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

15

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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.

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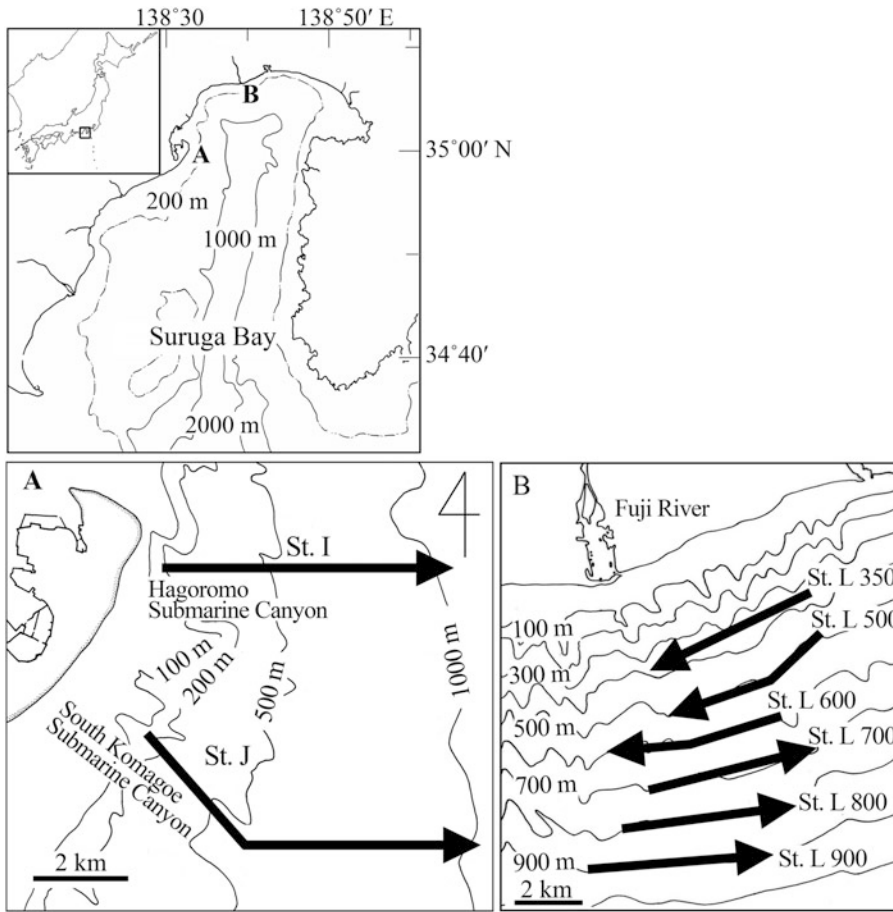
Fig. 15.1 Sampling stations for the near-bottom layer in Suruga Bay, southern Japan. *A* off mouth of Fuji River; *B* off Miho. Arrowed lines indicate range and direction of towed larval net

