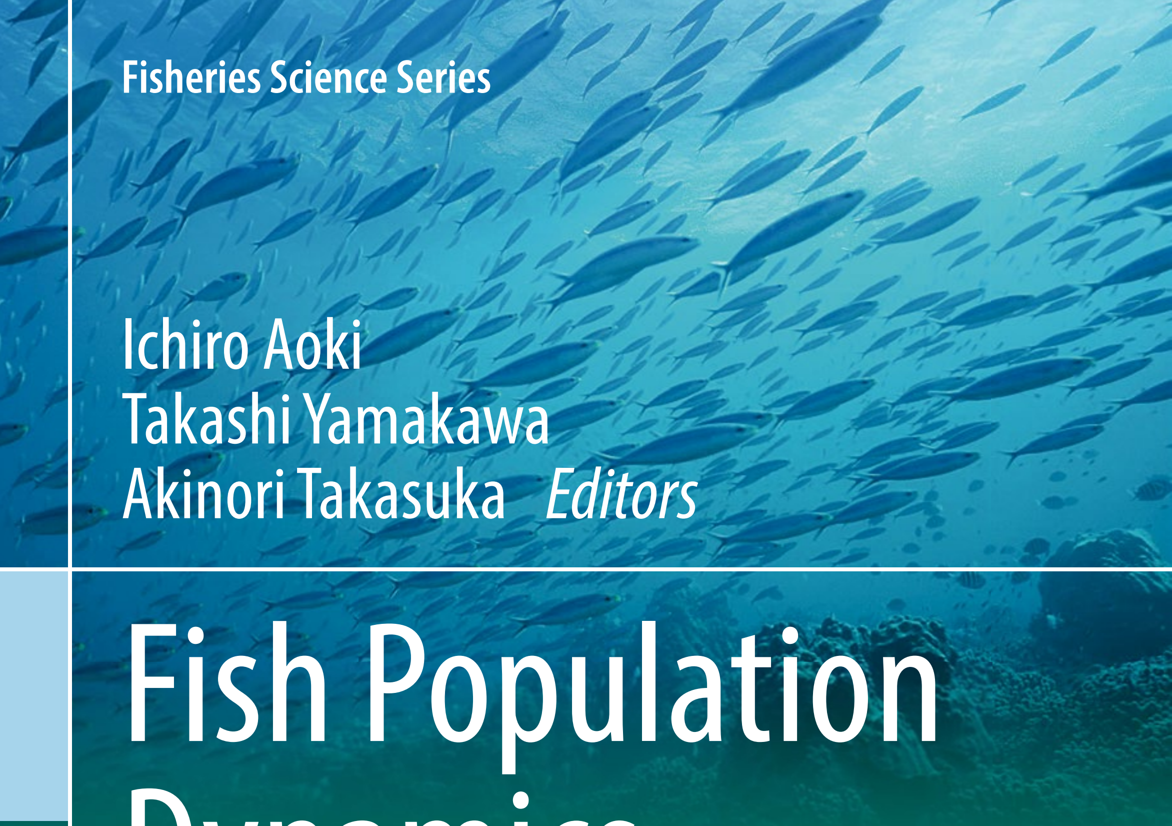

Fisheries Science Series

Ichiro Aoki
Takashi Yamakawa
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Fish Population Dynamics, Monitoring, and Management

Sustainable Fisheries in the Eternal Ocean

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Editors

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Foreword to the Series

We all have to survive, and most of our food originates from that grown on land, but we can't overlook food from the sea. We catch creatures living in the water ecosystem by fishing techniques and eat them raw or cooked. That whole process and related activities are collectively called "fishery," and fishery is supported by fishery science that relates to a vast range of fields.

Fishery science brings us much knowledge—biological knowledge of the life in water; knowledge about their habitats and environment; knowledge to utilize these lives; political and administrative knowledge to organize social activities and system to distribute fishery products; technical and engineering knowledge of ships, fishing equipment, seaports, and harbors; and so on. It covers a great variety of subjects, and each subject contains both basic and applicative aspects relating to and essential to one another. To have fishery science prosper in human society, none of them can be ignored.

This series includes many of the aqua-bioscience fields and aquatic environment fields as the base of fishery science.

In this Fisheries Science Series, we provide you with carefully selected up-to-date topics of excellent works in the fields of fishery science. We hope our series can contribute to the development of fishery and the welfare of people worldwide.

Tokyo, Japan
July 2017

Katsumi Aida
Series Editor-in-Chief

Preface

We humans since prehistory might have received benefits of the ocean in the belief that the seemingly vast ocean holds unlimited and eternal resources that can be exploited. However, such an assumption was shown to be false in the twentieth century. The issue of overfishing has been extensively examined for various ocean ecosystems all over the world. Moreover, climate impacts on fisheries resources have received much attention during the last decades. This combination of natural and human impacts has led to difficulties in reliable prediction of resource availability. Despite considerable research progress, accurate prediction of resources remains a serious challenge for fisheries science in the twenty-first century. To achieve sustainable exploitation so that it is an eternal ocean, we will need to understand population dynamics of fisheries resources, monitor fisheries and ecosystems, and adopt sound management strategies. This book is intended to evoke discussion about optimizing resource use to enable "sustainable fisheries in the eternal ocean" for both the present and future generations. Our perspectives are presented in the last chapter. The editors thank all the authors for their efforts to contribute to this book. Sincere thanks are also due to reviewers, Series editors, and the staffs of the Japanese Society of Fisheries Science for providing helpful suggestions and supports.

