservation action for improving the riverbeds was regularly performed.

This type of small-scale mitigations is reactive and cannot address the underlying threats to fish species. The density of natural spawning substrates for *T. fasciatus*, namely, shells of oysters and fun-mussels, has to be restored at their spawning grounds because these bivalves were decreased by anthropogenic impacts. Moreover, the maintenance of artificial spawning substrates requires time and effort because sessile macroinvertebrates attached with the artificial substrates should be removed annually (Takeshita and Onikura 2011). Iyooka et al. (2013) also noted that sustainable use of spawning grounds for *L. petersii* is difficult because riverbeds constantly need to be maintained. The authors emphasized that the recovery of sediment transportation to the Muromi-gawa River mouth is necessary to maintain the spawning grounds of *L. petersii*; thus, the relocation, elimination, or consolidation of the estuarine barrage is needed (Iyooka et al. 2013).

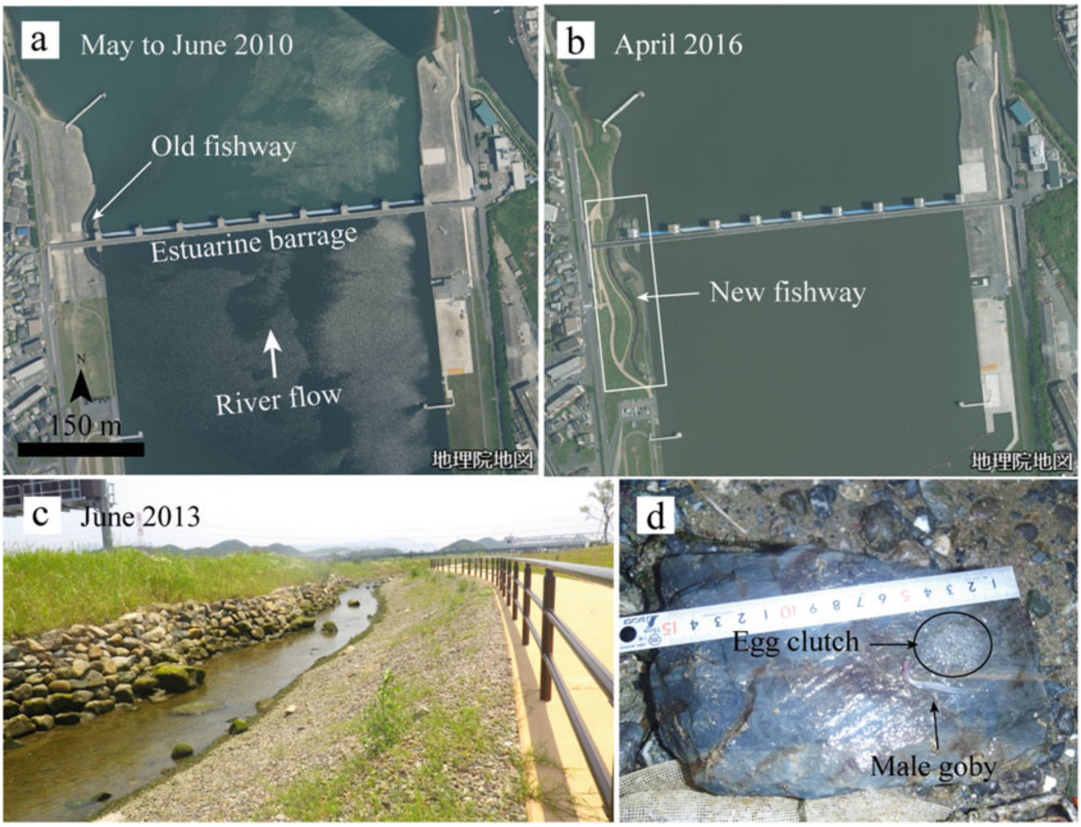

Fig. 22.4 Aerial photographs by Geospatial Information Authority of Japan at the Onga-gawa River mouth (**a**: before new fishway construction and **b**: after construction), (**c**) landscape of the fishway at low tide during spring tide, and (**d**) spawning of *Leucopsarion petersii*. The circle in (**d**) indicates an egg clutch attached with a boulder in which the goby spawned

22.5.2 Selecting Conservation Areas Using Indicator Species

In addition to the construction of artificial habitats, the selection of priority conservation intertidal areas is important for managing fish diversity. In general, estuarine fishes respond to environmental changes associated with anthropogenic impacts and are therefore effective environmental indicators for assessing these impacts (Whitfield and Elliott 2002). However, as fishes with various lifestyle and lifecycle appear in estuaries, a lot of effort and money is required to accurately evaluate the status of all estuarine fishes. Moreover, the ecological role of intertidal habitats among regions may be misevaluated by transient and accidental species (Kunishima and Tachihara 2020). Thus, it is necessary to identify the most effective indicator fish species that can be used to select priority conservation areas.

In recent years, gobies have been recognized as effective indicator species for evaluation of intertidal environmental health (Rudneva et al. 2016) and conservation and restoration of estuarine environments (Murase et al. 2017; Harding et al. 2020). Gobies are common resident benthic fishes found in estuarine habitats worldwide. Their distribution depends on the gradient of biotic and abiotic factors in intertidal zones (Polgar et al. 2010; Yokoo et al. 2012; Inui et al. 2018). In particular, gobies have high fidelity to the spawning substrate (Harding et al. 2020), and sediment conditions are one of the major factors affecting their spatial distribution (Koyama et al. 2019a). Cuevas et al. (2016) showed that sediment contamination can be assessed by observing multiple organs of common gobies inhabiting the Ibaizabal estuary in Spain. In Japan, the effects of several intertidal mitigations and restorations have been assessed using gobies as indicator species (Suzuki et al. 2003; Koyama et al. 2018, 2019b). Furukawa et al. (2019) suggested that the records of *A. flavimanus* fished by the citizen scientists were useful for planning estuarine restoration in Tokyo Bay; thus, gobies can also be used as flagship species for estuarine conservation actions.

In Japan, identification of the river mouths that need conservation was attempted using the distributional data of gobies as indicator species. Based on the distributional data of ten threatened and near threatened goby species, Inui et al. (2016) defined 47 river mouths that should be preferentially conserved in 189 rivers flowing in the Seto Inland Sea. Koyama et al. (2020) defined 63 priority conservation tidal rivers in 158 rivers in the Kyushu region based on the distribution information of 14 threatened and near threatened goby species. In Japan, the Seto Inland Sea and the Kyushu region have particularly large tidal flat areas (Fig. 22.1); consequently, the information on the rivers indicated by the two studies is expected to be used as a basis for estuarine biodiversity conservation in Japan. Both studies indicated that rivers with large basins have high conservation priority because large rivers are likely to form various types of intertidal flats, and species diversity of goby is high in such river mouths. However, priority conservation areas for gobies do not completely match those for estuarine brachyuran crabs (Koyama et al. 2020). Thus, more effective conservation areas for fishes and other organisms could be identified using indicator species of various taxa.

22.6 Conclusion

Japan has the 35th largest area of intertidal tidal flats in the world with diverse ecosystem services, but approximately 40% of these tidal flats have disappeared since 1945, resulting in the extinction crisis of many fish species. However, the extent to which anthropogenic environmental changes in tidal flats and salt marshes influence these threatened fishes has not been fully assessed. Thus, it is necessary to study the ecological traits of estuarine fishes to assess anthropogenic impacts on them. Naturally, threatened species as well as common species not listed in the Red Data Book should be actively investigated. There are very few studies on salt marshes compared to studies tidal flats, and the conservation and restoration planning for the sustainable use of fishes in salt marshes are unclear. Thus, the relationship between salt marshes and fishes in Japan should be studied.

Previous studies that focused on the mitigation and restoration of intertidal habitats in Japan have suggested that the construction of artificial intertidal habitats contributes to fish conservation; however, these artificial habitats are small. In Japan, more than 30,000 ha of tidal flats have already disappeared, which is why larger intertidal habitat restoration will be required in the future. We must investigate specific solutions to achieve the restoration of intertidal habitats and river management for disaster prevention at the same time, because they sometimes compete with each other in Japan.

Moreover, most of the reviewed studies have shown that artificial intertidal habitats are unstable and their environments change due to various factors. This finding reminds us that in order to maintain appropriate artificial habitats, adaptive management should be conducted based on the results of monitoring. To date, various management actions have been adapted, such as extermination of invasive species, introduction of dredged sediment, transplantation of reed plans, and maintenance of spawning substrates.

In addition to mitigation and restoration, the identification and conservation of intertidal habitats with high biodiversity are urgently needed. Gobies are effective indicators for assessing the conditions in estuarine environments and may help solve this issue; thus, these species could be used to identify intertidal habitats that should be prioritized for conservation.

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23

Conservation of Freshwater Fish Diversity in Japan

Kazumi Hosoya

Abstract

The current situation for Japanese freshwater fishes is discussed in terms of biodiversity by comparing the Red List and the Red Data Book (Japanese versions). As a threat to Japanese freshwater fishes, rice paddy field remodeling to improve the efficiency of rice cultivation is thought to have the greatest negative impact. This can be shown by the fact that 24 out of 75 species (32%) categorized as “Critically Endangered” and “Extinct,” live around paddy fields. Furthermore, Largemouth Bass *Micropterus salmoides* and Bluegill Sunfish *Lepomis macrochirus* introduced from the United States of America are having serious negative effects on small native cyprinids. Steps to protect Japanese freshwater fishes are proposed by referring to “in situ conservation,” “ex situ preservation,” and “social enlightenment.”

Keywords

Ex situ preservation · Invasive alien fishes · In situ conservation · IUCN · Neonicotinoids · Radioactive contamination · Red Data Book · Rice paddy field remodeling · Social enlightenment · Threatened species

23.1 Introduction

The Japanese Archipelago is located at latitudes 20–46° north and consists of islands of various sizes, with its main islands comprising Hokkaido, Honshu, Shikoku, Kyushu, and the Ryukyu Islands. The archipelago is long and narrow from north to south, and the Oyashio cold current from the north and the Kuroshio warm current from the south carry various fishes of marine origin along the Pacific coast. From a meteorological point of view, the archipelago can be classified as a heavy rain zone belonging to the temperate monsoon. The annual rainfall is about 1800 mm, which is about twice the world average. When heavy rain falls on rivers in Japan, floods are frequently caused and create diversified habitats including temporal breeding grounds for freshwater fishes. In addition to this, the Japanese Archipelago has been connected to the Asian continent, and several continental strains of freshwater fishes have been established in the archipelago. These geological circumstances have resulted in a relatively diversified freshwater ichthyofauna in Japan.

Unfortunately, many Japanese freshwater fishes are now declining in various areas of the archipelago as result of excessive anthropogenic activity, and some are on the verge of extinction. In this chapter, the current situation of Japanese freshwater fishes is reported first, and then steps to protect them are discussed. In the following pages freshwater fishes are defined as the primary

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and secondary freshwater fishes (sensu Myers 1938).

23.2 Freshwater Fishes in the Red Data Book

To promote the protection of wildlife, it is prerequisite to objectively grasp the current situation of species and to scientifically analyze the factors that threaten their habitat. The “Red List” (RL) and the “Red Data Book” (RDB) are important indicators for this purpose regardless of the taxon. The former contains a list of endangered species, and the latter is its commentary.

It is well known that the RL and RDB each bears red on its cover. This binding color was originally selected by the International Union for Conservation of Nature (IUCN) in Switzerland in 1966 according to the degree of danger of endangered organisms on the earth. Since then, “red” has become the symbol color of endangered species (Fig. 23.1a).

23.2.1 Publication of the Red Data Book

In 1991, the Environment Agency (now the Ministry of the Environment), Government of Japan published the RDB for the first time entitled “Japanese Endangered Wildlife: Vertebrates” (Environment Agency 1991). Since then, many local governments such as prefectures or municipalities have followed the policy of the Environment Agency, and each published their own RL and RDB. In addition, the Fisheries Agency published a similar version, the “Databook on Rare Wild Aquatic Organisms in Japan” (Fisheries Agency 1998).

The RDB of the Ministry of the Environment has been selected and revised four times by 2015 and has become a Japanese standard, the most important and reliable source in both name and reality (Fig. 23.1b).

The selection criteria for the RL of the Ministry of the Environment were reviewed for the first time in 1997. The quantitative evaluation criteria by the IUCN were adopted from the second RL in the same year (Ministry of the Environment 2003) and now follow the IUCN criteria ver. 3.1 second edition (IUCN 2012; Fig. 23.1a). However, qualitative requirements are also used to prevent underestimation due to a lack of quantitative data (Ministry of the Environment 2020a).

23.2.2 Definition of Threatened Species

In the RL of the Ministry of the Environment, each species falls into one of eight categories (Fig. 23.2). Aside from “extinct,” not all categories on the RL indicate “threatened.” Strictly speaking, threatened species are limited to three categories: endangered IA, IB, and II. These categories are defined by how “the current state was brought about.” In addition, if the negative factors continue to act, species ranked in these categories are estimated as having difficulty in surviving in the wild. In fact, fishes ranked in IA are facing an “extremely high risk of extinction in the wild in the very near future,” and IB is “as much as IA.” Endangered species II may move to the category of “endangered species I” in near future, if the negative factors that brought about the current state continue to act as “species with an increased risk of extinction.” Quantitative criteria are defined by (A) reduction rate, (B) area, (C) mature population + reduction rate, (D) mature population, and (E) extinction probability. In the case of the Ministry of the Environment RL, qualitative criteria have been used in addition to quantitative criteria as well.

At first, regarding the handling of fishes in the RDB of the Ministry of the Environment, freshwater fishes, brackish water fishes, and some seawater fishes migrating to inland water for some life stages were comprehensively considered. However, at present, two special committees are set up to treat “freshwater fishes” and “seawater fishes” independently, though its sorting of some brackish water fishes to be charged, is tough and very confusing on affiliation.

In Japanese biota, freshwater fishes are in a particularly critical situation among various

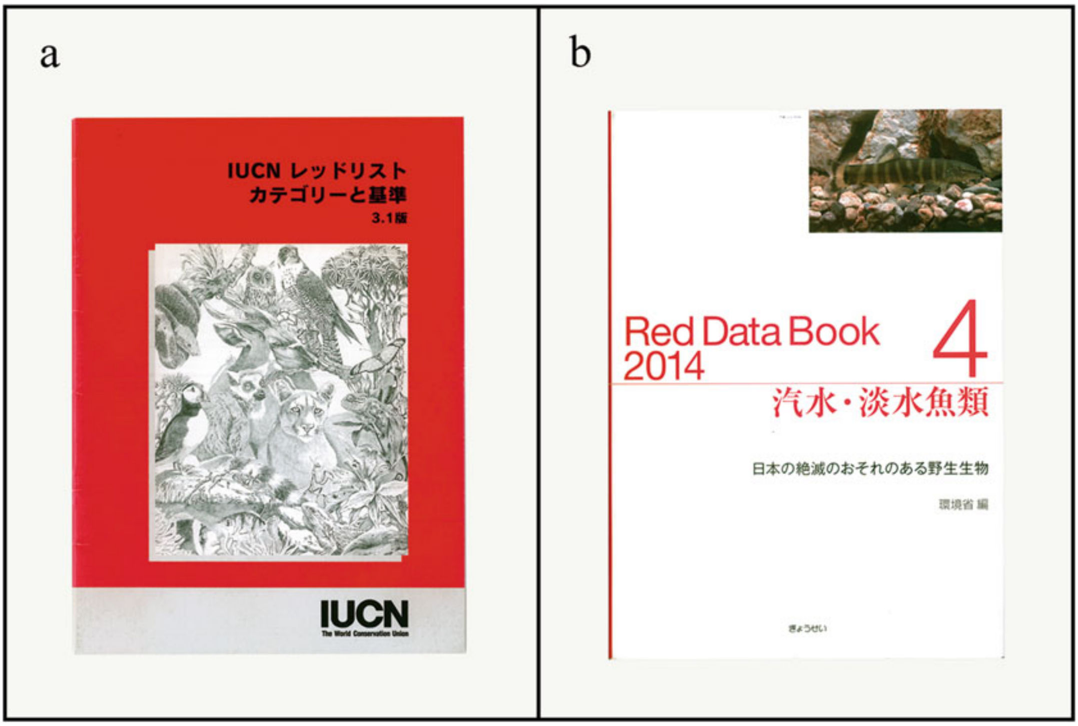

Fig. 23.1 IUCN Red List and Japanese Red Data Book. (**a**) The IUCN Red List Categories and Criteria, version 3.1 (2001) translated into Japanese; (**b**) Red Data Book—Threatened Wildlife of Japan 4. Pisces–Blackish and Freshwater Fishes, Ministry of the Environment (2015)

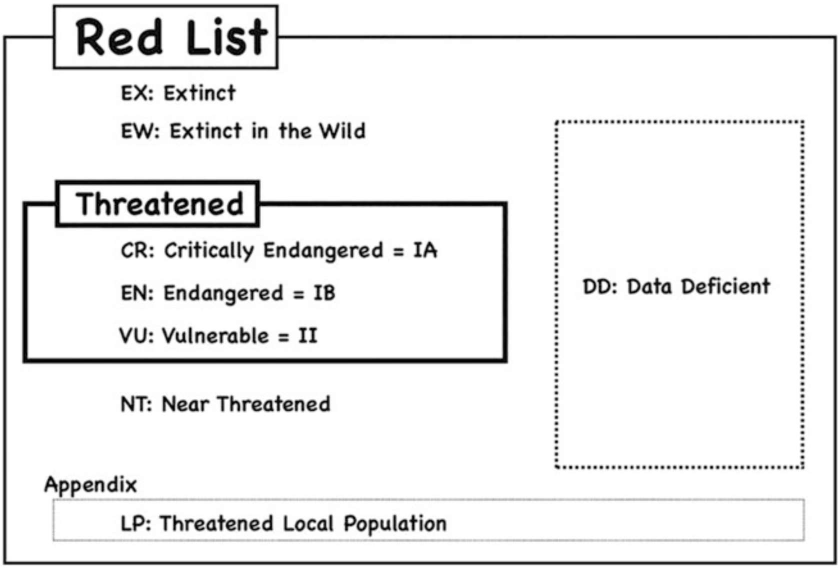

Fig. 23.2 Category classification and hierarchy structure in the Red List, issued by the Ministry of the Environment, Government of Japan

threatened animals. The RDB 2014 version (Ministry of the Environment 2015) preceded as the RL in 2013 lists a total of 167 threatened species of freshwater fishes (IA, IB, II). About 500 species of Japanese native freshwater fishes were evaluated. The total number of threatened species of freshwater fishes on the list exceeds 40% of the total number of native freshwater fishes. This ratio is significantly higher than in other fields or taxa such as insects and plants. Unfortunately, the number of listed species has clearly increased with successive revisions (Fig. 23.3). This increase includes the number of species examined and taxonomic subdivision, but it is true that the number of threatened species of freshwater fishes has increased in the last 20 years or so.