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
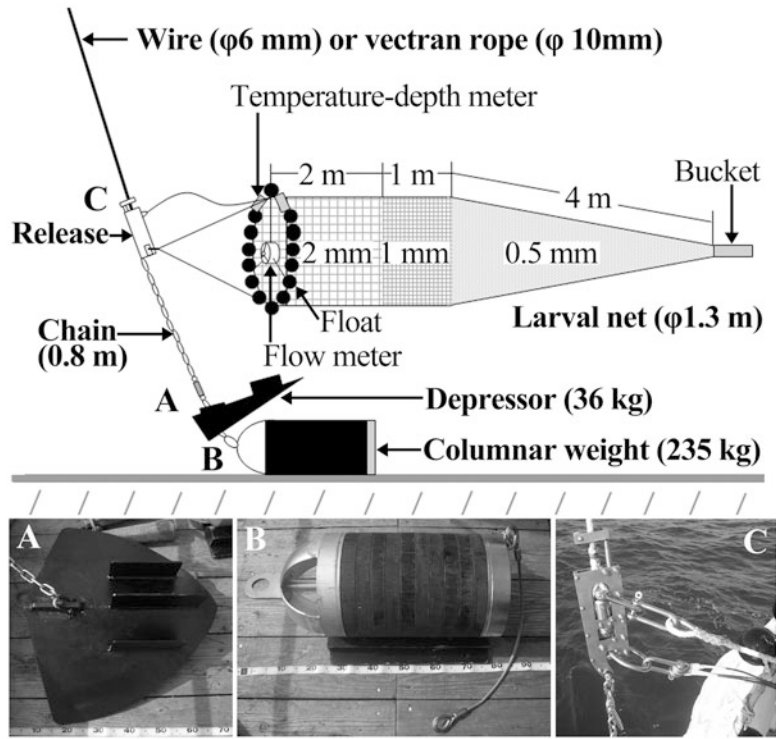
A total of 582 fishes, representing 57 species (plus unidentified taxa) in 38 genera (23 families), were collected by near-bottom sampling. Species and individual numbers were highest for adults (53.3%, 55.0% respectively), followed by juveniles (29.4%, 39.8%) and larvae (17.3%, 5.2%) (including postflexion, 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)
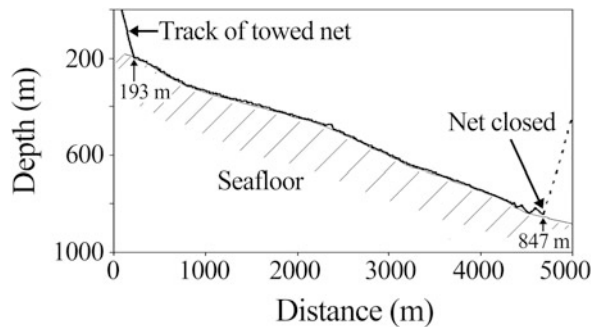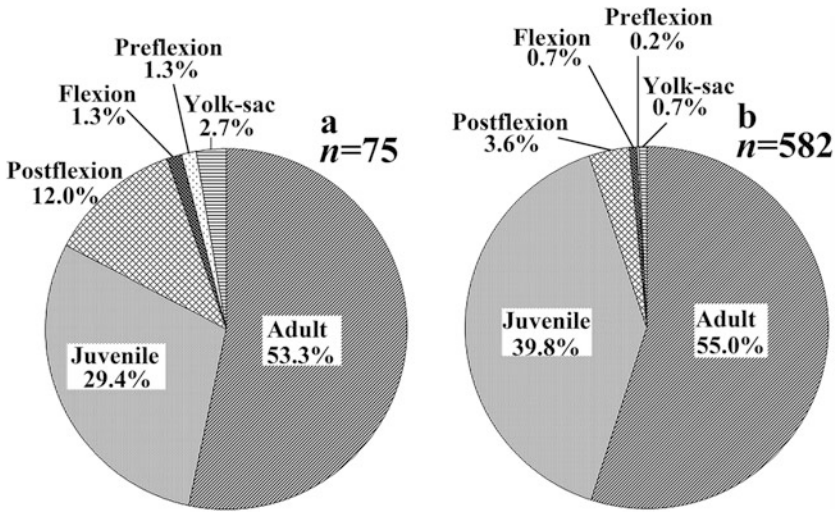
Fig. 15.4 Species (including unidentified taxa) (**a**) and individual (**b**) numbers in each developmental stage of deep-sea fishes occurring in the near-bottom layer of the upper continental slope in Suruga Bay