Tokyo, Japan
Tokyo, Japan
Yokoham, Japan
April 2018

Ichiro Aoki
Takashi Yamakawa
Akinori Takasuka

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Part II Monitoring Systems

Part III Management Models

Part IV Perspectives

Chapter 1
Introduction

Ichiro Aoki, Takashi Yamakawa, and Akinori Takasuka

Abstract This introductory chapter begins by describing trends in the world's marine capture fisheries and outlines what are the unique features of fisheries resources and what are the critical issues faced in optimizing their exploitation. Adaptive strategies in response to natural variability will increasingly enable the sustainable exploitation of fisheries resources and development of effective response to optimize fisheries. Multidisciplinary monitoring for real-time information and nowcasting is required to manage fisheries resources which are inherently variable. The aim and concept of this book as well as the structure and relationship of each theme are also briefly introduced.

Keywords Fisheries resources · Sustainable exploitation · Uncertainty

1.1 Trends in World Marine Capture Fisheries

Water covers about 70% of the surface of the earth. Since prehistoric times humans have caught and utilized marine organisms living in marine ecosystems. In our diet, on a global average for 2013, seafoods provide 17% of animal protein and 6.7% of all protein (FAO 2016a). As the world's population is increasing, the supply of marine products is bearing a greater importance not only for the supply of animal

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protein but also the maintenance of life and health since seafood contains a variety of essential micronutrients with beneficial health effects.

The world production of marine capture fisheries made rapid progress since the 1950s by innovation of fishing technologies and exploitation of new fisheries resources and fishing grounds. Total global marine capture production increased from 17 million tons in 1950 to a peak of 88 million tons in 1996 (Fig. 1.1). The sustained growth corresponds to an average annual growth rate of 9% during this period. Since this peak, however, the marine capture production has shown a slight tendency to decline, being 81.5 million tons in 2014, in contrast to the world's marine aquaculture production that has continued to grow in the twenty-first century (FAO 2016a). There has been no increase in the marine capture production levels in the last two decades (Fig. 1.1). The world's capture fishery yields seem to be approaching an upper limit of potential yield from the sea, considering discards and unreported catches (Garcia and de Leiva Moreno 2003).

Global marine fishery catches are dominated by anchovies and sardines which commonly belong to Clupeiformes, notably by the Peruvian anchovy (*Engraulis ringens*), Japanese sardine (*Sardinops melanostictus*), and South American sardine (*Sardinops sagax*). Their stock levels fluctuate widely because of natural causes (Chavez et al. 2003). In the early 1970s, catches of Japanese sardine and South American sardine began to increase while those of Peruvian anchovy decreased (Fig. 1.1). In the 1980s, the two species of sardines were very abundant and accounted for 10–15% of world marine capture production. Then in the 1990s, Peruvian anchovy catches again began to increase, and alternation occurred in the

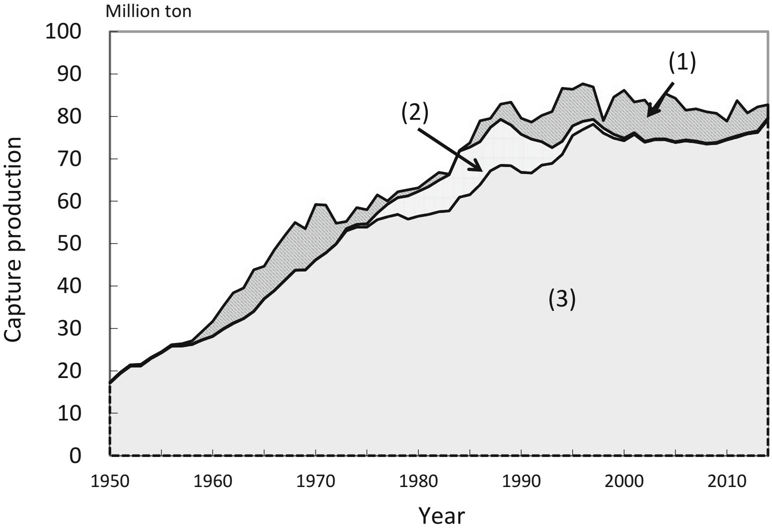

Fig. 1.1 Trend in world marine capture production, divided into three groups: (*1*) Peruvian anchovy, (*2*) Japanese sardine and South American sardine, and (*3*) others excluding these three fish species (Data from FAO 2016b)

catches of sardines and anchovy (Fig. 1.1). It is well known that catches of anchovies and sardines fluctuate with opposite phases in various sea regions over a scale of decades (see Chap. 3). Although world marine catches have shown a gradual decrease in the twenty-first century, catches excluding these three fish species have stabilized in the range of 73–75 million tons and have recently shown a slight increase from 2010 (Fig. 1.1).

According to an FAO assessment of global trends in the state of world marine fish stocks from 1974 to 2013 (FAO 2016a), the proportion of fully fished stocks has changed little at a level of 50%; then recently it has risen to 58.1% in 2013. The fraction of overfished stocks has continued to increase from 10% in 1974 to 31.4% in 2013. In contrast, the percentage of underfished stocks has decreased from 40% in 1974 to 10.5% in 2013. Global capture fisheries production can be considered to be in an unstable equilibrium. We are now standing at a critical watershed for the sustainable exploitation of marine fisheries resources. It is likely that if fish stocks continue to be exhausted, this unstable balance will be lost, and global catches even excluding anchovies and sardines will decline.