23.2.3 Application of IUCN Criteria

Currently, 36 out of a total of 123 species (29.3%) that are classified as endangered IA and IB on the Ministry of the Environment RL, and the oldest RLs (ver. 2.3, not the current standard ver. 3.1) were also evaluated by the IUCN. Among them only two species [*Parabotia curtus*, Ministry of the Environment version IA; *Parahucho perryi* (listed as *Hucho perryi*), IB; 1.6%] correspond to IUCN IA and IB, respectively. Overall, there are few contradictions in the difference between the global (IUCN) evaluation and that of Japan about widely distributed species not endemic to Japan. In the current situation where only *Parabotia curtus*, which was newly evaluated as IA in November 2015, is listed at the top of the IUCN list among Japanese endemic species, and the crisis and conservation status of Japanese freshwater fishes are being discussed worldwide. International evaluations by the IUCN and others have triggered a great deal of domestic attention, as seen with *Anguilla japonica* and *Parabotia curtus*. Furthermore, international information sharing on the biodiversity crisis is an important criterion for clarifying the issues and responsibilities of Japan in ratifying the “Convention on Biological Diversity” and realizing more appropriate conservation measures and efforts. The main idea is that the creation of a system in which valuable information compiled by the Ministry of the Environment is effectively reflected in the IUCN RL should be led by the national government, not by individual researchers. For that purpose, it is strongly desired that the Ministry of the Environment considers its approach, especially in the handling of qualitative requirements.

On the other hand, the Japanese versions of the RL or the RDB differ in that they have two major features regarding taxonomic targets compared with those of the IUCN. First, the Japanese versions cover even undescribed species as targets that are tentatively included by indicating these as “sp.” or “type.” For example, Musashitomiyo, a ninespine stickleback, is confined to small area near Tokyo and categorized as IA, under the name of “*Pungitius* sp. 1” without proper scientific name. In addition, the Japanese version is unique in including an extra category “Lp,” which stands for a local population of the species possibly classified as “Least concerned” or “Data deficiency.” This approach focuses on the protection of peripheral populations of some species that are candidates as new subspecies.

23.3 Threats to Japanese Freshwater Fishes

There are 33 causes that threaten the survival of wildlife listed by the Ministry of the Environment, Government of Japan in the RDB (edited by the Ministry of the Environment 2015). The causes of the decrease differ depending on the fish species, but all causes have human activity at the root (Fig. 23.5).

23.3.1 Dam Construction and Crossing Work

The biggest threat to fish species is that the natural environment is being converted to artificial structures by various developments. In fact, the Japanese Archipelago, which has a small land area, is even more susceptible to this.

When geographic structures such as dams are created in rivers, they affect the run-up of migratory fishes that make a round trip between a river and the sea. Arctic Lamprey *Lethenteron camtscaticum* is a typical anadromous species whose life history cannot be completed unless the parent fish return to the breeding ground to lay eggs in the river and then migrating down the river after the fry have grown. The designation of this species as Endangered on the third RL, 2007 suggested that it is more difficult for mature adults from the sea to reach their breeding grounds. Though the lamprey mainly occurs in Hokkaido, they are distributed along the coastal area of the Sea of Japan southward to the San-in and Hokuriku districts in Honshu where the decrease in individuals has accelerated.

The extinction of Japanese sturgeon, *Acipenser medirostris* (Fig. 23.4a), which was rated as it was in 2007, once had run-up large rivers in Hokkaido emptying into the Sea of Japan such as the River Teshio and the River Ishikari (Hosoya 2016).

23.3.2 Rice Paddy Field Remodeling

The impact of agricultural modernization is also enormous throughout the Japanese Archipelago. Remodeling rice paddy fields is thought to have the greatest negative impact on Japanese freshwater fishes (Hosoya 2009). Widespread public works to improve the efficiency of rice crops started from the 1960s. Since then, about 60% of paddy fields in Japan have been changed to unnatural structures, characterized by unification of several small traditional paddy fields to a large modern one in a rectangle; separation of canals into drainage and water injection in some cases even replaced with irrigation pipelines; expansion of the heading distance by more than 1 m between paddy fields and drainage channels; three-sided concrete walling of canals; and alternation from small soil grooves to U-shaped concrete grooves (Fig. 23.6).

As a result, the parental fishes cannot move from the drainage channel or stream to the paddy field, which should be their spawning ground. Thus, the reproduction of fishes is inhibited. Furthermore, because the waterways for drainage are protected by concrete on three sides, there is no sediment, and it becomes difficult for aquatic plants to grow. As a result, the flow becomes too strong and rapid, and fishes that use these plants as a refuge and feed on them cannot remain in the drainage canals anymore. These construction methods have left even medaka fishes *Oryzias latipes* and *Oryzias sakaizumii*, which are so-called symbol fishes of paddy fields, as endangered species (Category II).

The total number of freshwater fish species inhabiting the Japanese Archipelago is 512, including exotic species (Hosoya 2019). Of these, 115 species live around paddy fields, which is equivalent to 22% of freshwater fishes in Japan. On the other hand, there are 71 species categorized as “Critically Endangered” (Fig. 23.3) and four species as “Extinct” (Fig. 23.4) in the Ministry of the Environment version of RL (2020a), of which 24 species live around rice paddy fields, accounting for 32% of IA plus extinct species. These facts show how many freshwater fishes live around paddy fields in the Japanese Archipelago, but now are in danger of extinction.

In fact, *Parabotia curtus* once successfully used the areas around rice paddy fields as an alternative to floodplains but has found it difficult to coexist with modern agriculture (Abe et al. 2007). Early rice cultivation that requires the start of irrigation earlier than the spawning season of this species has become common. Due to rice paddy field remodeling, the number of reliable breeding sites for *P. curtus* has now decreased to only three (Abe et al. 2007; Watanabe et al. 2009).

23.3.3 Invasion of Alien Species

The introduction of alien species has had irreparable consequences for native ecosystems. In Japan, the heavy negative effects of Largemouth Bass *Micropterus salmoides* and Bluegill Sunfish *Lepomis macrochirus* have become a major problem. After introduced from the United States of America, they have been secretly released into rivers and lakes for sport fishing. Some endangered species such as *Acheilognathus*

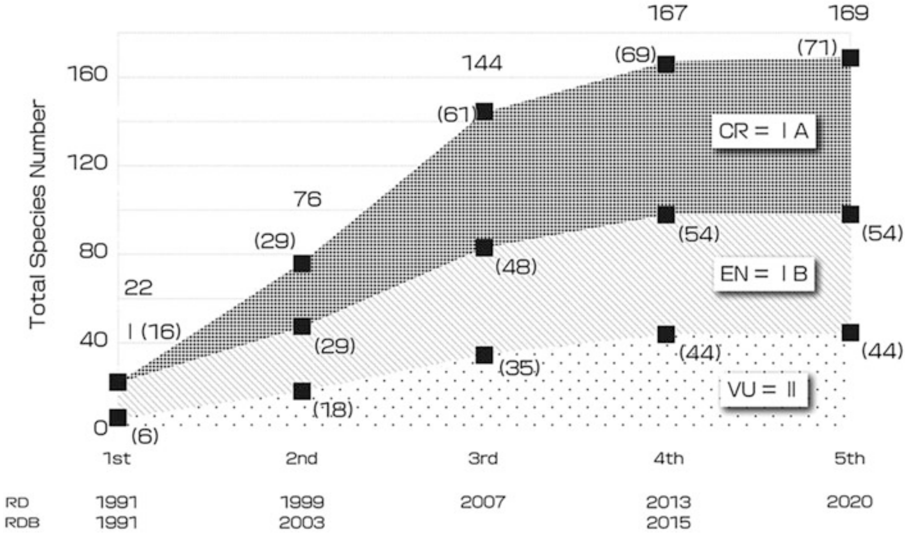

Fig. 23.3 Changes over time in the total number of categorical ranks of blackish and freshwater fishes listed on the Red List of the Ministry of the Environment, Government of Japan. (Modified from Hosoya et al. 2016)

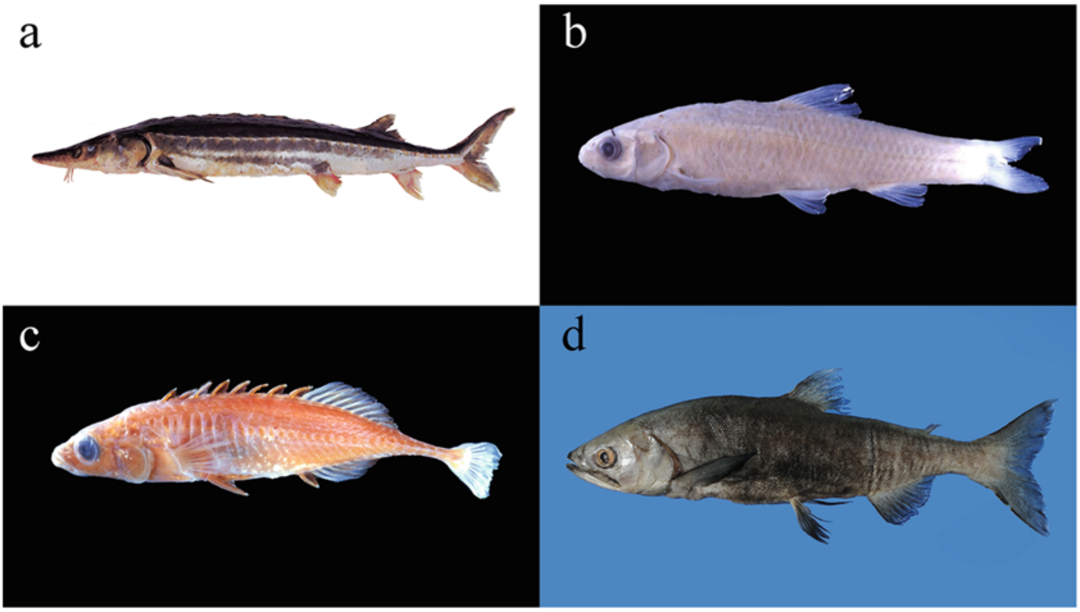

Fig. 23.4 Japanese freshwater fishes categorized as Extinct (**a**–**c**) and Extinct in the wild (**d**). (**a**) *Acipenser medirostris* (photo by Ryu Uchiyama); (**b**) *Gnathopogon elongatus suwae* (photo by Kazumi Hosoya); (**c**) *Pungitius kaibarae* (photo by Kazumi Hosoya); (**d**) Kunimasu *Oncorhynchus kawamurae*. (Photo by Tetsuji Nakabo)

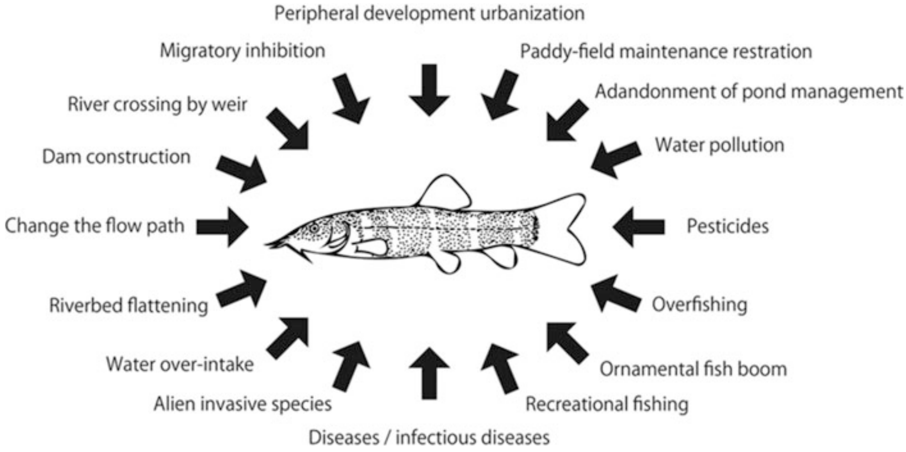

Fig. 23.5 Threats to Japanese freshwater fishes

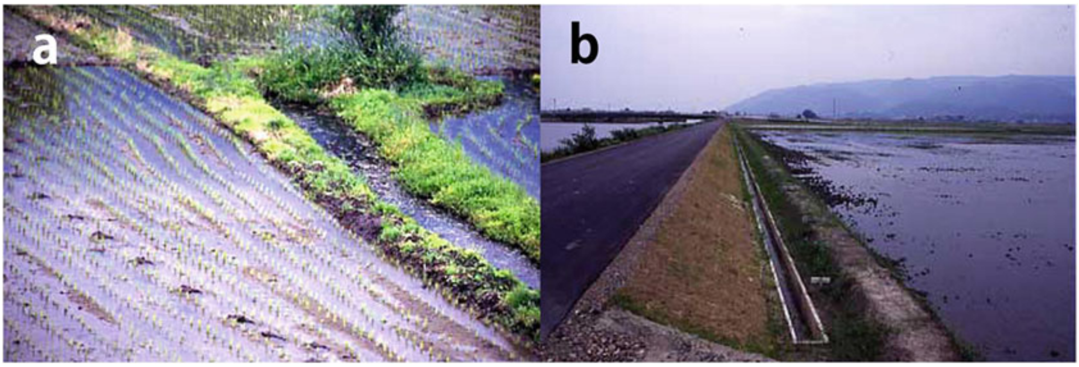

Fig. 23.6 Comparison of a traditional rice paddy field (**a**) and modern one during remodeling in the winter (**b**) in Gifu Prefecture, Japan

cyanostigma, *Acheilognathus typus*, *Pseudorasbora pumila*, and *Gnathopogon caerulescens*, which are all small cyprinids with a maximum total length of about 8–15 cm, have been severely damaged in ponds, lakes, rivers with weak currents, and agricultural waterways. It is thought that the rank up to Endangered IA is mainly due to the feeding damage by these predatory sunfishes. The habitat of *A. typus* has already disappeared in the Kanto region in central Honshu, and it is believed that there fewer than ten habitats remaining in the Tohoku region in northern Honshu. This rapid reduction in habitat has been accelerated by ecological competition with another alien bitterling, *Rhodeus occelatus occelatus* as well which happened to be contaminated into the seedlings of Chinese four major carps from the River Yangtze to the River Tone in the Kanto region, Japan to increase food production during the World War II. All these remaining habitats are irrigation ponds as the last fort because alien fishes cannot invade over high mounds. In recent years, Smallmouth Bass *Micropterus dolomieu*, which can live in running water, have been released illegally, and the distribution area is expanding rapidly from eastern Japan to western Japan. This results in accelerating the decrease and deterioration of Japanese biodiversity by the two species of *Micropterus*.

These foreign-derived exotic fishes should be called foreign exotic fishes. However, in practice, the distinction between exotic and native fishes must be made within and outside the natural distribution of individual species, not inside or outside a country border. This means that even fishes native to Japan, such as *Carassius cuvieri* endemic to Lake Biwa, will turn into exotic fish if they are transplanted to other areas beyond the original distribution area, and these should be called domestic exotic fishes (Hosoya and Takahashi 2006).