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 ($\geqq 5\%$) were *Polymetme elongata* (Phosichthyidae) ($n = 76$), *Coelorinchus kishinouyei* (Macrouridae) ($n = 55$),
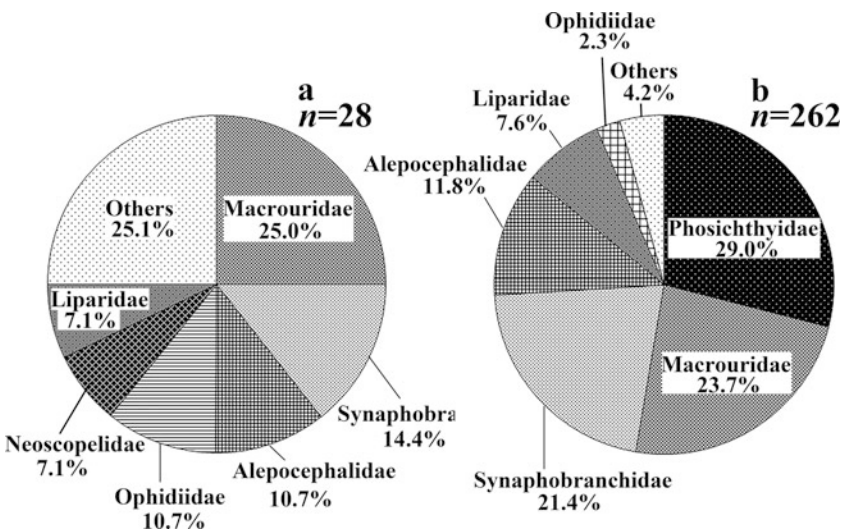

Fig. 15.5 Species (including unidentified taxa) (**a**) and individual (**b**) numbers in each family of larvae and juveniles occurring in the near-bottom layer of the upper continental slope in Suruga Bay

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

Type	Family	Species (types)	Near-bottom						Water column			
			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-

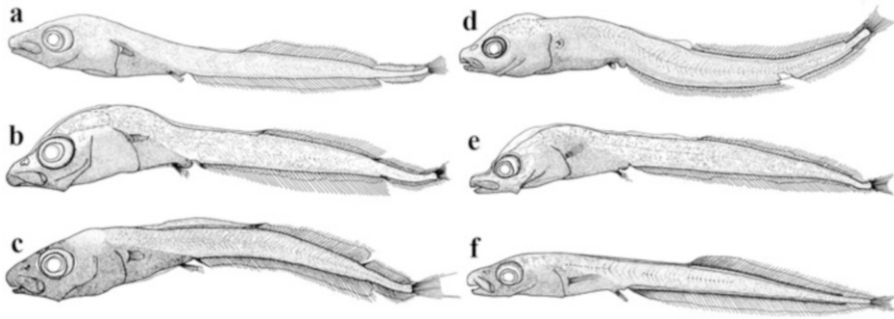**Fig. 15.6** Larvae and juveniles of *Leptoderma lubricum* (**a**–**c**) and *Leptoderma retropinnum* (**d**–**f**). (**a**) 26.9 mm SL, postflexion stage; (**b**) 31.8 mm SL, juvenile stage; (**c**) 42.9 mm SL, juvenile stage; (**d**) 22.2 mm SL, yolk-sac stage; (**e**) 28.4 mm SL, juvenile stage; (**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 $\pm$ standard deviation, 2389.0 $\pm$ 475.7) (*L. retropinnum*), the number of well-developed ovarian eggs being 69 (maximum diameter 3.45 mm) and 22–46 (34.3 $\pm$ 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
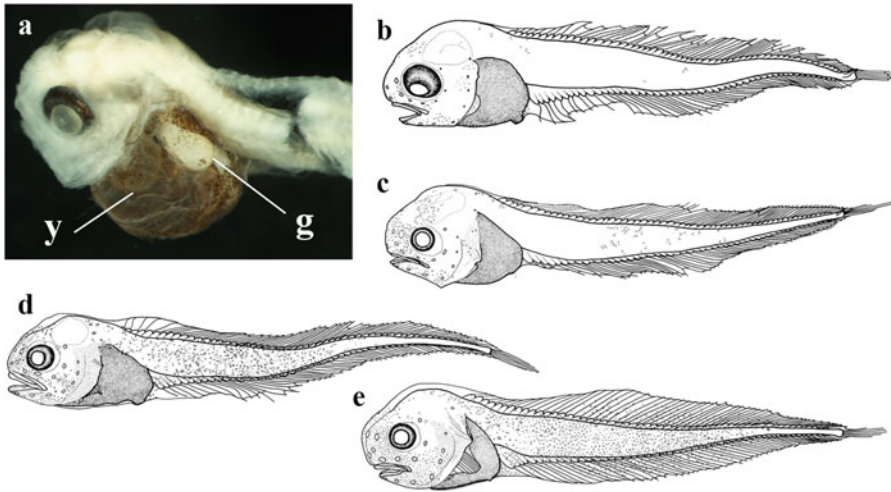
Fig. 15.7 Larvae and juveniles of *Paraliparis dipterus*. (**a**) photograph of 5.6 mm SL, yolk-sac stage; (**b**) 6.4 mm SL, yolk-sac stage; (**c**) 7.3 mm SL, flexion stage; (**d**) 10.1 mm SL, postflexion stage; (**e**) 11.2 mm SL, juvenile stage. *y* Yolk-sac, *g* gut