1.2 Nature of Fisheries Resources

Fisheries resources have three important features (Fig. 1.2). First, fish stocks are reproducible and renewable resources that can increase in abundance by reproduction and decrease by mortality. The turnover rate (P:B ratio), the ratio of production (P) to biomass (B) of primary producer (phytoplankton), is two orders higher in the sea than on land (Furuya 2009). The difference leads to the higher P:B ratio of marine animals. Therefore material circulation and organic production turn over at a considerably higher rate in marine ecosystems where primary production is controlled by microscopic phytoplankton. This means that fish stocks naturally possess a high capability for renewability and restorability, though a limit of the carrying capacity is imposed. Optimization of this biological function of reproduction leads to efficient sustainable utilization of fisheries resources.

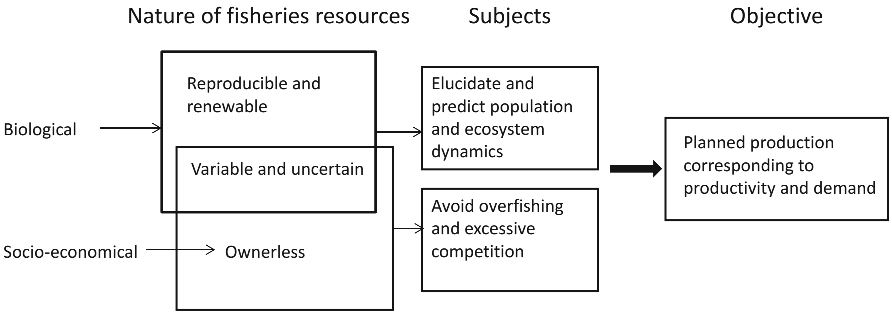

Fig. 1.2 Nature of fisheries resources and their sustainable exploitation

The second feature is that fish stocks show inherent variability and uncertainty in space and time. In general, a female fish spawns hundreds of thousands to millions of small eggs of about 1 mm diameter. The high fecundity of fish ensures a high renewability in stocks and, on the other hand, is a cause of the large variability in abundance. The abundance and distributions of fish stocks are under the influence of oceanic and climatic variability. Fisheries resources are renewable but subject to large and sometimes unpredictable change. This uncertainty is the crux of fisheries management and a potential cause of overfishing (Fig. 1.2).

The third feature is that fish in the sea before being caught are ownerless, common things of which no one has the property rights while fishing effort or catch amount can be regulated. This characteristic brings fishers into competition on a "first come, first served" basis and leads to overfishing and financially costly fishing (Fig. 1.2). However, being different from the first and second features which are based on biological processes, this is a socioeconomic problem that can be solved by changes in human behavior.

The above three features enable insights into a way forward for sustainable exploitation of marine biological resources. The first feature of reproduction and the second feature of uncertainty present positive and negative aspects of biological properties, respectively. We must consider ways of deriving benefits of the first feature, while avoiding risks and competition induced by the second and third features. Planned production in fisheries corresponding to ocean productivity and social demands can be realized by elucidation and prediction of stock and ecosystem dynamics and by avoiding overfishing and excessive competition (Fig. 1.2).

1.3 Fish Stock Variability and Marine Ecosystem Dynamics

Most marine fish species spawn a large number of small eggs. The survival of eggs and larvae in the early life stages is extremely low and varies among cohorts or among years with the environmental variations in the oceans. The growth and development of larvae and juveniles are key processes in the linkage between variations in the oceans and variability in fish abundances. Environmental variability, such as changes in temperature and food availability, affects growth and development of larvae and juveniles. Their conditions determine the survival rates of larvae and juveniles and ultimately the recruitment to and abundance of fish stocks. The proximate factors affecting growth and development are the suitability of temperature and the food environment that larvae encounter primarily by physical forcing in ocean dynamics in terms of optimal temperature and feeding habit for the larvae. The suitability is a basic principle in the mechanism of fish stock variability.

In the last two decades, it has been clarified that many fish stocks show wide fluctuations driven primarily by cyclical fluxes of climatic and oceanic variations that occur over periods of decades (Drinkwater et al. 2010). Structural changes in the whole system including the climate, oceanographic features, and marine ecosystem have been called a regime shift (Kawasaki 2013). The concept of a regime shift forms a new principle in the pattern of marine fish population dynamics. It implies that, first, individual fish populations alternate between high and low abundance levels in response to large-scale environmental regimes with a periodicity of several decades. Secondly, at the same time, dominance of species switches among species as a response at the community level. Long-term changes in abundance related to climate variations are observed in clupeoids, salmonids, gadoids, squids, and shellfish (e.g., Kawasaki 1991; Drinkwater et al. 2010; Rothschild 1991; Sakurai et al. 2000; Kodama et al. 2002). These species can be classified into two groups by favorable climatic regime and corresponding changes in abundance (Klyashtorin 2001): one represented by sardine and another by anchovy. It is interesting that in Japanese waters, the catches of Japanese common squid (*Todarodes pacificus*), though not fish, have fluctuated synchronizing with catches of Japanese anchovy and jack mackerel (*Trachurus japonicus*) in terms of phase and amplitude over the last several decades (Sakurai et al. 2013).