23.3.4 Ornamental Fish Boom

In Japan, there are a few cases where freshwater fishes have been overfished for food purposes, but collection for viewing purposes is frequent. *Acheilognathus cyanostigma*, which is a relatively slender bitterling with a maximum total length of about 10 cm, has a habit of spawning in bivalves, but in the habitat of the Lake Biwa/Yodo River system, bivalves that raise eggs and fry have been poached. The threatened freshwater fishes listed in the RDB are all pretty and relatively easy to breed. However, personal collection of these freshwater fishes for viewing purposes is no longer necessary in many habitats. Even if it is not directly involved in collecting but the demand for rare freshwater fishes is high, it will lead to an increase in collecting pressure by traders and indirectly reduce the number of rare freshwater fishes. It is now time for the collection and sale of rare wildlife for commercial purposes to be severely restricted (See Sect. 23.5).

In 1993, Japan ratified the Convention on Biological Diversity, a global treaty aimed at preserving biodiversity. Since then, the government has been presenting a national strategy to protect Japan's native organisms, with several revisions. Among them, the goals are the idea of nature conservation, expansion of the scope of protection, nature restoration, concrete proposals for that purpose, cooperation, and collaboration. Unfortunately, the number of animals and plants listed on the RL and the RDB has continued to increase since then, and the results of efforts cannot be read from them. This is probably because many protection measures are not sufficiently effective.

23.3.5 Water Pollution

Water pollution cannot be overlooked as a cause of deteriorating habitats of freshwater fishes. This includes eutrophication, inflow of industrial wastewater, sewage, and mine wastewater, and the toxic effects of pesticides. Of the four extinct freshwater fishes in Japan, *Oncorhynchus kawamurae* originally inhabited only Lake Tazawa in Akita Prefecture (Fig. 23.4d). This species became extinct in 1940s when the water from the River Tama was introduced into Lake Tazawa for hydroelectric power generation. This is because the water from Tamagawa-Onsen hot spring, which is known for its hypochlorous acid water, had begun to flow into Lake Tazawa. Later, it was found that individuals of *O. kawamurae* transplanted from Lake Tazawa to Lake Saiko, Yamanashi Prefecture before the World War II still survive (Nakabo et al. 2011). Therefore, this finding compels the Ministry of the Environment to change the category of *O. kawamurae* from "Extinct" to "Extinct in the wild" based on the extant distribution out of original site.

Certainly, the water quality of Japanese rivers has improved dramatically since the 1980s due to the development of sewage treatment plants, legislative restriction of water pollution, and increasing public awareness of environmental protection. The achievement rate of the public environmental standard for organic water pollution by 2019, reached 94.1% of 2572 waters in rivers in BOD while it remains in 50% of 188 waters in lakes in COD (Ministry of the Environment 2020b). These changes in aquatic circumstances appear to lead to improved habitats for Japanese freshwater fishes.

On the other hand, various kinds of synthetic organic chemicals have been utilized in the terrestrial environments and flow into the aquatic ones including freshwater and marine water area, recently. For example, pesticides including oraganophosphates (fenitrothion, diazinon, dichlorvos, IBP, etc.), neonicotinoids (acetamiprid, clothianidin, imidacloprid, etc.), and fipronil (phenylpyrazole) have been much applied. Since the 1990s, neonicotinoids and fipronil, which are effective for rice cultivation, have been much used, and drastically reduced the number of aquatic organisms such as dragonfly larvae and *Daphnia* that freshwater fishes feed on. The EU already prohibited to use some neonicotinoids in 2013 after heavy colony collapse disorder (CCD) of honeybees. It has been warned that this effective pesticide not only acts directly on pests, but also has unpredictable negative effects on ecosystems through the food chain. In fact, neonicotinoids have been reported to act indirectly not only on arthropods but also on vertebrates (Frank and Tooker 2020). In Lake Shinji, Shimane Prefecture, the biomass of zooplankton and chironomid larvae, has plummeted since the beginning of the application of neonicotinoids to agricultural fields in the 1990s. This phenomenon may be the indirect negative impact to fishes represented by commercially caught fishes through trophic cascades (Yamamuro et al. 2019). For example, the catch of *Hypomesus nipponensis* and *Anguilla japonica* has dropped sharply since 1993. That time coincided with the time when neonicotinoid insecticides were started to use. Many kinds of pesticides have been applied in the terrestrial environment and are introduced into aquatic one. The levels of these pesticides in river water were generally less than the acute toxic concentration in fishes (Kawai et al. 2018). However, neonicotinoids and organophosphorus pesticides act on the nervous system of vertebrates and invertebrates, especially on acetylcholine esterase receptor that has very important role of excitatory transmission in animals. Therefore, these pesticides may affect behavioral activity of aquatic organisms such as fishes, and researches concerning behavioral ecotoxicological approaches seem to be essential (Kurokawa and Kawai 2019).

On 11 March 2011 the Pacific coast of northern Honshu was attacked by a huge tsunami caused by a large earthquake. This caused heavy damages to human lives and a significant disastrous impact on various ecosystems including the hydrosphere, both directly and indirectly. Unfortunately, the Fukushima First Nuclear Power Station of TEPCO (Tokyo Electric Power Company) located on the tsunami-attacked area was given serious damages in this disaster. This resulted in the scatter of huge amounts of radioactive materials into the air which highly contaminated the surrounding land and water bodies. As a result, radioactive cesium was detected in *Plecoglossus altivelis* at 3093 Bq/kg wet and *Pseudaspius hakonensis* at 2500 Bq/kg wet, compared with 100 Bq/kg wet as a standard value, in the River Mano, Soma City, Fukushima Prefecture. Freshwater fishes seem to bioaccumulate radionuclides through the food chain from pelagic fishes to demersal fishes, and from omnivorous fishes to carnivorous fishes (Mizuguchi 2012). Among radioactive substances, cesium-137 released has been confirmed to be highly concentrated in the waters around the Tohoku region and adjacent areas. Moreover, high level of radio cesium (^{134}Cs and ^{137}Cs) was detected in *Salvelinus leucomaenis* in a river close to the Nuclear Power Station at the level of 25,600 Bq/kg wet (Wada et al. 2019). Cesium-137 has a long half-life, or decay period, of about 30 years. It was revealed that the factors affecting radio cesium levels in riverine organisms did not necessarily influence radio cesium levels in organisms from lakes (Ishii et al. 2019). Namely, feeding habits had a major influence in the case of piscivorous fishes in lakes, but not in rivers. These findings show that biotic and abiotic factors affecting radionuclide accumulation in fishes are clearly dependent on the ecosystem. After the Fukushima nuclear power plant accident, managing environmental radionuclide contamination efficiently has become greatly important because of two reasons, one is the acute and chronic effects of radionuclide to all animals including humans, of course, and the second is the effect on the inland fisheries for safe supply of fishes.

Overall, regarding the recent negative effects of environmental changes on Japanese freshwaters, it is necessary to carefully monitor how they affect freshwater fishes, not only the health hazards to humans.

23.4 Red List Challenges

The RL and its manual, the RDB, are an important collection of data that can be used in various forms as statistical data on the current situation and factors for the critical situation of species diversity for each taxon.

The purpose of creating the RL should be to accurately comprehend endangered species and spread this understanding to the public so as not to lead to artificial extinction of wildlife. It has been pointed out that selection does not impose any legal restrictions, so the disappearance of habitats due to development will not end, and the value of rare organisms will increase. Nevertheless, when viewed comprehensively, many experts judge that it has the effect of promoting efforts toward biodiversity conservation. However, there are various issues even when focusing on fishes, and it is necessary to understand them to a certain extent when using the RL.

23.4.1 Insufficient Basic Data

A problem frequently seen in the evaluation process is the lack of basic data for quantitative criteria that are important in determining the rank of endangered species. To address this issue, qualitative requirements are also provided for evaluation. However, there is a common understanding that evaluation should be carried out objectively, leading to a way only using quantitative criteria. From a scientific point of view, fishes are animals that live freely in water, and it is generally difficult to make reliable estimates of populations across habitats. Even if catch statistics are available, it is not uncommon to know how many individuals exist outside the fishing grounds, and it is not uncommon for multiple species to coexist, such as "sardines." Furthermore, even for countable species, no system has been established for continuous monitoring at a national level. In other words, it is extremely difficult to obtain accurate quantitative information for most species. At present, it is necessary to take into consideration that the tendency to underestimate extinction risk does not occur while making good use of qualitative evaluation, and environmental administration will promote the construction of a system to focus on scientific research.

In addition, the rate of decrease that is emphasized in the evaluation is stipulated as a longer period of 10 years or three generations. However, as is the case with many Japanese freshwater fishes, it is often inappropriate to apply this criterion to species that declined earlier and are now in minority equilibrium. This is because freshwater fishes that once proliferated in the plains may have already declined from the 1960s to the 1980s, when rice paddy field remodeling was active (Hosoya 2009), or from the 1980s to 2000s, when Largemouth Bass was released nationwide (Hosoya and Takahashi 2006). This is because the rate of decrease is expected to be underestimated. Therefore, in such organisms, it is difficult to individually predict the causes of extinction such as loss of habitat due to development, introduction of alien species, and overfishing before problems occur on the biological side such as genetic deterioration and demographic fluctuations. However, the anthropogenic factors that have been involved pose a far greater threat. This is not limited to freshwater fishes in minority equilibrium, but in assessing species for which quantitative data are lacking, we are fully aware of the endangering nature of anthropogenic factors.

23.5 Protection Measures

Listing on the RL itself is not subject to legal restrictions. In the RDB published in February 2015, species with the highest priority for protection were defined as those where necessary protective measure will be taken, such as designating it as a domestic rare wild animal and plant species based on the "Act on the Conservation of Endangered Wild Animal and Plant Species" (Ministry of the Environment 2015). However, only four species, *Tanakia tanago*, *Acheilognathus longipinnis*, *Rhodeus smithii*, and *Parabotia curtus* had been designated at first, then *Acheilognathus tabira nakamurae*, *Cobitis striata hakataensis*, *Cobitis takenoi*, *Neosalanx reganius*, and *Gymnogobius nakamurae* were added in 2020. Finally, total number remains at only 15% of the endangered IA species. At the same time, *Hemigrammocypris neglecta* were designated as the "Specified second species" under the act which prohibits sales for commercial purposes but permits sampling for research and conservation activities. The purpose is to inform the plight of endangered rare wildlife as well as to publish the RL and the publication of the RDB, and to proceed with protection from there. Of course, there are various possible developments in protection (e.g., Hosoya 2002). However, the concrete steps are left specified and are not connected to efficient protection. It is necessary to promptly respond to the challenges posed by the RL.

23.5.1 Three Basic Steps for Protection

"Protection" can be defined as the way to protect threatened species (Hosoya 2008; Yokoi 2009; Kitagawa 2018). Protection methods include "in situ conservation" which conserves the field habitat where a threatened species is originally located, and "ex situ preservation" which maintains the strain of threatened species in a research facility. In addition, to implement "protection," the value of the threatened species must be socially promoted as a prerequisite. Therefore, in "protection" of threatened species, "in situ conservation" and "ex situ preservation," plus "social enlightenment" can be compared to three basic steps (Hosoya 2002, 2008) (Fig. 23.7). All three steps are indispensable, and each must have an organic connection.

23.5.2 In Situ Conservation

This refers to the conservation of threatened species that live in an original distribution area in their natural state. Many threatened fishes occur in rural areas including paddy fields, streams, and ponds (See Sect. 23.2.2). To conserve these fishes, it is desirable to isolate the population in a fish sanctuary to block the negative effects of anthropogenic activities. However, these fishes are often unevenly distributed in now open habitats without being conserved. The current situation is that they are directly susceptible to human influences such as rice paddy field remodeling, excessive spraying of pesticides, and disorderly release of foreign fishes such as black bass (Largemouth Bass and Smallmouth Bass), Bluegill Sunfish, and Mosquitofish *Gambusia affinis*. To conserve native threatened fishes, local governments need to give some rating to local groups and impose legal restrictions. In fact, they are on the RL of each local government, but no effective decree that imposes penalties has been found so far.

23.5.3 Ex Situ Preservation

This refers to accommodating threatened species in zoos, aquariums, research institutes, etc. to maintain the lineage, and plays the role of "Noah's Ark." In fact, this term is internationally confusing. For example, the IUCN per se consistently uses the term "ex situ conservation" (IUCN/SSC 2014), whereas the World Resources Institute and the United Nations Environment Program uses "ex situ preservation" (WRI et al. 1992; see Frankel and Soulé 1981 as well). Like the IUCN, the Ministry of the Environment also follows the term "ex situ conservation." It is undeniable that the reason for this was the excessive interference of ecologists with terms in the protection measures for rare organisms in Japan. Though it can be admitted that "ex situ conservation" can be contrasted with "in situ conservation" as a word, it is not realistic as a concept. Because the properties that can be extracted from within a habitat are always limited, and the act of protecting the lineage is preservation itself, as shown by cryopreservation of sperm (Frankel and Soulé 1981).

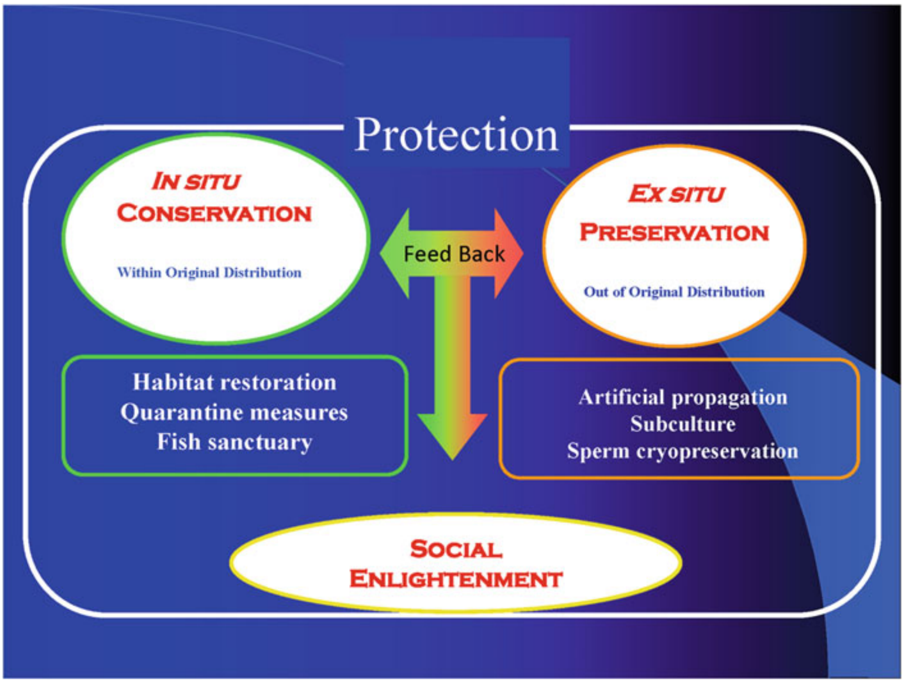

Fig. 23.7 Scheme for the protection of threatened species using three basic steps: "in situ conservation", "ex situ preservation", and "social enlightenment"

It is well known that having a small number of breeding parents reduces the genetic diversity of the offspring. For example, it was reported *Oryzias latipes* became completely clonal populations after 20 generations (Arii et al. 1987). Such long-term sub-cultured populations carry the risk of being transformed into a population that is genetically different from the wild population. This tendency is even more likely to appear in small freshwater fishes, which have a short lifespan and a fast generation rate. The goal of "ex situ preservation" is how to faithfully maintain the genetic traits of wild populations.

23.5.4 Social Enlightenment

Japan is traditionally a fishing nation, and fishermen and officers have used fish seedings. In the name of environmental education, artificially improved varieties of *Oryzias latipes* such as "Himedaka" were released into natural waters where native *O. latipes* had disappeared (Munakata et al. 2020). This activity was often reported as positive news. The easy transfer of artificially improved varieties of unknown origin and wild *O. latipes* from other regions clearly deviates from the idea of biodiversity protection. Because the addition of heterogeneous elements will have some negative effect on the stability of the ecosystem, and if crossed with a native wild *O. latipes* population, genetic disturbance is inevitable (Nakao et al. 2017).

Unfortunately, the public is not aware of *O. latipes*, and few people understand the plight of wild *O. latipes*. In many cases, fry of common cyprinid species such as *Opsariichthys platypus* and *Pseudorasbora parva*, or *Gambusia affinis* of a specific exotic species are mistaken for *O. latipes*. Even in textbooks whose educational goal should be nature maintenance, the explanation of wild *O. latipes* is not sufficient. It is required now to have the public accurately understand the uniqueness and diversity of not only wild *O. latipes* but also other native freshwater fishes in Japan.

On the other hand, there are many NPO bodies for *O. latipes* conservation activities. In Kanagawa Prefecture, the "Fujisawa Medaka School Creation Association" and the "Odawara Medaka Protection Association" actively protect the local native *O. latipes*. Higashiyama Zoo and Botanical Garden in Nagoya City, the Medaka Museum, is noteworthy as an aquarium specializing in *O. latipes*. Finally, it is deeply desired that the circle of these protection and enlightenment activities will expand.