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-
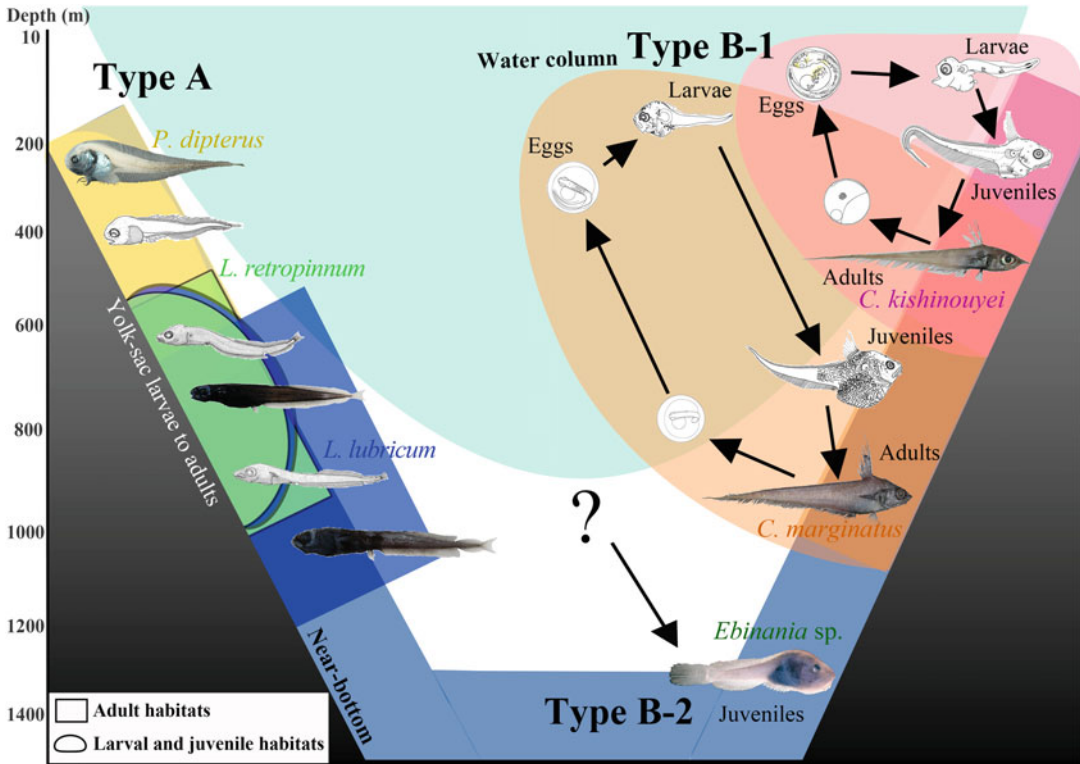
Fig. 15.8 Illustration of three ecological types based on the ontogeny of near-bottom layer species on the upper continental slope of Suruga Bay. *Leptoderma lubricum* and *Leptoderma retropinnum*: Takami and Fukui (2010);

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], Paralepidae[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	Antennariidae, 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, Draconettidae, 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, Mugilidae, 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	Notacanthiformes[b], Chaunacidae
>60 to ≦70	Nemichthyidae, Clupeidae, Diretmidae, Pegasidae, Cheilodactylidae, Bathymasteridae, Pholidae, Trichonotidae, Caproidae, Gempylidae	Bregmacerotidae, Malacanthidae, Paralichthyidae,	Congridae, Ceratiidae, Callanthiidae,	
>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 ($\leqq$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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