It is of importance that there are apparent opposite changes of decreases in some stocks while increases in others. Assuming that this is the provision of nature in the production of marine living resources and an intrinsic property of fish population variability, it is appropriate to manage total fish productivity based on multispecies integration at a fish community level instead of a single species approach. We need to improve the present situation where utilization and market values are different among fish species. A critical aspect is whether we can adapt to long-term stock fluctuations caused primarily by environmental change that we cannot control. While high stock abundance enables high levels of exploitation, we should note that the exploitation rate easily becomes excessive for stocks that are forced to low abundance in an unfavorable environmental condition. An adaptive strategy in response to natural variability enables us to sustain exploitation of fisheries resources and the development of fisheries.

Physical environmental changes such as circulation and mixing in the oceans owing to climate change affect the primary production and ecosystem productivity and ultimately the abundance and distribution of commercially important fish stocks. The regime shift of a marine system constitutes characteristic features of alternation of the dominant fish species and, more importantly, changes in the productivity of marine ecosystems (Chavez et al. 2003). An adaptive way to manage and exploit such systems is from a viewpoint of the total fishery productivity of a fish community beyond the specific fish populations. Thus, it is increasingly important to understand the dynamics of marine ecosystems and their response to environmental changes and human activities.

Ecosystem-based fisheries management (EBFM) takes into account interactions among species and environmental influences in the ecosystem beyond mere considerations of specific single species. The view of EBFM has been implied in the 1995 FAO Code of Conduct for Responsible Fisheries, which includes effective conservation, management, and development of living aquatic resources in relation to ecosystem and biodiversity (FAO 1995). Since then, EBFM has been recognized as an evolutional direction for fisheries management (Pikitch et al. 2004). It is noted by Fogarty (2014) that EBFM is designed to be adaptive in response to changing conditions and that it can encompass uncertainty and various objectives and also enables scope for human exploitation of resources to be included as an element of the ecosystem. A necessity of EBFM is perceived universally in the world (Gascuel et al. 2016). An example in Japan is shown as “Shiretoko approach” in which fisheries co-management was expanded to EBFM to achieve ecosystem conservation (Makino et al. 2009).

Given that healthy marine ecosystem and sustainable fisheries are closely interrelated, a diagnosis of the status of marine ecosystems is required as in human health management. Ecosystem indicators are key elements of EBFM procedures and have been used to provide scientific diagnosis and advice for management decision (Fogarty 2014; Coll et al. 2016).

Ecosystem modeling has been also developed to support EBFM (see Chap. 12). Recently, effects of management action and socioecological trade-offs on the ecosystem have been explored using Ecopath with Ecosim (Wang et al. 2016), Atlantis (Weijerman et al. 2016), and size-spectrum model (Zhang et al. 2016).

1.4 Fishery and Ecosystem Monitoring

Multidisciplinary monitoring for real-time information and nowcasting is required to manage fisheries resources with uncertainty in changing marine ecosystems. In Japan, observational networks for fisheries and oceanography have been long established by national and prefectural institutes, providing a valuable database for monitoring studies in the Northwest Pacific. Especially in the fisheries sector, monitoring to collect a variety of information on the physical environment, eggs and larvae, and caught fish has been conducted since the 1930s for the purpose of forecast to fishery and oceanic conditions (see Chap. 7). For fish species targeted by fisheries, stock assessment and management are carried out using extensive data set and knowledge accumulated on biological traits including abundance, distribution, compositions of body length and age, and patterns of growth and maturity.

If fisheries management is developed from an individual population basis to an ecosystem-based approach, monitoring will also be required on a new framework that corresponds to the change from monitoring individual species to monitoring ecosystem as a whole. Ecosystem indicators for fisheries management may contain various traits of the ecosystem such as abiotic environments, organisms in lower and upper trophic levels, biological community, trophodynamics, and size spectrum at various ecologically important temporal and spatial scales. Development and introduction of new observation and information technologies are essential to meet the expanding requirements of ecosystem-based fisheries management. Fishery-independent surveys are needed especially for plankton, micronekton, sea birds, and marine mammals. Quantitative biological sampling, hydroacoustics, underwater optics, and imaging, and satellite remote sensing offer prospects of visualization and quantification of the underwater world. If models are integrated with the collection and management of data from in situ observational networks that consist of organized deployment of various platforms and sensors, it may be possible to promote understanding of ecosystem dynamics and implement ecosystem-based fisheries management.

1.5 Aim and Structure of This Book

The aim of this book is to explore how we can solve the urgent problem of optimizing the use of variable, uncertain but finite fisheries resources while maintaining sustainability from the viewpoint of conservation of the marine ecosystem. The process bringing a solution can be a cycle interconnected by three elements: elucidating population dynamics of fish stocks, monitoring changes in fisheries resources and marine ecosystems, and developing harvest control rules in correspondence with changes in stock abundance and management objectives. The framework of this book is based on this process (Fig. 1.3). The book gives readers a broad understanding of the existing findings, methods, and theory for sustainable exploitation of fisheries resources and introduces recent findings and technological developments.