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Using *Gyotaku* to Reveal Past Records of Fishes Including Extinct Populations

24

Yusuke Miyazaki and Atsunobu Murase

Abstract

Japan has developed unique customs related to recreational fishing. *Gyotaku*, which means "fish impression" or "fish rubbing" in English, has become common since the last Edo Period. A *gyotaku* is made by copying an image of a fresh fish specimen to paper using ink. Information such as capture locality and sampling date were often written on a *gyotaku* sheet, and these can be useful with respect to past biodiversity data. Some fish targets of *gyotaku* (i.e., popular targets of recreational fishing) have been listed as threatened species in the Japanese red lists because their habitats have been seriously degraded. Some *gyotaku* targets are able to be identified to species using *gyotaku* alone, particularly if external morphologies such as number of scales or scale rows are distinguishing characters. Two examples of the families Sparidae and Sillaginidae are discussed, and the latter includes new distributional records for *Sillago parvisquamis*. This species has been listed as critically endangered, and only one *gyotaku* sheet of the species caught from the Tokyo Bay was previously known. Additional sheets from Tokyo Bay are reported here, with identifications based on the *gyotaku* alone. As shown herein, data mining from historical materials such as *gyotaku* can help clarify past biodiversity.

Keywords

Citizen science · Distribution · Museum · Natural history · Time limit

24.1 Introduction

The Japanese Archipelago, one of the world's most populated areas, was identified by Marchese (2015) as a global biodiversity hotspot. It has many endemic species, in particular freshwater fishes, and negative factors such as habitat degradation have been rapidly extended by human impacts over recent decades (Boufford et al. 2004). Regrettably, three known species of freshwater fishes have been lost in this archipelago, i.e., Japanese wild populations of *Acipenser medirostris*, *Pungitius kaibarae*, and *Oncorhynchus kawamurae* (see Ministry of the Environment 2015). The last species was found outside its distributional range in 2010 (Nakabo et al. 2011), meaning that the trout is not extinct but does require ex situ conservation [its category has been changed from "extinction (EX)" to "extinction in wild (EW)" (Hosoya 2015;

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Miyazaki et al. 2019)]. In addition, the sustainability of many populations of Japanese fishes, particularly those from brackish water and freshwater, is in crisis; the Japanese red list records some as extinct (EX) and others trending toward EX (e.g., Ministry of the Environment 2015; Nature Conservation Committee of Ichthyological Society of Japan et al. 2016). Seven species of fishes have been listed as EX by the regional red list of the Tokyo Metropolis, which is the largest megacity of the world (Maruyama et al. 2021).

For conservation and/or restoration of threatened species and populations, the previous environments, prior to human impact, can function as important reference points (e.g., Dobson et al. 1997; Young 2000; Feinsinger 2001). However, such past information, whether from literature, specimens or other materials, is often limited. That said, some can be mined from sources other than natural history collections and published literature. For example, Hayashi (2014) demonstrated that *Honzou Gaku*, which is a classic monograph for Japanese medicine, provides evidence for past distributions of whales and barnacles. Such monographs, widely neglected by modern biologists, are a potentially useful source for mining biodiversity data.

Japan's recreational fishing culture has grown significantly since the Edo period (1603–1868), as the methods and tools used have also developed (e.g., Matsuzaki 1939; Fukuoka City Museum 2016; Tsuribito-sha 2020). *Gyotaku* (fish rubbing with ink) is one of the unique examples of memorial records of recreational fishing in Japan (e.g., Hiyama 1964a, b; Fukuoka City Museum 2016). Such images often have attached information such as locality and sampling date, and therefore these can function as voucher records of past distributional information (Miyazaki and Murase 2020).

Here, we introduce the possibilities and future prospects of using *gyotaku* as a source of past biodiversity information. We give special emphasis to the current knowledge of this material for scientific purposes, the accuracy of species-level identifications, and its validity regarding identifying extinct populations of critically endangered species.

24.2 Using *Gyotaku* for Past Biodiversity Information

The origin of *gyotaku* is unclear, but the oldest example currently known is dated 1867 (the last Edo period) at Kinshi-bori, Edo (Nakajima 2005; Fig. 24.1). The current oldest prints were made by the samurais from the Shonai clan, who pursued recreational fishing to improve their concentration, and their spiritual and physical fitness and abilities (e.g., Nagatsuji 1996). Since the 1950s, *gyotaku* has become increasingly popular with recreational fishers nationwide (e.g., Hiyama 1964a, b).

Gyotaku techniques have also developed over time (e.g., Hiyama 1964a, b). Many kinds of brushes, inks, and other materials have existed since the Edo era in Japan. Direct and indirect methods have been used to capture images. Using the direct method, a fish specimen is painted, and then a sheet of paper is pressed onto the painted fish. The indirect method involves placing a sheet of thin paper or silk onto the fish specimen, and then painting the characteristics of the fish onto the paper or silk while it is resting on the specimen. Various color paints are used to create art pieces, whereas simple and uniform colors are usually used for memorial records of recreational fishing. The latter examples of *gyotaku* frequently include attribute information (i.e., sampling dates and localities) written on the sheet, while the art pieces usually do not. Therefore, some *gyotaku* sheets (particularly ones produced for art) are excluded as vouchers for past distributional information of fishes because they lack distributional data. In the recent years, digital *gyotaku* have become common, but these are based on color photographs, not on a fish-rubbing technique (Miyazaki and Murase 2020). We regarded the digital examples as equivalent to photographic data, not as *gyotaku*.

Miyazaki and Murase (2020) demonstrated that many leisure fishing and boating stores own *gyotaku* sheets with useful distributional data.

Fig. 24.1 The oldest known example of *gyotaku*, from the Tsuruoka City Folk Museum in the Tsuruoka City Library, Yamagata Prefecture, Japan. The subject is the Japanese crucian carp, *Carassius* sp., caught at Kinshi-bori, Edo in 1867

The *gyotaku* sheets roughly reflected regional fish faunas and common fishing targets of the stores' locations, and were useful for determining past distributional information of threatened species (Fig. 24.2). However, exhibitions at stores deteriorate over time, with a lifespan of approximately 30–35 years observed at some stores. Therefore, while *gyotaku* is a useful source of past biodiversity information, examples from leisure fishing and boating stores should be researched and accessed in a timely manner to maximize this opportunity.

Both *gyotaku* and photographs are very useful representations or secondary sources of specimen information. Photographs are generally more reliable than *gyotaku* due to more accurate representations of morphology and colors.

24.3 Identifications of Fishes Based on *Gyotaku*

Miyazaki and Murase (2020) also discussed the evaluation of identifications made from *gyotaku*. This can be done by examining the external morphology captured in the printed image and possibly by trying to obtain biological material from the print for molecular analysis. If a fish is able to be identified by using only *gyotaku* sheets, *gyotaku* could adopt the function of a primary source.

External morphology visible in *gyotaku* is sometimes sufficient to delineate species. A group of sister species that can be separated by characters such as general morphology or the number of scales can sometimes be identified to species using *gyotaku*. For example, Fig. 24.3 shows photographs of the following three species of the family Sparidae, one of the popular fishing targets in Japan, and the specimens' *gyotaku* sheets: *Pagrus major*, *Acanthopagrus schlegelii*, and *Acanthopagrus latus*. These species can be distinguished from one another by the number of transverse scales between the lateral line and the median spinous portion of the dorsal fin (TRac) (Akazaki 1962, 1984; Hayashi and Hagiwara 2013a). Their ranges of TRac are 6.5–7.5 for *P. major*, 5.5–6.5 for *A. schlegelii*, and 3.5 for *A. latus*. The ranges of *P. major* and *A. schlegelii* are slightly overlapping, but additional

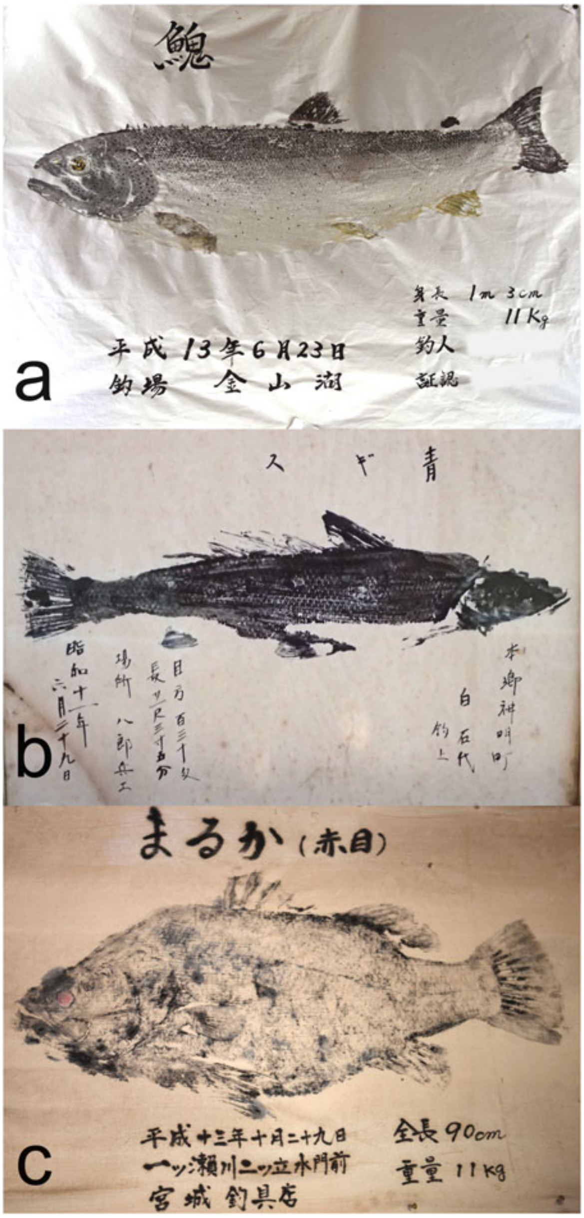

Fig. 24.2 Three species targeted in leisure fishing and listed as threatened in the Japanese national red list (Miyazaki and Murase 2020). (**a**) *Parahucho perryi* from the fishing tackle store, Kamiya-tsuriguten, Hidaka Town, Saru County, Hokkaido. (**b**) *Sillago parvisquamis* from the boating shop, Funayado-Yoshinoya, Urayasu City, Chiba Prefecture. (**c**) *Lates japonicus* from the fishing tackle store, Miyagi-tsuriguten, Miyazaki City, Miyazaki Prefecture

characteristics such as the shape of their snouts and the arrangement of head scales differ. As represented in the figure, differences in the above external morphologies are recognizable and countable from both photographs and *gyotaku* sheets.

Similarly, an additional example of a threatened species, *Sillago parvisquamis*, is provided here. This species has been listed as critically endangered (CR) on the national red list since 2007, and its populations in Tokyo and Ise bays and other regions except for in and around the Sea of Suo-nada, western Japan, have been strongly suggested as extinct (Shigeta and Usuki 2011; Shigeta 2015). Information on these uncertain populations is somewhat limited. For example, museum specimens collected from Tokyo Bay amount to only a few individuals at

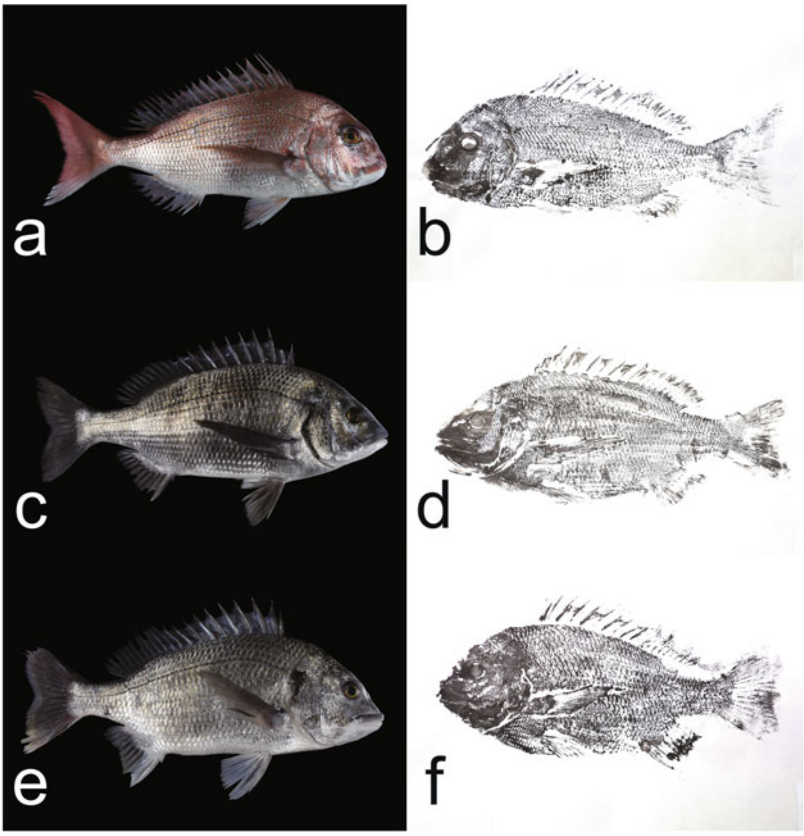

Fig. 24.3 The specimens (**a–c**) and their *gyotaku* sheets (**d–f**) of three species belonging to the family Sparidae. (**a**) KPM-NI 44097, *Pagrus major*, photo by AM, trawl by Y. Nagata, off Nobeoka City, Miyazaki Prefecture on 23 March 2017; (**b**) *gyotaku* of the same individual (a) made by M. Matsumura. (**c**) KPM-NI 44098, *Acanthopagrus schlegelii*, photo by AM, set net by H. Wada, Kadogawa Bay, Miyazaki Prefecture on 23 March 2017; (**d**) *gyotaku* of the same individual (c) made by M. Matsumura. (**e**) KPM-NI 44099, *Acanthopagrus latus*, photo by AM, set net by S. Hamada, Kadogawa Bay, Miyazaki Prefecture on 23 March 2017; (**f**) *gyotaku* of the same individual (e) made by M. Matsumura

Table 24.1 List of the registered specimens of *Sillago parvisquamis* (probably) collected from Tokyo Bay at two museums, the National Museum of Nature and Science (NSMT), and the University Museum, University of Tokyo (ZUMT)

Registration no.	Locality	Date	Remarks
NSMT-P 78318	The mouth of Ara-Kawa River (Tokyo Metropolis)	21 September 1960	164.4 mm SL
NSMT-P SK 1489	The mouth of Edo-Gawa River (Ichikawa City, Chiba Prefecture)	19 March 1960	Five individuals (103.8–172.4 mm SL)
ZUMT 4469	Tokyo Market	Unknown	
ZUMT 12735	Tokyo Market	Unknown	
ZUMT 15506	Unknown	Unknown	Donated by Shusuke Miyashiro from the Kanagawa Technical School; this individual could not be found

the National Museum of Nature and Science, Tokyo (NSMT) and The University Museum, University of Tokyo (ZUMT) (Table 24.1; Fig. 24.4). A color photograph of a specimen from Tokyo Bay has not been found. The first color photograph of the species was provided by a fishing magazine, Weekly Sunday Fishing, from the population of Yoshino-gawa River, east of Shikoku Island in 1976 (Konishi and Konishi 1976). This population has also been suggested

Fig. 24.4 The museum specimen of *Sillago parvisquamis* caught by set net (tsubo-ami) from the mouth of the Ara-kawa River, Tokyo on 21 September 1960. This specimen was registered to the National Museum of Nature and Science (NSMT-P 78318)

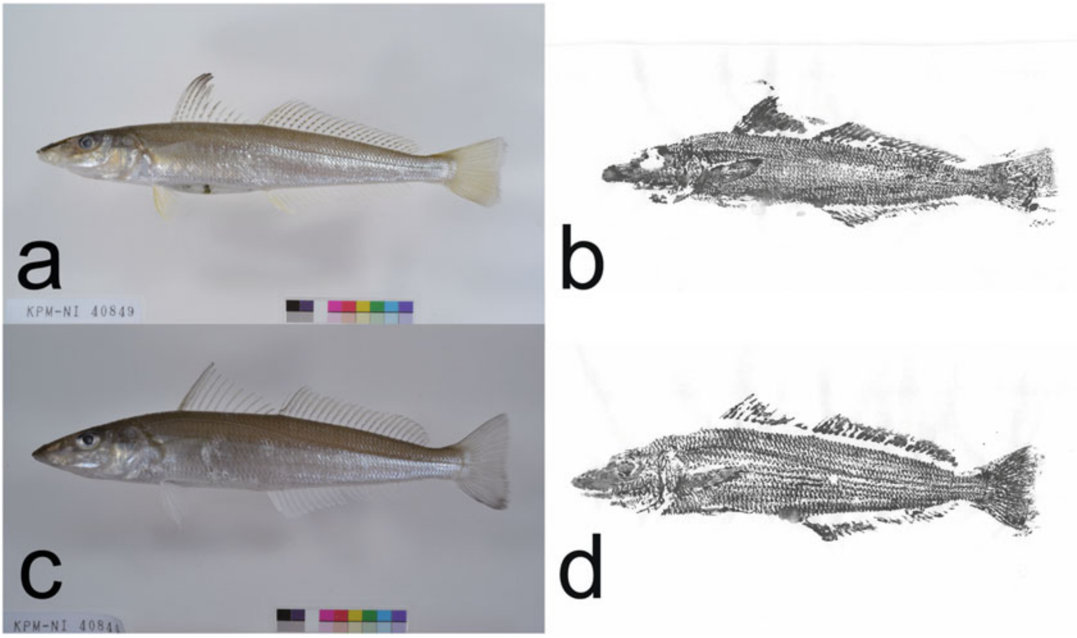

Fig. 24.5 The specimens (left side) and their *gyotaku* sheets (right side) of two species belonging to the family Sillaginidae. (**a**) KPM-NI 40849, *Sillago parvisquamis*, photo by YM, hook and line by N. Aratake, the Sea of Suo-nada, Oita Prefecture, 28 May 2016; (**b**) *gyotaku* of the same individual (a) made by YM. (**c**) KPM-NI 40844, *Sillago japonica*, photo by YM, hook and line by Y. Ogata, the mouth of Kaeda-gawa River, Miyazaki Prefecture, 4 July 2016; (**d**) *gyotaku* of the same individual (c) made by YM

as extinct after the reclamation of the tidal flats at the river mouth (Konishi 2002; Shigeta and Usuki 2011).