Following this introductory chapter, the book is constituted of three parts along topics of fish stock dynamics, monitoring systems and management models, and a part of "Perspectives" (Fig. 1.3). Each part of Parts I to III begins with an introductory overview including some other topics than contents in the following chapters. Part I illustrates how ecological processes in life histories and biological interactions

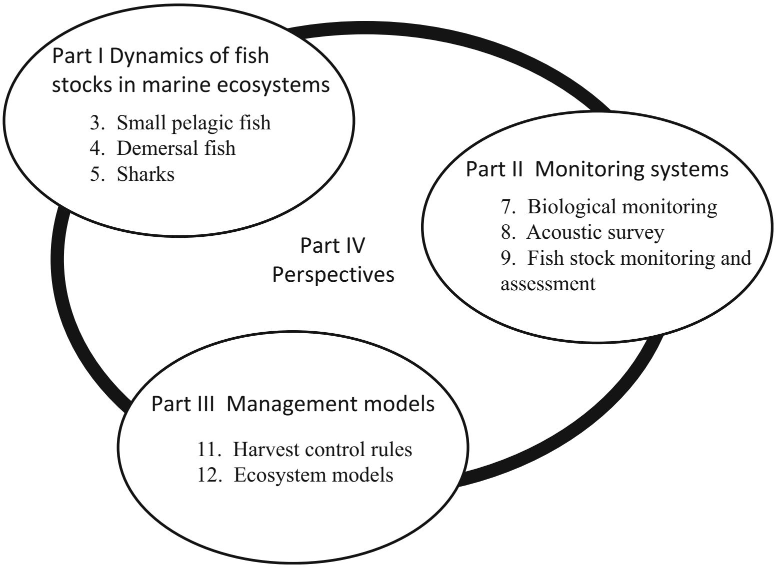

Fig. 1.3 Structure of the contents in this book

and marine environments lead to fish stock variability in space and time in major fish groups: small pelagic fish, demersal fish, as well as sharks which differ from teleost fishes in their life history. These understandings enable explanation of the mechanism underlying in the variability in the dynamics of fish stocks and form the essential, biological basis for fisheries management. Part II considers technologies and systems that monitor changes in fisheries resources and marine ecosystems through two approaches, fishery-dependent and fishery-independent data. It becomes very significant to advance high technology of collecting and analyzing information on changing fisheries resources and marine ecosystems. Observation methods of acoustic surveys and biological sampling and stock assessment methods are described. Part III examines management models effective to assess the natural variability in fisheries resources. The authors discuss how we are to determine the allowable catch in response to changes in stock abundance and how to incorporate ecological processes and monitoring procedures within management models. Finally, the last chapter provides perspectives relating to the management of sustainable fisheries.

Implementation of fisheries management is a synergy of monitoring, modeling, and prediction. A fishery integrated by such information may be called as "precision fishery" analogous to precision agriculture on land which is a farming management concept for optimizing crop production by observation, measurement, and response to environmental variability (Shibusawa 2006). To realize planned production, sound management, and stable supply to the market while preserving natural resources, information is essential on when and how fishing efforts are exerted to harvest natural resources which are inherently hard to control. The readers will gain an overall understanding of sustainable exploitation and how various factors interrelate and enable insights into fisheries management of the next generation.

Part I: Dynamics of Fish Stocks in Marine Ecosystems

Chapter 3 reviews biological mechanisms underlying climate impacts on population dynamics of small pelagic fish, taking examples from the species alternations between anchovies and sardines. The chapter discusses how environmental variability can regulate the survival probability of small pelagic fish, introducing hypotheses for biological mechanisms of species alternation. Lastly, directions of future studies are also proposed.

Chapter 4 reviews the relationships of recruitment to spawning stock biomass and environmental factors and recruitment prediction models in consideration of such relationships, focusing on walleye pollock as an example of an important demersal fish resource. In addition, the chapter discusses linkages of recruitment studies with stock assessments and fisheries managements. Lastly, recommendations for future fisheries management strategies are also provided, with an emphasis on connections to fisheries economics.

Chapter 5 focuses on sharks, which maintain the role of top predator in marine ecosystems, have a reproductive strategy quite different from those of teleosts including internal fertilization and the live birth of only a few well-formed neonates, and show conspicuous sexual differences in the life history. The sex-specific life history traits are illustrated including growth, reproduction, and mating system in sharks. Implications of the intersexual differences in the life history traits are discussed from both the evolutional and exploitative points of view.

Part II: Monitoring Systems

Chapter 7 introduces technological advances and data applications of fishery-independent monitoring surveys, after briefly reviewing their history and current status in Japan and worldwide. These reviews include (1) long-term zooplankton monitoring, (2) long-term fish egg and larval surveys and spawning monitoring, and (3) samplings of fish larvae and juveniles (pre-recruit stages). Moreover, the chapter provides recommendations for monitoring systems and perspectives in the future for continuity of long-term monitoring.

Chapter 8 describes how acoustic methods can be utilized to enable monitoring marine organisms: (1) discrimination of zooplankton, as well as larval, juvenile, and adult fish by frequency characteristics of backscattering strengths and estimation of their biomasses, (2) advances in acoustic applications for ecological monitoring, and (3) an acoustic monitoring system for *shirasu* (Japanese anchovy post-larvae) fishery now in operation. Finally the author details how acoustic monitoring system can be integrated for ecosystem-based fisheries management.

In Chap. 9, both survey-based and model-based stock assessment methods are briefly reviewed giving advantages and disadvantages of each method. Then VPA, which has been used worldwide for many stocks, is reviewed and discussed on its reliability and validity based on actual experience in Japanese fisheries stock assessment for estimating allowable biological catch (ABC). Finally, future perspectives on stock assessment methods are discussed.

Part III: Management Models

Chapter 11 reviews the management strategy evaluation (MSE) framework to evaluate the performance of harvest control rules (HCRs) and management procedures (MPs), which utilize operating models (OMs) to simulate virtual stock dynamics. The authors also report on harvest strategies, the impact of uncertainty on the use of MSE, and on the use and simulations of HCRs in Japan. Finally, the authors discuss the use of HCRs in the context of coping with climate change.

Chapter 12 reviews the ecosystem models published and used so far in fisheries science around the world. The authors then propose a new ecosystem assessment model that is used even for data-poor situations and conduct a simple simulation test to investigate the performance of the new model, applying it to North Pacific multispecies data. The merits and demerits of the model and the future direction of ecosystem modeling in data-poor situations are discussed.

Part IV: Perspectives

In Chap. 13, we bring together the conclusions of previous chapters to seek a new synthesis of fish biology, environmental and biological monitoring, and management modeling. The chapter identifies future research direction and discusses successful implementation of management procedures in fishery systems.

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Part I
Dynamics of Fish Stocks in Marine Ecosystems

Chapter 2
Part I: Description

Akinori Takasuka

Abstract Numerous studies have been conducted to understand the mechanisms regulating the dynamics of fish stocks in marine ecosystems. The leading motive has been predicting the future trends of population dynamics for better fisheries management toward sustainable fisheries. However, we now have to confront the complexity of the ecosystems and phenomena and consider how to achieve resource sustainability at the ecosystem level. Part I provides concrete examples of the biology and ecology related to the dynamics of fish stocks in marine ecosystems, reviewing the mechanisms of the population dynamics of small pelagic fish and demersal fish and the reproductive strategies of sharks.

In 2014, we passed the 100th anniversary of contemporary science on fish population dynamics, after Hjort (1914) proposed that fish populations are regulated by survival success during the early life stage right after hatching. Since then, numerous studies have been conducted to understand the mechanisms regulating the dynamics of fish stocks in marine ecosystems. The leading motive has been predicting the future trends of population dynamics for better fisheries management toward sustainable fisheries.

During the last century, the efforts of scientists led to substantial progress in this field of science. Leggett and Frank (2008) listed seven paradigms which have heavily influenced advances in fisheries oceanography over the past century and reviewed the progress, current status, and future directions of research. As one of several concluding remarks, they stated "the dynamics of the systems and phenomena we seek to understand are invariably more complex than initially meets the eye" and "ecosystems rather than individuals or populations are rapidly becoming the object of study as the search for solutions to traditional problems such as recruitment dynamics are pursued." Now, we have to confront the complexity of the ecosystems

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and phenomena and consider how to achieve resource sustainability at the ecosystem level.

The complexity in understanding the mechanisms regulating the dynamics of fish stocks in marine ecosystems has increased as our understanding has progressed. Although earlier studies focused on the early life stage right after hatching, we now recognize that vital parameters related to survival rates are important throughout the life stages (Petitgas et al. 2013). Although regulating fishing pressure has long been the principal method to achieve sustainable fisheries (Pauly et al. 1998; Myers and Worm 2003), assessment of acceptable exploitation levels for wild stocks in relation to the risk of overfishing has been a controversial issue worldwide (Worm et al. 2009; Hilborn 2012). During the last several decades, however, the effects of climate variability on fish and fisheries have been identified (Stenseth et al. 2005; Checkley et al. 2009; Barange et al. 2010, 2014). The concept of "regime shifts," which are abrupt shifts from one ocean environmental state to another, has prevailed in fisheries oceanography (Hare and Mantua 2000; Kawasaki 2013). Hence, a combination of natural and human impacts on fisheries resources is to be considered. Further, life histories are different among different taxonomic groups (Winemiller and Rose 1992). As such, even if we discuss climate impacts on fish at the ecosystem level, we need to examine the biology and ecology of each species, as the observed effects of climate variability on fish result from physiological changes at molecular, cellular, and whole organism levels and the ultimate effects of climate variability at the ecosystem level will build on species-specific responses to environmental factors (Pörtner and Peck 2010).

The concept of ecosystem-based fisheries management (EBFM) is currently recognized as the desired direction for fisheries management (Pikitch et al. 2004; Berkes 2012). In the context of EBFM, all the components of the ecosystem as well as the target fish species should be considered. Therefore, knowledge of the biology and ecology of pelagic, demersal, and deep-sea fish are of mutual benefit to one another in terms of fisheries management. In a similar manner, understanding top predators cannot be ignored in understanding forage fish (small pelagic fish) and vice versa.

Obviously, it is impossible to cover all the topics, taxonomies, and ecosystems in a review of studies on the dynamics of fish stocks in marine ecosystems. Here, we focus on several topics and taxonomies by taking examples mainly from the waters around Japan. Even so, we try to extend the discussion and references to include generality and applicability as much as possible for an international readership. Undoubtedly, technological and methodological developments have been essential in studies on the dynamics of fish stocks. For example, stable isotope ratios have been adopted as natural tracers and tools for characterizing trophic structures in marine food webs (Michener and Kaufman 2008). The discovery of daily periodicity in the microstructure of otoliths has enabled fine scale aging of fish (Pannella 1971), and otolith chemistry has been useful in studies on migration and population structures (Campana 2005). Recently, next-generation sequencing technology has been adopted in studies on fish physiology at molecular levels; for example, transcriptional responses to environmental factors were tested in a study on climate impacts on fish (Olsvik et al. 2013). Even though these technological and methodological aspects are not covered here, we note that they have been rapidly evolving.