Figures 24.5 and 24.6 represent the examples of *Sillago japonica* and *S. parvisquamis*. The main islands of Japanese Archipelago have only these two species of Sillaginidae, although *S. aeolus*, *S. macrolepis*, and *S. sihama* have been recorded in the Ryukyu Islands (Hayashi and Hagiwara 2013b). The two species are identifiable by the number of scales; that is, the number of the scales above the lateral line (TRa) is 3–4 for *S. japonica* and 7–9 for *S. parvisquamis* (Sano and Mochizuki 1984; Hayashi and Hagiwara 2013b). As shown in the figures, these two species could be identified by using only *gyotaku*

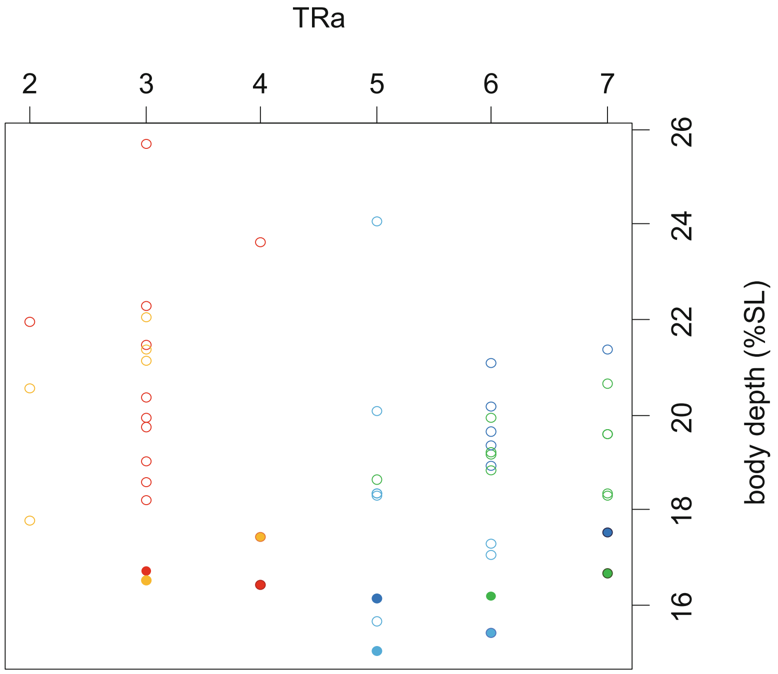

Fig. 24.6 The relationship between the numbers of scale rows of TRa (the transverse scales above the lateral line) and the body depth (%SL) that were counted and measured from the specimens, their photographs, and their *gyotaku* sheets. *Solid circles with dark grid-line* indicate the original specimens. *Solid circles without grid-line* indicate the photographs of the specimens. *Open circles* indicate the *gyotaku* sheets made from the specimens. Data for each individual is displayed using its own color. *Bluish and greenish colors* indicate the three specimens (KPM-NI 40847–40849) and their copies of *Sillago parvisquamis*, whereas *reddish and yellowish colors* indicate the two specimens (KPM-NI 40843–40844) and their copies of *Sillago japonica*

sheets and photographs. Based on this, the specimens represented in the *gyotaku* sheets were able to be identified even without the species name being recorded on the sheet itself.

Figure 24.7 shows three *gyotaku* sheets stocked at the fishing boating shop, Funayado-Yoshinoya, Urayasu City, Chiba Prefecture. These individuals were caught in the inner Tokyo Bay in the period from 1954 to 1963. Similarly, Fig. 24.8 is a color photograph provided by a recreational fisherman who read an outreach article written by the first author in the offshore fishing magazine, Tsuri-joho (Miyazaki 2017). This specimen was caught at the Onuki Fishing Port, Uraga Suido Channel, the Sea of Sagami in March 1966, and probably originated from the population of the Banzu intertidal flat of the Obitsu-gawa River of Tokyo Bay; its capture location was close to the biogeographic boundary between Tokyo Bay and the Sea of Sagami (i.e., edge effect in the context of ecology). Based on *gyotaku* sheets and a color photograph provided by citizens, it was determined that the number of scale rows corresponds with the number in *S. parvisquamis*, not *S. japonicus* (i.e., TRa ≥5). Only one *gyotaku* sheet of *S. parvisquamis* caught in Tokyo Bay has been known (Onoue 2001; Miyazaki and Murase 2020), so those shown in Fig. 24.7 are additional and secondary *gyotaku* records of *S. parvisquamis* from the bay. In addition, the image is the first color photograph of a specimen from the Tokyo Bay population, and is the oldest known color photograph of the species; moreover, it is the first verifiable record from the Uraga Suido Channel, the Sea of Sagami (see also Senou et al. 2006).

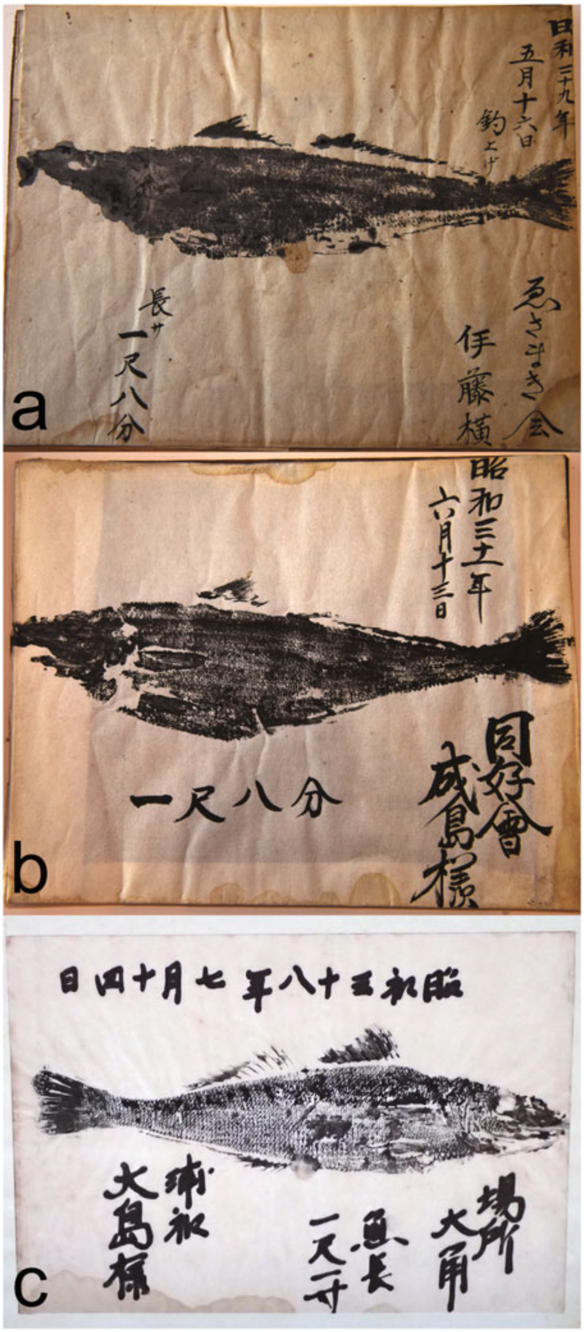

Fig. 24.7 Three additional sheets of *gyotaku* identified as *Sillago parvisquamis* from individuals collected from inner Tokyo Bay on 16 May 1954 (**a**), on 13 June 1956 (**b**), and on 14 July 1963 (**c**), have been stored at the fishing ship shop, Funayado-Yoshinoya, Urayasu City, Chiba Prefecture

In addition to assessing characters such as morphology and scale numbers, it may be possible to obtain DNA residue off *gyotaku* sheets, which could be used to provide data for studies in conservation or phylogeography. If so, *gyotaku* would have additional value as a primary source.

24.4 Applications and Future Prospects

Recent technological advancements of smart phones, waterproof digital cameras, and social

Fig. 24.8 Color photograph of *Sillago parvisquamis* caught at the fishing port of Onuki, Chiba Prefecture on March 1966 (KPM-NR 212427). (Photo by K. Kawashima)

networking services (SNS) have made easier the acquisition of biodiversity data via citizen science (e.g., Kobori et al. 2016; Toivonen et al. 2019). On one hand, Japanese society including companies and public officers promote the Sustainable Development Goals (SDGs) as their ideals to be achieved (e.g., Monitor Deloitte 2018; Acuti et al. 2020) but at the same time, developments causing biodiversity losses continue in Japan (e.g., Nishida et al. 2019). In the face of ongoing losses, the mining of current and historical biodiversity information such as those can be obtained from citizens' *gyotaku* sheets should continue. The positive effects of citizen science have been recognized by policy makers and the general public, and its influence and perceived value are increasing. For example, photographs of fishes provided by citizens contributed to the conservation for Japanese fish diversity, in particular regarding unusual phenomena and the prevention of the spread of non-native species (Miyazaki et al. 2020).

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25

Convention on Biological Diversity and Its Impact on Research, with Special Reference to Ichthyology

Masanori Nakae

Abstract

Outlines and backgrounds of the Convention on Biological Diversity and related international frameworks, in particular the Nagoya Protocol, and Access and Benefit-Sharing, that have been significantly impacting scientific studies, including ichthyological research, are reviewed. The Convention objectives have sometimes been misunderstood as referring only to "conservation of biological diversity," although two other objectives exist: "sustainable use of the components of biological diversity" and "fair and equitable sharing of the benefits arising out of the utilization of genetic resources." On the basis of Articles 19, 6, and 15 of the Convention, the Cartagena Protocol, National Biodiversity Strategies and Action Plans, and the Nagoya Protocol on Access and Benefit-Sharing were also established. The Cartagena Protocol was set up to ensure adequate levels of protection in the safe transfer, handling and use of living modified organisms that may have adverse effects on the conservation and sustainable use of biological diversity, with special focus on transboundary movements. To enrich biodiversity in Japan and achieve a society in harmony with nature through the maintenance and recovery of biodiversity, and the sustainable use of its components, the National Biodiversity Strategy of Japan 2012–2020 was established with long- and short-term targets, basic strategies, 13 national targets consistent with the five strategic targets of the Aichi Biodiversity Target, indicating 41 key action goals for the achievement of national targets, and 81 indicators for determining the achievement status of the latter. The Nagoya Protocol is a legally binding international framework, the main objective being fair and equitable sharing of benefits arising from the utilization of genetic resources, including appropriate access to such resources. However, the Protocol also clarifies that a person who wish to access/use biological resources of a foreign country has to establish mutually agreed terms with the provider, obtain a prior informed consent from the providing country, and share benefits arising from their utilization fairly and equitably. Because of the procedures, researchers are currently required to expend significant time and cost to newly access/use biological resources of foreign countries, even in non-commercial academic studies. In addition, domestic measures taken in Japan are also reviewed, with an emphasis on procedures for accessing fishes within Japan for research activities.

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Keywords

ABS · Access and benefit-sharing · Cartagena protocol · Laws · Nagoya protocol · Strategic plan for biodiversity

25.1 Introduction

Convention on Biological Diversity (CBD), adopted in 1993, has made a significant contribution to the conservation of biodiversity, through promoting the adoption of international frameworks for biodiversity conservation (e.g., *Cartagena Protocol*, *Strategic Plan for Biodiversity*, and *Nagoya Protocol*), establishment/determination of relevant domestic laws and strategies in each country (e.g., *National Biodiversity Strategy* and *ABS Guidelines* in Japan), and improvement of public awareness of world biological diversity. On the other hand, because each country has sovereign rights over its own natural resources, the CBD, especially in regard to accessing genetic resources and benefit-sharing, has had a significant impact not only on economic activities but also on scientific studies (including taxonomic, phylogenetic and ecological studies, and inventory surveys) related to conservation of biodiversity. Consequently, any researchers intending to access the biological resources of a foreign country must do so under the dictates of the CBD and Nagoya Protocol, even for non-commercial academic studies. In order to improve understanding of the convention and related frameworks, and reduce the risk of problems or difficulties for researchers (with particular emphasis on ichthyologists), outlines of and backgrounds to the CBD and related international frameworks, in particular the Nagoya Protocol and Access and Benefit-Sharing, and domestic measures taken in Japan are reviewed, and the procedures for accessing fish specimens in Japan for research activities emphasized.

25.2 Convention on Biological Diversity (CBD)

25.2.1 Pre-CBD

The importance of conservation of natural resources (including flora and fauna, and ecosystems) was initially set forth in the *United Nations Conference on the Human Environment* (also known as the *Stockholm Conference*) held in Stockholm, Sweden in June 1972 (United Nations 1973; Saishu 2011). Subsequently, the *United Nations Environment Programme* (UNEP) was established in the same year to “serve as a focal point for environmental action and coordination within the United Nation system” (United Nations Environment Programme 1994). UNEP convened an Ad Hoc *Working Group of Experts on Biological Diversity* (first meeting held in November 1988) following the 1987 Governing Council’s decision 14/26 of UNEP, being the origin of negotiations for the CBD (Secretariat of CBD 2005, 2021a). UNEP also established the Ad Hoc *Working Group of Technical and Legal Experts* in May 1989 to prepare an international legal instrument for the conservation and sustainable use of biological diversity (Secretariat of CBD 2021a). The Ad Hoc Working Group, which became the *Intergovernmental Negotiating Committee* (INC) in February 1991, contributed greatly to the charter of the CBD (*Nairobi Final Act of the Conference for the Adoption of the Agreed Text of the Convention on Biological Diversity*), adopted on May 22, 1992 (Secretariat of CBD 2005, 2021a).

UNEP stated “The Objective of this Convention is to conserve the maximum possible biological diversity for the benefit of present and future generations and for its intrinsic value. . .” (United Nations Environment Programme 1992), although the conservation of biological diversity was the only objective listed in “Article 1. Objectives” in an initial draft of the text (even in the informal proposal by the Chairman of INC and Executive Director of UNEP) on May 11, 1992. However, because delegations from developing countries at the seventh negotiating session/fifth session of the INC (May 11–19, 1992) claimed that two other objectives (i.e., sustainable use of the components of biological diversity, and fair and equitable sharing of the benefits arising from the utilization of genetic resources) should be included (Saishu 2011), the draft text of the CBD charter was expanded to include three main objectives (see below).

25.2.2 Outline of the CBD

After the charter of the CBD was adopted on May 22, 1992 at the *Conference for the Adoption of the Agreed Text* (held in Nairobi, Kenya), the CBD was ready for signature in June 1992 at the *United Nations Conference on Environment and Development* (UNCED; also known as the *Earth Summit*), held in Rio de Janeiro, Brazil (Secretariat of CBD 2005). It came into force on December 29, 1993 and currently has 196 Parties (168 Signatures; Secretariat of CBD 2021b), including Japan, which signed on June 13, 1992.

The CBD has three main objectives: (1) the conservation of biological diversity, (2) the sustainable use of the components of biological diversity, and (3) the fair and equitable sharing of the benefits arising out of the utilization of genetic resources (United Nations 1992, Article 1; see also Table 25.1). As shown in the Preamble of CBD, the contracting Parties are “conscious of the intrinsic value of biological diversity and of the ecological, genetic, social, economic, scientific, educational, cultural, recreational, and aesthetic values of biological diversity and its components” and “conscious also of the importance of biological diversity for evolution and for maintaining life sustaining system of the biosphere.” The CBD also reaffirmed that states have sovereign rights over their own biological resources, but are also responsible for conserving their biological diversity and for using their biological resources in a sustainable manner, and recognizing the desirability of sharing equitably any benefits arising from the use of traditional knowledge, innovations, and practices relevant to the conservation of biological diversity and the sustainable use of its components.

Because of the CBD, the relevant international frameworks, domestic laws, and domestic strategies of each signatory party have been adopted or determined (e.g., with respect of Article 6, 192 of 196 parties have currently developed one or more National Biodiversity Strategies and Action Plans; Secretariat of CBD 2021c). Regarding scientific studies, including ichthyology, it should be noted that Article 15 is related to the Nagoya Protocol and has had a significant impact (see below).

25.2.3 Related Initiatives in Japan

After the signing off the CBD in June 1992, Japan enacted the *Basic Environment Act* on November 19, 1993 (Act revised on 1 December 2018) (Government of Japan 2018). Although the purpose of the Act is to comprehensively and systematically promote policies for environmental conservation, it included conservation of biodiversity in the formulation of policies for environmental conservation (Article 14, paragraph 1, subparagraph ii).

Furthermore, the Government of Japan enacted a *National Biodiversity Strategy*, providing directions and targets for government measures regarding conservation and sustainable use of biological diversity, in October 1995 (Government of Japan 1995). The Act set forth two long-term targets (conservation of biodiversity and sustainable use of its components in Japan, including each biogeographical region, and each prefecture and municipality; and the appropriate management of large protected areas together with securing ecosystem connections between protected areas), and three short-term targets (ensuring no threat of extinction of fauna and flora in Japan; appropriate conservation of areas important for the conservation of biodiversity; and use of biodiversity components in a sustainable manner), together with additional requirements (e.g., designation and management

Table 25.1 Important articles of the Convention on Biological Diversity, mainly related to the Cartagena Protocol and Nagoya Protocol in terms of scientific studies

Cartagena Protocol	
Article 8	**In-situ Conservation**
(g)	Establish or maintain means to regulate, manage or control the risks associated with the use and release of living modified organisms resulting from biotechnology which are likely to have adverse environmental impacts that could affect the conservation and sustainable use of biological diversity, taking also into account the risks to human health
Article 19	**Handling of Biotechnology and Distribution of its Benefits**
3	The Parties shall consider the need for and modalities of a protocol setting out appropriate procedures, including, in particular, advance informed agreement, in the field of the safe transfer, handling and use of any living modified organism resulting from biotechnology that may have adverse effect on the conservation and sustainable use of biological diversity
4	Each Contracting Party shall, directly or by requiring any natural or legal person under its jurisdiction providing the organisms referred to in paragraph 3 above, provide any available information about the use and safety regulations required by that Contracting Party in handling such organisms, as well as any available information on the potential adverse impact of the specific organisms concerned to the Contracting Party into which those organisms are to be introduced
Nagoya Protocol	
Article 2	**Use of Terms**
	“Biological resources” includes genetic resources, organisms or parts thereof, populations, or any other biotic component of ecosystems with actual or potential use or value for humanity
	“Country providing genetic resources” means the country supplying genetic resources collected from in-situ sources, including populations of both wild and domesticated species, or taken from ex-situ sources, which may or may not have originated in that country
Article 15	**Access to Genetic Resources**
1	Recognizing the sovereign rights of States over their natural resources, the authority to determine access to genetic resources rests with the national governments and is subject to national legislation
3	For the purpose of this Convention, the genetic resources being provided by a Contracting Party, as referred to in this Article and Articles 16 and 19, are only those that are provided by Contracting Parties that are countries of origin of such resources or by the Parties that have acquired the genetic resources in accordance with this Convention
4	Access, where granted, shall be on mutually agreed terms and subject to the provisions of this Article
5	Access to genetic resources shall be subject to prior informed consent of the Contracting Party providing such resources, unless otherwise determined by that Party
7	Each Contracting Party shall take legislative, administrative or policy measures, as appropriate, and in accordance with Articles 16 and 19 and, where necessary, through the financial mechanism established by Articles 20 and 21 with the aim of sharing in a fair and equitable way the results of research and development and the benefits arising from the commercial and other utilization of genetic resources with the Contracting Party providing such resources. Such sharing shall be upon mutually agreed terms

of protected areas; ex situ conservation of endangered species; and promotion of nature education, research, and international cooperation). The Government of Japan revised this Act in March 2002, November 2007, March 2010, and September 2012 (see also below).

On June 6, 2008, the *Basic Act on Biodiversity*, establishing fundamental principles for conservation and sustainable use of biodiversity in line with the Basic Environment Act, came into force in Japan (Government of Japan 2008). The Act recognized fundamental principles for conservation and sustainable use of biodiversity (Article 3) and stipulated the formulation of a National Biodiversity Strategy (Article 11) and government responsibility for 13 fundamental policies, including preparation of a document clarifying policies to be implemented in consideration of biodiversity status, promotions of surveys, scientific and technological research, and environmental impact assessments pertaining to biodiversity at project planning stages (Articles 14–27).

25.3 Cartagena Protocol

Cartagena Protocol on Biosafety to the Convention of the Biological Diversity (Cartagena Protocol), an international treaty governing the movements of living modified organisms (LMOs), was adopted on January 29, 2000 at the *Extraordinary Meeting of the Conference of the Parties to the Convention of the Biological Diversity* (*EXCOP 1*; held in Montreal, Canada) and came into force on September 11, 2003 (Secretariat of CBD 2000a, 2021c). To date, 173 parties have ratified the Protocol (Secretariat of CBD 2021e).

The objective of the Protocol is "to contribute to ensuring an adequate level of protection in the field of the safe transfer, handling and use of LMOs resulting from modern biotechnology that may have adverse effects on the conservation and sustainable use of biological diversity, taking also into account risks to human health, and specifically focusing on transboundary movements" (Article 1). The Protocol includes 40 stipulated articles and three annexes, mainly to avoid adverse effects on the conservation and sustainable use of biological diversity by LOMs, by, for example, taking necessary and appropriate legal, administrative, and other measures by each Party (Article 2, paragraph 1), so as to ensure a manner that prevented or reduced risks of LMOs to biological diversity by those Parties (Article 2, paragraph 2), and establishment of a Biosafety Clearing House (Article 20).

The Cartagena Protocol was accepted by Japan on November 21, 2003, coming into force in Japan on February 19, 2004 (Secretariat of CBD 2021d). Furthermore, to devise measures that regulated the use of LMOs in order to protect conservation strategies and the sustainable use of biological diversity through international cooperation, *Act on the Conservation and Sustainable Use of Biological Diversity through Regulations on the Use of Living Modified Organisms* (*Cartagena Act*) came into force in Japan on February 19, 2004 [the current (revised) Act coming into force on April 1, 2019; Government of Japan 2021]. The Act categorizes the use of LMOs in Japan regarding Type 1 and 2 Uses: Type 1 Use not subject to measures required for Type 2 Use; and Type 2 Use undertaken with measures to prevent the dispersal of LMOs into the air, water, or soil outside facilities, equipment, or other structures in accordance with such measures or other measures as stipulated by the appropriate ministries (Article 2, paragraphs 5 and 6). Anyone wishing to make Type 1 Use (including creation or import) of LMOs must stipulate the regulations for each type of LMO, obtain approval from the appropriate authority (Article 4, paragraph 1), assess any adverse effect on biological diversity caused by Type 1 Use of each type of LMO (as stipulated), and submit to the appropriate authority a document detailing the results of the assessment (Article 4, paragraph 2). Anyone wishing to make Type 2 Use of LMOs must take containment measures during the period of that use (Article 12). For example, a researcher making such use of LMOs in Japan must keep and use those LMOs in laboratories with containment measures, so as to prevent any dispersal of them to the outside environment. Because genetically modified fishes have at no time been approved for Type 1 Use, it is illegal to maintain them without containment measures in Japan. Information pursuant to the Act, related domestic regulations, and a list of the approved LMOs under the Act are provided by the *Japan Biosafety Clearing House* (Japan Biosafety Clearing House 2021).

The *Nagoya-Kuala Lumpur Supplementary Protocol on Liability and Redress to the Cartagena Protocol on Biosafety* was adopted on October 15, 2010 at the *fifth meeting of the Conference of the Parties serving as the meeting of the Parties to the Cartagena Protocol on Biosafety* (COP-MOP 5), held in Nagoya, Japan, and came into force on March 5, 2018 [currently 48 parties (including Japan); Secretariat of CBD 2021f]. The objective of the Supplementary Protocol is "to contribute to the conservation and sustainable use of biological diversity, taking also into account risks to human health, by providing international rules and procedures in the field of liability and redress relating to living modified organisms" (Article 1).

25.4 Strategic Plan for Biodiversity

25.4.1 Strategic Plan 2002–2010, Including 2010 Biodiversity Target

The *Strategic Plan 2002–2010* was adopted at the *Sixth Conference of the Parties to the Convention of the Biological Diversity* (*COP 6*), held in the Hague, Netherlands, in April 2002 (Secretariat of CBD 2002a), whereby the Parties committed themselves "to achieve by 2010 a significant reduction of the current rate of biodiversity loss at the global, regional and national level as a contribution to poverty alleviation and to the benefit of all life on earth" (B. Mission). Subsequently, the *2010 Biodiversity Target* was endorsed by the *World Summit on Sustainable Development* (held in Johannesburg, South Africa, in 2002) and world leaders meeting at the *2005 World Summit of the United Nations* (held in New York, USA) (Secretariat of CBD 2006a). To facilitate the assessment of progress toward achieving the 2010 Biodiversity Target, the framework adopted at the COP 7 (held in Kuala Lumpur, Malaysia) in February 2004 included seven focal areas: reducing the rate of loss of biodiversity components; promoting sustainable use of biodiversity; addressing the major threats to biodiversity; maintaining ecosystem integrity; protecting traditional knowledge, innovations, and practices; ensuring the fair and equitable sharing of benefits arising out of the use of genetic resources; and mobilizing financial and technical resources. For each of the focal areas, 11 goals (e.g., promotion of the conservation of species diversity: Goal 2), 21 sub-targets (e.g., status of threatened species improved: Target 2.2), and many relevant indicators (e.g., coverage of protected areas) were identified (Secretariat of CBD 2004, 2006b).

Unfortunately, none of the 21 sub-targets of the 11 goals of the 2010 Biodiversity Target had been met at the global level by 2010 (Secretariat of CBD 2010). Four of the sub-targets (1.1: at least 10% of each of the world's ecological regions effectively conserved; 1.2: areas of particular importance to biodiversity protected; 3.1: genetic diversity of crops, livestock, and of harvested species of trees, fish, and wildlife and other valuable species conserved, and associated indigenous and local knowledge maintained; and 7.2: reduce pollution and its impacts on biodiversity) were categorized as "Not achieved globally but significant progress," three (4.2: unsustainable consumption, of biological resources, or that impacts upon biodiversity, reduced; 8.2: biological resources that support sustainable livelihoods, local food security, and health care, especially of poor people; and 9.1: protect traditional knowledge, innovations, and practices) as "Not achieved globally," and the remainder as "Not achieved globally but some progress." In the *Global Biodiversity Outlook 3* (GBO 3), the Secretariat of CBD (2010) noted one of the main reasons for the failure to meet 2010 Biodiversity Targets at the global level as "actions tended to focus on measures that mainly responded to changes in the state of biodiversity, such as protected areas and programmes targeted at particular species, or which focused on the direct pressures of biodiversity loss, such as pollution control measures." Subsequently, the Strategic Plan for Biodiversity was revised and updated as the *Strategic Plan for Biodiversity 2011–2020* (see below).

25.4.2 Strategic Plan for Biodiversity 2011–2020, Including Aichi Biodiversity Targets

The *Strategic Plan for Biodiversity 2011–2020*, adopted at the COP 10 (held in Nagoya, Aichi Prefecture, Japan) in October 2010, comprised six key elements, as follows: Rationale; Vision; Mission; Strategic Goals and the *Aichi Biodiversity Targets*; Implementation, Monitoring, Review, and Evaluation; and Support Mechanisms (Secretariat of CBD 2018). The Vision for the Strategic Plan was "Living in Harmony with Nature" wherein "By 2050, biodiversity is valued, conserved, restored and wisely used, maintaining ecosystem services, sustaining a healthy planet and delivering benefits essential for all people," the Mission being to "take effective and urgent action to halt the loss of biodiversity in order to ensure that by 2020 ecosystems are resilient and continue to provide essential services, thereby securing the planet's variety of life, and contributing to human well-being, and poverty eradication." Five goals within "Strategic Goals" included: (A) address the underlying causes of biodiversity loss by mainstreaming biodiversity across government and society; (B) reduce the direct pressures on biodiversity and promote sustainable use; (C) improve the status of biodiversity by safeguarding ecosystems, species, and genetic diversity; (D) enhance the benefits to all from biodiversity and ecosystem services; and (E) enhance implementation through participatory planning, knowledge management, and capacity building, incorporating the 20 Aichi Biodiversity Targets [e.g., "by 2020 all fish and invertebrate stocks and aquatic plants are managed and harvested sustainably, legally and applying ecosystem based approaches, so that overfishing is avoided, recovery plans and measures are in place for all depleted species, fisheries have no significant adverse impacts on threatened species and vulnerable ecosystems and the impacts of fisheries on stocks, species and ecosystems are within safe ecological limits" (Target 6) and "by 2015, the *Nagoya Protocol on Access to Genetic Resources and the Fair and Equitable Sharing of Benefits Arising from their Utilization* is in force and operational, consistent with national legislation" (Target 16)] (Secretariat of CBD 2020a). The CBD Parties were invited to set their own targets within the framework, taking into account national needs and priorities, while bearing in mind national contributions to the achievement of global targets (Secretariat of CBD 2018).

Based on a range of indicators, research studies and assessments (in particular the global assessment report on biodiversity and ecosystem services by the *Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*: *IPBES*), as well as national reports provided by parties on their implementation of the CBD, the progress made in implementing the Aichi Biodiversity Targets were assessed in the GBO 5 (published in September 2020). None of the 20 targets had been fully achieved at the global level, although six (Targets 9, 11, 16, 17, 19, and 20) had been partially achieved (Secretariat of CBD 2020b). Furthermore, within the 60 specific elements of the 20 targets, seven had been achieved (e.g., "17% of terrestrial and inland water areas conserved"), 38 showed progress (e.g., "aquaculture is sustainable"), 13 showed no progress or indicated a move away from the target (e.g., "conservation status of threatened species improved"), and two had unknown levels of progress (e.g., "pressures on vulnerable ecosystems minimized") (Secretariat of CBD 2020b).

25.4.3 National Biodiversity Strategy of Japan 2012–2020

Following the adoption of the *Strategic Plan for Biodiversity 2011–2020*, including the *Aichi Biodiversity Targets*, the Government of Japan established the *National Biodiversity Strategy of Japan 2012–2020, Roadmap towards the Establishment of an Enriching Society in Harmony with Nature* on September 28, 2012 (Government of Japan 2012). The National Biodiversity Strategy consisted of three parts (Part 1: strategy towards conservation and sustainable use of biodiversity, Part 2: roadmap for the achievement of the Aichi Biodiversity Targets, and Part 3: action plan on conservation and sustainable use of biodiversity), and set forth a long-term target for 2050 and a short-term target for 2020, as follows: "through the maintenance and recovery of biodiversity and the sustainable use of its components, current biodiversity in Japan will be enriched further and a society in harmony with nature will be achieved where humans can benefit from ecosystem services into the future" (long-term target); and "in order to halt the loss of biodiversity, effective and urgent action will be taken with the aim of achieving the Japanese national targets towards the achievement of the Aichi Biodiversity Targets" (short-term target). The National Biodiversity Strategy also set forth the five basic strategies (1—mainstreaming biodiversity in daily life; 2—reviewing and rebuilding relationships between man and nature in local communities; 3—securing linkages between forests, the countryside, rivers, and the sea; 4—taking action with a global perspective; and 5—strengthening the scientific foundation and utilizing it in policy making), 13 national targets (e.g., significantly reduce the rate of loss of natural habitats, as well as their degradation and fragmentation, by 2020: National Target B-1) consistent with the five strategic targets of the Aichi Biodiversity Targets, 41 key action goals (e.g., reduce the rate of loss of natural habitats by at least half or bring this close to zero in cases where it is possible to do so by 2020: key action goal B-1-2) for the achievement of its national targets, and 81 indicators [e.g., percentage of wetlands restored in particularly important water systems (a related indicator group of National Target B-1)] for determining the achievement status of the national targets. The National Biodiversity Strategy also showed approximately 700 (ca. 770 after revision) specific measures and policies aimed at implementing the conservation of biodiversity and the sustainable use of its components, in the form of the Government's action plan for the next 5 years.

In January 2021, the Government of Japan assessed the progress achieved in implementing the National Biodiversity Strategy of Japan 2012–2020 and reported that (1) although various measures and policies had been implemented in line with the five basic strategies, further strengthening of initiatives and launch of new initiatives were needed; (2) five of 13 national targets had been achieved and the other eight targets progressed; and (3) 45.2% of the ca. 770 specific measures and policies had been achieved, and 54.4% progressed (Inter-Ministerial Coordinating Committee to the CBD 2021). Furthermore, the Government of Japan concluded that in order to halt the loss of biodiversity and achieve the long-term target for 2050, further strengthening of initiatives, introduction of new initiatives to bring about changes in social and economic factors that indirectly affect biodiversity loss and their underlying values and behaviors, and improvement of structures within the national strategy, including evaluation approaches, were needed (Inter-Ministerial Coordinating Committee to the CBD 2021).