This part of the book comprises three chapters. The dramatic and cyclic population dynamics of small pelagic fish can be a good example of the dynamics of fish stocks under climate variability at multi-decadal time scales. Chapter 3 reviews the biological mechanisms underlying climate impacts on the population dynamics of small pelagic fish. Climate variability also influences demersal fish, but recruitment mechanisms and appropriate management strategies may be different between pelagic and demersal fish. For example, fish of longer lifespans may be more susceptible to fisheries, but the stocks can be more efficiently managed by controlling catch. Chapter 4 reviews the population dynamics of demersal fish focusing on walleye pollock. To achieve EBFM, we should not ignore the biology of the top predators. A unique contribution comes from Chap. 5, which focuses on sharks. This chapter reviews the reproductive strategies of sharks, which are quite different from those of teleosts. Understanding the sex-specific ecological and life history traits is important for the sustainable exploitation of sharks. Further, the information is also useful in the context of EBFM. Overall, Part I provides concrete examples of the biology and ecology related to the dynamics of fish stocks in marine ecosystems, which are connected to Part II and Part III.

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Chapter 3
Biological Mechanisms Underlying Climate Impacts on Population Dynamics of Small Pelagic Fish

Akinori Takasuka

Abstract Small pelagic fish account for more than 30% by weight of the total landings of marine fisheries in Japan and around the world. Their population dynamics have tended to be dramatic and cyclical in response to climate variability on multi-decadal time scales. However, the biological mechanisms linking climate variability to population dynamics are still unresolved. This chapter reviews the biological mechanisms underlying climate impacts on the population dynamics of small pelagic fish, taking examples from the species alternations between anchovy and sardine in the Kuroshio Current system. First, the chapter examines how environmental variability regulates the survival probability of small pelagic fish, highlighting the role of vital parameters such as growth rate and physiological condition as an amplifier linking subtle changes in environmental variables to dramatic changes in the population dynamics. Then, the chapter introduces hypotheses for the biological mechanism of species alternation, showing how environmental conditions differently affect the population dynamics of different small pelagic fish species. Lastly, recommendations for future research directions are presented.

Keywords Growth · Population dynamics · Small pelagic fish · Spawning · Species alternation · Survival

3.1 Population Dynamics of Small Pelagic Fish

Small pelagic fish are relatively small-sized fish which are broadly distributed in the surface layer from coastal to oceanic waters in various regions of the world. Typically, they have a planktonic larval stage and metamorphose to the juvenile stage while being transported from the spawning ground to the nursery ground and migrate seasonally in schools from the feeding ground to the spawning ground. In

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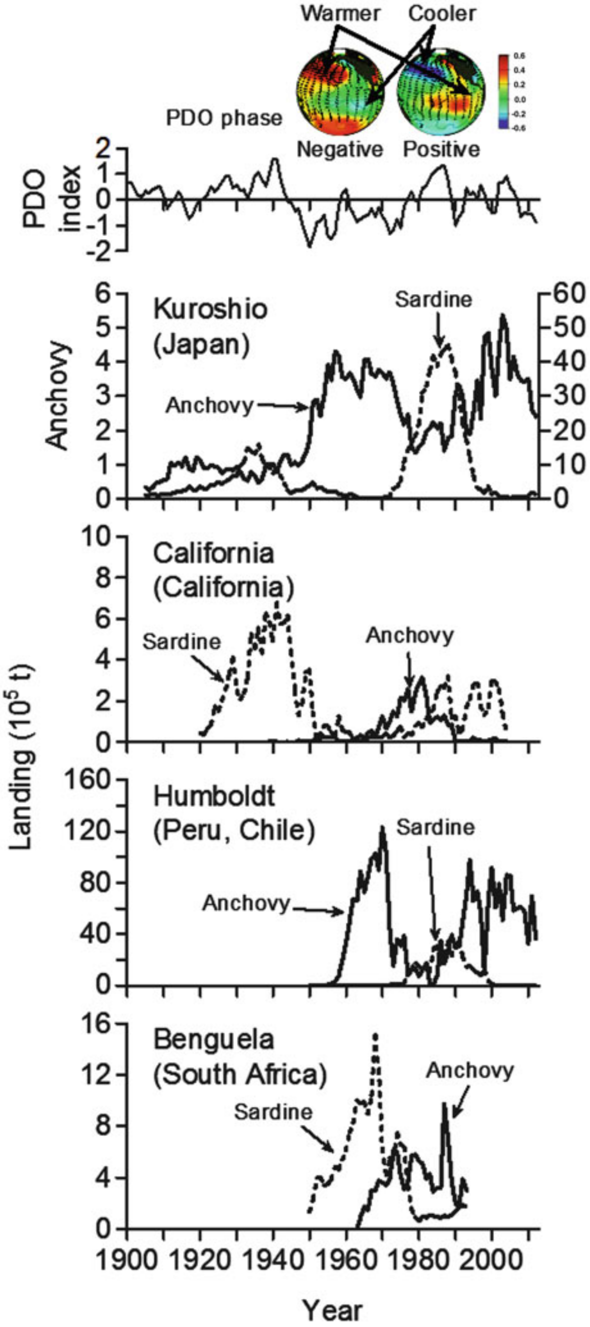

Fig. 3.1 Species alternations between anchovy and sardine in response to climate variability. The Pacific Decadal Oscillation (PDO) index, which is an index of the Pacific climate variability, is defined as the leading principal component of monthly SST anomalies in the North Pacific, poleward of 20°N (monthly mean global average SST anomalies were removed) (Mantua and

general, they feed on phytoplankton and zooplankton using filter and/or particulate feeding strategies (e.g., anchovy, sardine, herring, saury), although some species are piscivorous with a raptorial feeding strategy (e.g., mackerel). On the other hand, they are preyed upon by many predatory fish species. Thus, they are also called forage fish, and within food webs play an important role of energy transfer in mid-trophic positions (Peck et al. 2014). Their commercial impact is also significant. Indeed, small pelagic fish account for more than 30% by weight of the total landings of marine fisheries in Japan and around the world. However, as fisheries resources these stocks are far from stable.