25.4.4 The Post-2020 Biodiversity Framework

To achieve the *2050 Vison for Biodiversity*, the need to depart from "business as usual" and make transformative change was mentioned in GBO 5. Eight transitions needed in aspects of the interface between human activity, human well-being, and nature were highlighted, as follows: (1) the land and forest transition, (2) the sustainable freshwater transition, (3) the sustainable fisheries and oceans transition, (4) the sustainable agriculture transition, (5) the sustainable food systems transition, (6) the sustainable cities and infrastructure transition, (7) the sustainable climate action transition, and (8) the biodiversity-inclusive One Health transition (Secretariat of CBD 2020b).

Although the post-2020 global biodiversity framework was supposed to be adopted during the COP 15, scheduled to take place on October 15–28, 2020 in Kunming, China, the Conference was postponed until May 17–30, 2021 and again until October 11–24, 2021, due to the COVID-19 pandemic (Secretariat of CBD 2020c, 2021g).

The post-2020 biodiversity framework will comprise 11 key elements in its first draft as follows: A: Background, B: The purpose, C: Relationship with 2030 Agenda for Sustainable Development, D: Theory of change, E: 2050 Vision and 2030 Mission, F: 2050 Goals and 2030 Milestones, G: 2030 action targets, H: Implementation support mechanisms, I: Enabling conditions, J: Responsibility and transparency, and K: Outreach, awareness, and uptake (Secretariat of CBD 2021h). The framework will have four long-term goals for 2050 (increase of natural ecosystems while reducing the number of threatened species and maintaining genetic diversity; evaluation, maintaining or enhancement of nature's contributions through conservation and sustainable use sharing benefits equitably; and benefits shared equitably, ensuring availability of means of implementation), one mission (i.e., 2030 Mission; "to take urgent action across society to put biodiversity on a path to recovery for the benefit of the planet and people"), eight milestones (2030 Milestones), to assess in 2030 progress toward the 2050 Goals (e.g., access and benefit-sharing mechanisms established in all countries), and 21 action-oriented targets for 2030 which, if achieved, will contribute to the 2030 Milestones and outcome-oriented goals for 2050 (e.g., Target 5: Ensure that the harvesting, trade, and use of wild species are sustainable, legal, and safe for human health). Detailed contents of the framework will be also discussed at the COP 15, for example, recommendations by the *Open-ended Inter-sessional Working Group* (established to support the preparation of the framework) on how to address digital sequence information on genetic resources within the context of the former (Secretariat of CBD 2021i).

25.5 Access to Genetic Resources and the Fair and Equitable Sharing of Benefits Arising from Their Utilization to the Convention on Biological Diversity (Access and Benefit-Sharing: ABS)

25.5.1 Background

Although the CBD came into force on December 29, 1993, Article 15 (Access to Genetic Resources) was not seriously considered until 1998 (Secretariat of the CBD 2002b). Access and Benefit-Sharing (ABS) was an official agenda item for the first time at the COP 4 (held in Bratislava, Slovakia, in May 1998) (Sumida and Watanabe 2011). Decisions made at the Conference resulted in the establishment of a *Panel of Experts on Access and Benefit-Sharing*, which made many suggestions at its first meeting (held in San Jose, Costa Rica) in October 1999 (e.g., "parties should establish a national focal point and one or more competent national authorities," "access and benefit-sharing strategies should be a component of national biodiversity strategies," "prior informed consent is the core requirement of effective access and benefit-sharing measures," and "contractual arrangements are presently the main mechanism for concluding access agreements and implementing benefit-sharing, and mutually agreed terms are at the heart of the contracting process") (Secretariat of CBD 1999). Thereafter, the Ad Hoc *Open-Ended Working Group on Access and Benefit-Sharing*, mandated to develop guidelines and other approaches to assist Parties with the implementation of access and benefit-sharing, was established at the COP 5 (held in Nairobi, Kenya) in May 2000 (Secretariat of CBD 2000b).

25.5.2 Bonn Guidelines on Access to Genetic Resources and Fair and Equitable Sharing of the Benefits Arising Out of Their Utilization (Bonn Guidelines)

The first draft of the *Bonn Guidelines on Access to Genetic Resources and Fair and Equitable Sharing of the Benefits Arising Out of Their Utilization* (*Bonn Guidelines*) was prepared at the first meeting of the Ad Hoc *Open-Ended Working Group on Access and Benefit-Sharing* (held in Bonn, Germany, on October 22–26, 2001), and adopted at the COP 6 (held in the Hague, Netherlands) in April 2002 (Secretariat of CBD 2001, 2002b). The Guidelines were prepared as a voluntary guide for both users and providers of genetic resources, thereby promoting transparency in the negotiation and implementation of access and benefit-sharing arrangements [paragraph 7, subparagraph (a), (h)], and showed the roles and responsibilities in access and benefit-sharing pursuant to Article 15 of the CBD (paragraphs 13–16), (e.g., "each Party should designate one national focal point for access and benefit sharing, and make such information available through the clearing-house mechanism") (paragraph 13), and steps in the access and benefit-sharing process (paragraphs 22–50). Furthermore, the Guidelines provided examples in developing and drafting legislative, administrative, or policy measures on access and benefit-sharing and contracts and other arrangements under mutually agreed terms (MAT) for access and benefit-sharing, in addition to an indicative list of typical mutually agreed terms (e.g., type and quantity of genetic resources, limitations on the possible use of material, and whether or not genetic resources could be transferred to third parties: paragraph 43), suggested elements for material transfer agreements (e.g., preambular reference to the CBD, description of genetic resources covered by the agreements, terms of benefit-sharing arrangements, and obligation to comply with the material transfer agreement; Appendix I), and provided examples of monetary and non-monetary benefits (e.g., access fees/fee per sample collected or otherwise acquired, research funding, sharing of research and development results, and collaboration, cooperation and contribution in education and training; Appendix II).

However, because the Guidelines were voluntary (not legally binding), some Parties called for the development of a legally binding international framework (Japan Bioindustry Association and Ministry of Economy, Trade and Industry, Japan 2012).

25.5.3 Nagoya Protocol on Access to Genetic Resources and the Fair and Equitable Sharing of Benefits Arising from Their Utilization to the Convention on Biological Diversity (Nagoya Protocol)

The *Nagoya Protocol on Access to Genetic Resources and the Fair and Equitable Sharing of Benefits Arising from Their Utilization to the Convention on Biological Diversity* (Nagoya Protocol), a legally binding international framework, was adopted on October 29, 2010 at the COP 10 (held in Nagoya, Aichi Prefecture, Japan) and came into force on October 12, 2014 (Secretariat of CBD 2011, 2015). To date, 131 parties (including Japan) have ratified the Protocol (Secretariat of CBD 2021j), the main objective of which is fair and equitable sharing of the benefits arising from the utilization of genetic resources, including by appropriate access to genetic resources (Article 1). The Protocol outlines core obligations for the Parties, e.g., appropriate access to genetic resources or traditional knowledge associated with genetic resources (e.g., Articles 6 and 7), benefit-sharing (e.g., Article 5), and compliance (e.g., Articles 15 and 16). Furthermore, the Protocol requires the Secretariat of the CBD to provide relevant information on national focal points and competent national authorities, received from the Parties, through the *Access and Benefit-Sharing Clearing-House* (ABSCH) (Article 13, paragraph 5). Accordingly, the Protocol has provided a transparent legal framework for the effective implementation of fair and equitable sharing of benefits arising out of the utilization of genetic resources (Secretariat of CBD 2015).

However, the Protocol also includes many articles that significantly affect many researchers (including ichthyologists) (Table 25.2) and clarifies the requirement for a researcher (or research team), who wishes to access and use biological (i.e., genetic) resources of a foreign country (i.e., a Party) for study, to enter into a contract with a related institution/department (e.g., to which a counterpart belongs) with mutually agreed terms, and obtain a prior informed consent (PIC) or approval (if needed) from a competent national authority of the Party providing the resources, in accordance with applicable national legislative, administrative, or policy measures of the Party, and also share benefits arising from such utilization fairly and equitably. Because of these procedures, it has been pointed out that the Protocol may be detrimental to promotion and encouragement of research that contributes to the conservation and sustainable use of biological diversity, particularly in international studies (e.g., Nakae et al. 2015; Schindel et al. 2015; Smith et al. 2017). In fact, some articles on arthropod taxonomy, which failed to follow the biodiversity law of another Party, have been retracted because approval had not been obtained from a competent national authority, or the relevant law had not been understood (e.g., Editor and Publisher of Journal of Natural History 2020; Kim et al. 2020).

Table 25.2 Key articles of the Nagoya Protocol

Article 5	**Fair and Equitable Benefit-Sharing**
1	. . . benefits arising from the utilization of genetic resources as well as subsequent applications and commercialization shall be shared in a fair and equitable way with the Party providing such resources that is the country of origin of such resources or a Party that has acquired the genetic resources in accordance with the Convention. Such sharing shall be upon mutually agreed terms
3	To implement paragraph 1 above, each Party shall take legislative, administrative or policy measures, as appropriate
Article 6	**Access to Genetic Resources**
1	In the exercise of sovereign rights over natural resources, and subject to domestic access and benefit-sharing legislation or regulatory requirements, access to genetic resources for their utilization shall be subject to the prior informed consent of the Party providing such resources that is the country of origin of such resources or a Party that has acquired the genetic resources in accordance with the Convention, unless otherwise determined by that Party
3	Pursuant to paragraph 1 above, each Party requiring prior informed consent shall take the necessary legislative, administrative or policy measures, as appropriate, to: (a) Provide for legal certainty, clarity and transparency of their domestic access and benefit-sharing legislation or regulatory requirements; (b) Provide for fair and non-arbitrary rules and procedures on accessing genetic resources; (c) Provide information on how to apply for prior informed consent;. . .; (e) Provide for the issuance at the time of access of a permit or its equivalent as evidence of the decision to grant prior informed consent and of the establishment of mutually agreed terms, and notify the Access and Benefit-sharing Clearing-House accordingly;. . .
Article 8	**Special Considerations**
	In the development and implementation of its access and benefit-sharing legislation or regulatory requirements, each Party shall: (a) Create conditions to promote and encourage research which contributes to the conservation and sustainable use of biological diversity, particularly in developing countries, including through simplified measures on access for non-commercial research purposes, taking into account the need to address a change of intent for such research; (b) Pay due regard to cases of present or imminent emergencies that threaten or damage human, animal or plant health, as determined nationally or internationally. . . .
Article 13	**National Focal Points and Competent National Authorities**
1	Each Party shall designate a national focal point on access and benefit-sharing . . . . The national focal point shall be responsible for liaison with the Secretariat
2	Each Party shall designate one or more competent national authorities on access and benefit-sharing. . . .
4	Each Party shall, no later than the date of entry into force of this Protocol for it, notify the Secretariat of the contact information of its national focal point and its competent national authority or authorities. . . .
5	The Secretariat shall make information received pursuant to paragraph 4 above available through the Access and Benefit-sharing Clearing-House. . . .
Article 14	**The Access and Benefit-Sharing Clearing-House and Information-Sharing**
1	An Access and Benefit-sharing Clearing-House is hereby established as part of the clearing-house mechanism under Article 18, paragraph 3, of the Convention. It shall serve as a means for sharing of information related to access and benefit-sharing. In particular, it shall provide access to information made available by each Party relevant to the implementation of this Protocol
Article 15	**Compliance with Domestic Legislation of Regulatory Requirements on Access and Benefit-Sharing**
1	Each Party shall take appropriate, effective and proportionate legislative, administrative or policy measures to provide that genetic resources utilized within its jurisdiction have been accessed in accordance with prior informed consent and that mutually agreed terms have been established, as required by the domestic access and benefit-sharing legislation or regulatory requirements of the other Party
2	Parties shall take appropriate, effective and proportionate measures to address situations of non-compliance with measures adopted in accordance with paragraph 1 above
Article 16	**Compliance with Domestic Legislation or Regulatory Requirements on Access and Benefit-sharing for Traditional Knowledge Associated with Genetic Resources**
1	Each Party shall take appropriate, effective and proportionate legislative, administrative or policy measures, as appropriate, to provide that traditional knowledge associated with genetic resources utilized within their jurisdiction has been accessed in accordance with prior informed consent or approval and involvement of indigenous and local communities and that mutually agreed terms have been established, as required by domestic access and benefit-sharing legislation or regulatory requirements of the other Party where such indigenous and local communities are located

(continued)

Table 25.2 (continued)

Article 17	Monitoring the Utilization of Genetic Resources
1	To support compliance, each Party shall take measures, as appropriate, to monitor and to enhance transparency about the utilization of genetic resources. . . .
2	A permit or its equivalent issued in accordance with Article 6, paragraph 3 (e) and made available to the Access and Benefit-sharing Clearing-House, shall constitute an internationally recognized certificate of compliance

25.5.4 Scientific Research and Studies Under the Nagoya Protocol

As mentioned above, any individuals or teams (users) intending to use and/or access biological resources from a foreign country (including field surveys) cannot currently avoid requirements of the CBD and Nagoya Protocol, even for non-commercial academic studies. For such studies, compliance with relevant measures (e.g., domestic ABS regulations of the providing country) is one of the most important aspects (also applicable to protected species or areas). Intending users must check for relevant measures in the providing country (e.g., by checking the website of the ABSCH: https://absch.cbd.int) and, if such measures are preset, must comply with them and obtain formal approval (i.e., a PIC) from a Competent National Authority (if necessary); if relevant measures are absent, intending users should endeavor to obtain approval from the government and establish a MAT with a provider (e.g., institution or organization in the providing country) as far as possible. To obtain the PIC, users are usually required to submit a copy of the MAT document, or in the case that such is unnecessary, must endeavor to establish a MAT with a provider as far as possible. The MAT should include, at least, requirements of the relevant measures, and (ideally) other items listed in the Bonn Guidelines or best practices of scientific communities [e.g., that of Consortium of European Taxonomic Facilities (Consortium of European Taxonomic Facilities 2015)]. After acquisition of the PIC and establishment of the MAT, the user accesses the biological resources to use them, if necessary, following a Material Transfer Agreement (MTA) contracted between the provider and user, and thereafter shares the benefits arising from their utilization fairly and equitably. The user may obtain an *Internationally Recognized Certificate of Compliance* (IRCC) from the ABSCH and provide related information to the Competent National Authority of the provider and/or the user's own country. Although the time and cost of obtaining a PIC and establishing a MAT are considerable, in the case of new access to or use of biological resources of foreign countries, the procedures are an unavoidable necessity.

A user wishing to access or use biological resources indirectly, subject to the CBD and Nagoya Protocol (e.g., museum specimens held outside the country of origin) should check the status of such resources; if they have been obtained with the compliance of related domestic measures of the providing country and are available for use by a third party, the latter can use the resources under the use conditions of the original PIC and MAT by contracting an MTA describing the use conditions of the material under the original PIC and MAT, and information about its legal provenance, including the country of access and date. If the status of such resources is unclear, the user is strongly encouraged against their use or advised to obtain new approval from the providing country.

Although it is not subject to the Nagoya Protocol, a person (or research team or institution) may need to consider regulations of access and benefit-sharing in the near future, regarding access to marine biological resources in areas beyond national jurisdiction, since the *United Nations Convention on the Law of the Sea* (UNCLOS), which came into force on November 16, 1994 (Division for Ocean Affairs and the Law of the Sea, United Nations 2020), stated that the International Seabed Authority shall provide for the equitable sharing of financial and other economic benefits derived from activities in the area (seabed and ocean floor and the subsoil thereof, beyond the limits of national jurisdiction) through any appropriate mechanism (Article 140, paragraph 2). Furthermore, *the Intergovernmental Conference on an international legally binding instrument under the United Nations Convention on the Law of the Sea on the conservation and sustainable use of marine biological diversity of areas beyond national jurisdiction*, that decided the convening of said Conference in accordance with resolution 72/249 (December 24, 2017) of *the 72nd session of the General Assembly of the United Nations* (United Nations 2018), will consider a draft of the text (comprising 70 Articles; United Nations 2019) of an international legally binding instrument under the United Nations Convention on the Law of the Sea, on the conservation and sustainable use of marine biological diversity of areas beyond national jurisdictions at its fourth session. Although the latter was intended to be held from March 23 to April 3, 2020, it was postponed to August 16–27, 2021, and re-postponed to the earliest possible available date in 2022 because of the COVID-19 pandemic (United Nations 2021).

25.5.5 Domestic ABS Measures in Japan (ABS Guidelines)

When Japan became a Party to the Nagoya Protocol (on August 20, 2017), the *Guidelines on Access to Genetic Resources and the Fair and Equitable Sharing of Benefits Arising from Their Utilization* (ABS Guidelines) also became effective (Minister of Finance, Japan et al. 2017). Key features in the Guidelines are as follows: (1) genetic resources or traditional knowledge accessed from a provider country prior to the date on which the Nagoya Protocol entered into force in Japan are not applicable (Chapter 2, No. 3, paragraph 1, subparagraph 5); (2) any person who obtained access to and imported genetic resources to which legislation in the provider country applies and has the relevant IRCC which posted on the ABSCH, has to report such to the Minister of the Environment, by stating that the genetic resources were lawfully accessed within 6 months of the date of the posting (Chapter 3, No. 1, paragraph 1); (3) the Minister of the Environment is to provide reported information to the ABSCH, and post information reported on the website of the Ministry of the Environment upon the request of the person who submitted the report (Chapter 3, No. 1, paragraph 4, subparagraph 1 and paragraph 5, subparagraph 1); (4) the Minister of the Environment is to request any person who reported relevant information regarding the obtaining and use of genetic resources to provide relevant information related to the utilization of genetic resources, after approximately 5 years have elapsed from the date on which the report was submitted, as appropriate (Chapter 3, No. 5, paragraph 1, subparagraph 1); (5) if any person is to provide genetic resources existing in Japan for utilization and seek the sharing of benefits arising from their utilization or is to utilize genetic resources existing in Japan and is requested to share benefits arising from their utilization, or who utilizes genetic resources to which the legislation in the provider country is applied in their access and is requested to share benefits arising from their utilization, that person is encouraged to conclude a contract on the said access for utilization that ensures the fair and equitable sharing of the said benefits (Chapter 4, No. 1, paragraphs 1–3); (6) any person who provides genetic resources existing in Japan for utilization, who utilizes genetic resources existing in Japan, and who utilizes genetic resources to which the legislation in the provider country is applied in their access is encouraged to include provisions on obligation of reporting concerning the implementation of the terms and other provisions for the sharing of information in the MAT established under the concluded contract (Chapter 4, No. 3); (7) the prior informed consent of the Government of Japan is not to be required for the provision of access to genetic resources existing in Japan (Chapter 5); (8) the guidelines are to be revised, as necessary, concerning access to genetic resources and the fair and equitable sharing of benefits arising from their utilization (Chapter 7, paragraph 2); (9) the need for developing laws and regulations concerning the provision of access to genetic resources existing in Japan is to be further considered within 5 years from the date on which the Guidelines come into effect, concerning access to genetic resources and the fair and equitable sharing of benefits arising from their utilization, and necessary measures are to be taken based on the results of the said consideration, as appropriate (Chapter 7, paragraph 3).

The Guidelines were mainly based on the report by the *Consultative Committee on the domestic measures to be taken for the ratification of the Nagoya Protocol* [15 experts from industries, academia, and NGO (Consultative Committee on the domestic measures to be taken for the ratification of the Nagoya Protocol 2013; Ministry of the Environment, Japan 2021a)]. The report, submitted to the Ministry of the Environment, with the expectation that specific work on domestic measures would be carried out based on the report, outlined five basic concepts for domestic legislation or regulatory requirements of the provider country on access to genetic resources or traditional knowledge associated with genetic resources to be taken, as follows: (1) it should contribute to the promotion of utilization in Japan of genetic resources, obtained in compliance with relevant laws and regulations of the providing country, and encourage voluntary efforts by users to comply with relevant laws and regulations of the providing country; (2) it should be designed to promote the utilization of genetic resources without interfering with academic and industrial activities, enabling Japanese users to gain the trust of providing countries; (3) it should be clear, certain, simple, and practical, without undue burden in implementation; (4) to ensure smooth international distribution of genetic resources, commonality of rules between Japanese laws (guidelines) and those of major advanced and other countries should be considered, as far as possible and appropriate; and (5) public awareness and support steps are needed (Consultative Committee on the domestic measures to be taken for the ratification of the Nagoya Protocol 2013).

25.5.6 Other Laws, Regulations, and Guidelines to be Aware of When Accessing Fishes in Japan for Scientific Research

Although the Government of Japan does not currently require prior informed consent for access to genetic resources existing in Japan (see above), a user intending to access fishes (including body parts) for scientific research may be subject to other existing regulations, in particular, for example, those relating to endangered species, protected areas, and fishery requirements (Table 25.3).

The *Act on Conservation of Endangered Species of Wild Fauna and Flora* came into effect in April 1993 (revised in 2019) primarily to conserve a satisfactory natural environment by ensuring the conservation of endangered species of wild fauna and flora (Government of Japan 1993). The Act set forth regulations of treatment of individuals (including body parts and processed products) of endangered species of wild fauna and flora, for example, prohibition of taking (Article 9), transfer (Article 12), export and import (Article 15), and display (Article 17). It also set forth regulations for habitat protection (Chap. 4). Unfortunately, the number of endangered species of wild fauna and flora in Japan, selected from the Red List of the Ministry of the Environment, has been increasing, currently numbering 395 (including species, subspecies, and variations) and including the following 10 fish species: *Acheilognathus longipinnis* (Cyprinidae), *Acheilognathus tabira nakamurae* (Cyprinidae), *Rhodeus smithii* (*Rhodeus atremius suigensis* in the list provided from the Ministry) (Cyprinidae), *Pseudorhodeus tanago* (*Tanakia tanago* in the list provided from the Ministry) (Cyprinidae), *Hemigrammocypris neglectus* (Cyprinidae), *Cobitis striata hakataensis* (Cobitidae), *Cobitis takenoi* (Cobitidae), *Parabotia curtus* (Botiidae), *Salanx ariakensis* (*Neosalanx reganius* in the list provided from the Ministry) (Salangidae), and *Gymnogobius nakamurae* (Gobiidae) (Ministry of the Environment, Japan 2021b). Any person who intends to

Table 25.3 A list of domestic laws related to biological diversity (particularly fish diversity) of Japan

Name of law	Act no.	Date of promulgation
Law for the Protection of Cultural Properties	214 of 1950	May 30, 1950
Natural Parks Act	61 of 1957	June 1, 1957
Nature Conservation Act[a]	85 of 1972	June 22, 1972
Act on Special Measures concerning Conservation of the Environment of the Seto Inland Sea[a]	110 of 1973	October 2, 1973
Act on Special Measures concerning Conservation of Lake Water Quality[a]	61 of 1984	July 27, 1984
Act on Conservation of Endangered Species of Wild Fauna and Flora	75 of 1992	June 5, 1992
Basic Environment Law	91 of 1993	November 19, 1993
Act on Special Measures concerning Rejuvenation of Ariake Sea and Yatsushiro Sea[a]	120 of 2002	November 29, 2002
Law for the Promotion of Nature Restoration	148 of 2002	December 11, 2002
Act on the Prevention of Adverse Ecological Impacts Caused by Designated Invasive Alien Species	78 of 2004	June 2, 2004
Basic Act on Biodiversity	58 of 2008	June 6, 2008
Act on Promoting the Treatment of Marine Debris Affecting the Conservation of Good Coastal Landscapes and Environments to Protect Natural Beauty and Variety[a]	82 of 2009	July 15, 2009
Act on Promotion, etc. of Activities for Conservation of Biodiversity through Coordination of Diversified Actors in Community[a]	72 of 2010	December 10, 2010
Act on the Promotion of Conservation and Sustainable Use of the Natural Environment in Local Natural Asset Areas[b]	85 of 2014	June 24, 2014
Act on concerning the Conservation and Restoration of Lake Biwa[b]	75 of 2015	September 28, 2015

[a] Translated from Japanese to English following the Japanese Law Translation Database System (2021)

[b] Translated from Japanese to English by the author

take or transfer living individuals of the above species for the purpose of academic research must first obtain permission of the Minister of the Environment (Article 10, paragraph 1 and Article 13, paragraph 1).

The *Law for the Protection of Cultural Properties*, which came into effect in August 1950, designated significant items of cultural properties as "Monuments," categorizing them as follows: shell mounds, ancient tombs, sites of castle towns, sites of forts or castles, old houses, and other sites of high historic or scientific value to Japan (Historic Sites); gardens, bridges, gorges, seashores, mountains, and other places of scenic beauty of high artistic or esthetic value for Japan (Places of Scenic Beauty); and animals, plants, minerals, and geological features of high scientific value to Japan (Natural Monuments) (Government of Japan 1950; Agency for Cultural Affairs, Japan 2021). The following four freshwater fishes are currently designated as Natural Monuments: *Acheilognathus longipinnis* (Cyprinidae), *Pseudorhodeus tanago* (Cyprinidae), *Parabotia curtus* (Botiidae), and *Tachysurus ichikawai* (Bagridae) (Database of National Designated Cultural Properties 2021). In addition, the following fishes living in nominated areas are also designated as Natural Monuments: *Anguilla japonica* (Anguillidae) in Kashiko-numa Pond (Fukushima Prefecture) and Kayugawa River (Gifu Prefecture), *Anguilla marmorata* (Anguillidae) in parts of Wakayama and Nagasaki Prefectures, and in Hahagawa River (Tokushima Prefecture), scarlet crucian carp ("Hibuna" in Japanese) *Carassius* sp. (Cyprinidae) in Harutori Lake (Hokkaido), long-finned crucian carp ("Tetsugyo" in Japanese) *Carassius* spp. (Cyprinidae) in Yutori-numa Pond (Miyagi Prefecture), *Pseudaspius hakonensis* (Cyprinidae) at Yokoyama (Miyagi Prefecture) and Yanaizu (Fukushima Prefecture), *Gasterosteus aculeatus* subsp. 1 (Gasterosteidae) in Hongan Shozu Pond (Fukui Prefecture), and *Pagrus major* (Sparidae) at Tainoura, east coast of Boso Peninsula (Chiba Prefecture). The habitats of the above fishes are also currently designated as Natural Monuments (*Pagrus major* at Tainoura is a Special Natural Monument) (Database of National Designated Cultural Properties 2021). Any alterations to the existing state of these protected species (including collection) and areas that would affect their preservation, requires approval from the Commissioner for Cultural Affairs or prefectural/municipal Board of Education (Article 125, paragraph 1; Committee for the Protection of Cultural Properties 1951). Because many areas, such as ponds and marshes in Japan are also designated as Natural Monuments, collecting fishes or other activities in these areas may be subject to Law.

National and Quasi-national Parks in Japan, 34 and 57 parks, respectively (Ministry of the Environment, Japan 2021c; National Parks Foundation 2021), also designate protected areas in each park by the *Natural Park Act* (revised in December 2019; Government of Japan 2019). Such protected areas include Special Protection, Special, and Marine Park Zones. To obtain fishes, all species in the Special Protection Zone, and designated species in the Special and Marine Park Zones require approval from the Minister of the Environment or a prefectural governor (Articles 20–24).

In addition to the Government of Japan, prefectural and municipal governments may also designate fish species as protected species (e.g., as prefectural endangered species of wild fauna and flora or as Natural Monuments) and their habitats as protected areas, by relevant ordinance. Furthermore, almost all prefectural governments designate no-fishing areas, no-fishing seasons, protected species (particularly small individuals), fishing methods to be used (e.g., electrofishing is not allowed), and other rules determined by regulations on fisheries (both for sea and inland waters).

25.5.7 Summary of Procedures for Access to/Use of Fishes Existing in Japan for Scientific Research

In cases of access to/use of fishes in Japan or fish specimens obtained from Japan after May 18, 2017, a person belonging to a foreign institution is strongly encouraged to conduct the following procedures (see also Fig. 25.1):

1. Check whether or not the fish (or sample, including tissue for DNA analysis) is a protected species; if so, that person is requested to obtain approval from the head of the related ministry (i.e., the Minister of the Environment or Commissioner for Cultural Affairs) or prefectural/city Board of Education.
2. In the case of a field survey, check whether or not the site of the survey includes a protected area; and whether or not the survey is subject to regulation of fisheries; if the area includes a protected area, a request for approval should be made to the head of the related ministry (i.e., the Minister of the Environment or Commissioner for Cultural Affairs) or prefectural/city Board of Education; if the survey is subject to regulation of fisheries, approval should be obtained from the prefectural government administering the survey site.
3. Check whether or not a PIC from a Competent National Authority is needed (note that the Government of Japan does not require a PIC, at the time of writing this chapter, July 2021; see above).

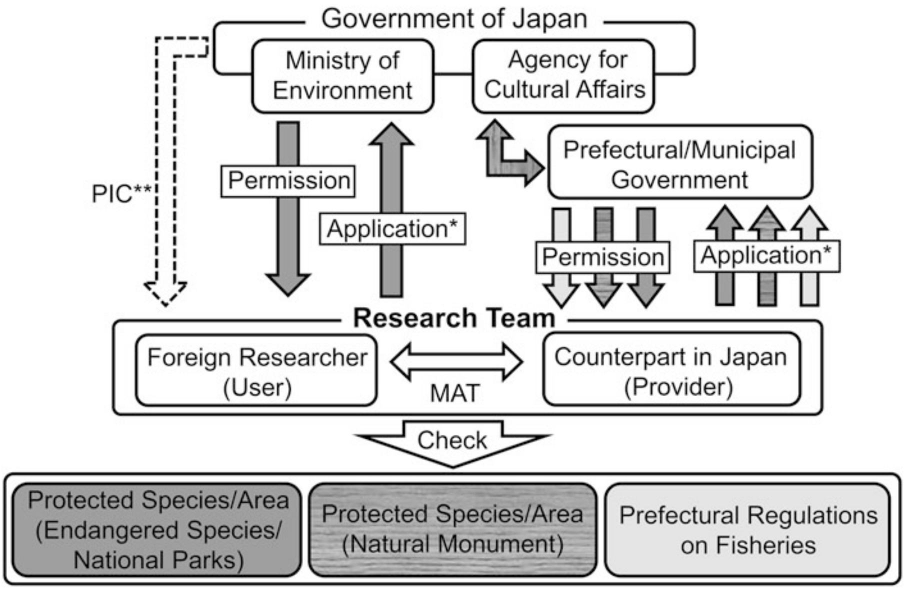

Fig. 25.1 Schematic chart of a summary of procedures to newly access/use fishes in Japan for scientific research. * if necessary; ** the Government of Japan does not require a PIC, as of 2021

4. Establish a MAT between institutions (home institution and a Japanese counterpart institution), such being encouraged to include items outlined in the Bonn Guidelines or best practices of scientific communities [e.g., fair and equitable benefit-sharing, allocation of benefits arising from the utilization of the biological resources (i.e., fishes/samples) to the conservation and sustainable use of the biological diversity, and sharing of information concerning implementation of the MAT through its provisions].

To obtain approval from a related public office or other organization smoothly, it is advisable to obtain the assistance of a Japanese counterpart (because of the language barrier), in particular regarding communication with local municipalities.

25.5.8 Consultation Services on the ABS in Japan

In Japan, six Ministries are concerned with the operation of ABS Guidelines, each having set up a consultation desk, as follows: Ministry of the Environment (relevant to overall operation of the Guidelines); Ministry of Education, Culture, Sports, Science and Technology (academic research); Ministry of Agriculture, Forestry and Fisheries [agriculture, forestry, fisheries (e.g., breeding), and the food industry]; Ministry of Health, Labour and Welfare (pharmaceuticals); Ministry of Economy, Trade and Industry [mining and manufacturing production (biochemical industry)]; and Ministry of Finance (alcoholic beverages and tobacco) (Ministry of the Environment, Japan 2021d).

With regard to academic research activities, the National Institute of Genetics has established the *ABS Support Team for Academia* since 2012, currently under the National BioResource Project (NBRP) of the Japan Agency for Medical Research and Development (AMED), at the request and with the support of the Ministry of Education, Culture, Sports, Science and Technology. The ABS Support Team helps researchers in Japan, via educational and support activities, including seminars, support for access to genetic resources, and establishment of systems in research institutions to deal with ABS matters (ABS Support Team for Academia 2021). Three institutions, the Material Management Center, Kyushu University (supporting the acquisition of genetic resources in the field of biotechnology and the development of tools such as contract templates), Tsukuba Plant Innovation Research Center, University of Tsukuba (supporting genetic resource acquisition, considering the role of genetic resources in the field of breeding and horticulture, and related seed banks). and Makino Herbarium, Tokyo Metropolitan University (supporting the acquisition and use of genetic resources in the field of biodiversity research based on studies of ABS-related case studies in Asia), have also been active since 2017 as sub-core Facilities of ABS support for the NBRP (National BioResource Project 2021).

The Japan Bioindustry Association (JBA) has made also great contributions to compliance for ABS of users in Japan, via a wide range of activities (Japan Bioindustry Association 2021). The JBA provides support mainly to the private sector, but also to academia and government, through collaboration with the Ministry of Economy, Trade and Industry (METI). The JBA and METI produced *Guidelines on Access to Genetic Resources for Users in Japan, Second Edition* in March 2012 (Japan Bioindustry Association and Ministry of Economy, Trade and Industry, Japan 2012).

Furthermore, many universities and institutions have established regulations, policies, and guidelines on the ABS (e.g., Kyushu University 2018; The University of Tokyo 2019; National Museum of Nature and Science 2015). Working groups on ABS have also been established in academic societies in Japan, for example, the Union of the Japanese Societies for Systematic Biology and the Japanese Society for Plant Systematics (Union of the Japanese Societies for Systematic Biology 2021; Japanese Society for Plant Systematics 2021). The ABS Working Group of the Ichthyological Society of Japan, established in 2015, has been also assisting members of the Society (Ichthyological Society of Japan 2021).

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