Dramatic and cyclical patterns in response to climate variability are representative of the population dynamics of small pelagic fish on multi-decadal time scales (Checkley et al. 2009). A typical example is the out-of-phase population oscillations between species of anchovy *Engraulis* spp. and sardine *Sardinops* spp. in various regions of the world (Fig. 3.1). Over a basin scale, the dominant species has historically shifted from anchovy to sardine and back approximately every 50 years (Kawasaki 1983; Lluch-Belda et al. 1989; Schwartzlose et al. 1999; Chavez et al. 2003). In the Kuroshio Current system off Japan including the warm Kuroshio Current, the cool Oyashio Current, and the transition regions, Japanese sardine *S. melanostictus* populations were very abundant during the 1980s, while Japanese anchovy *E. japonicus* populations were relatively scarce during the same period. However, sardine populations then decreased markedly at the end of the 1980s and subsequently have experienced very low levels during the last few decades, although signs of a population recovery during the last few years are currently being monitored. In contrast, anchovy populations have increased to be abundant during the period of low sardine biomass. Such a cycle has occurred twice during the last 100 years. The phenomenon of "species alternation" has also been observed between *E. mordax* and *S. sagax* in the California Current system off California, *E. ringens* and *S. sagax* in the Humboldt Current system off Peru and Chile, and *E. encrasicolus* and *S. sagax* in the Benguela Current system off South Africa. The species differ and the populations are separated geographically, but their population dynamics patterns have exhibited remarkable synchrony/asynchrony among these ecosystems (Kawasaki 1983; Lluch-Belda et al. 1989; Schwartzlose et al. 1999; Chavez et al. 2003). Overall, the pattern of species alternations has been roughly synchronous among the

Fig. 3.1 (continued) Hare 2002). Typical anomaly patterns of wintertime sea surface temperature (gradation), sea level pressure (contours), and surface wind stress (arrows) are indicated for the positive and negative phases of the PDO index. Landing histories are shown for *Engraulis japonicus* and *Sardinops melanostictus* in the Kuroshio Current system (Japan), *E. mordax* and *S. sagax* in the California Current system (California), *E. ringens* and *S. sagax* in the Humboldt Current system (Peru and Chile), and *E. encrasicolus* and *S. sagax* in the Benguela Current system (South Africa). The landing data were compiled and updated from Yatsu et al. (2005), Ito et al. (2006), and Takasuka et al. (2008a, b); the data from Peru were updated by courtesy of Blgo. Miguel Ñiquen Carranza

Pan-Pacific region (the Kuroshio, California, and Humboldt Current systems) while asynchronous between the Pan-Pacific region and the Benguela Current system, although the pattern observed in the California Current system has already been out of synchrony. Note however that in the Kuroshio Current system, the maximum biomass level and the extent of fluctuation for sardine were approximately one order higher than for anchovy. In contrast, anchovy population dynamics has been greater than sardine in the Humboldt Current system.

Therefore, these patterns of species alternations have been attributed to basin-scale climate variability rather than fishing pressure (Kawasaki 1983; Lluch-Belda et al. 1989; Schwartzlose et al. 1999; Chavez et al. 2003). Climate variability induces ocean regime shifts, which are abrupt shifts from one ocean environmental state to another. For example, the patterns of species alternations have been closely related to the Pacific Decadal Oscillation (PDO) index (Mantua and Hare 2002), which is an index of Pacific climate variability, and sea surface temperature anomalies. When the PDO index is positive, the sea surface tends to be cooler in the western North Pacific. During this period, sardine populations flourish in the Kuroshio Current system of the western North Pacific. In contrast, when the PDO index is negative, the sea surface tends to be warmer, and anchovy populations flourish in the Kuroshio Current system. Interestingly, the temperature regimes are reversed between the opposite sides of the Pacific during the same PDO phase (Mantua and Hare 2002; Chavez et al. 2003). In the California and Humboldt Current systems of the eastern Pacific, the phases of positive PDO index correspond to the warm temperature regimes in which sardine populations flourish, whereas the phases of negative PDO index correspond to the cool temperature regimes in which anchovy populations flourish. As such, climate impacts on species alternations have been clarified. However, the biological mechanisms linking climate variability to population dynamics of small pelagic fish are still unresolved.

Here emerge two key questions on biological mechanisms underlying climate impacts on species alternations (Takasuka et al. 2007a). First, why do even subtle environmental fluctuations sometimes trigger dramatic alternations? Climate fluctuations are big events at a basin scale, but the extent of the differences in the environmental factor itself could be subtle between the climate regimes. For example, a typical annual variability of the surface temperature is 2–3 °C in mid-latitude regions. Such an interannual temperature variability is interpreted as a great change in terms of physical oceanography. However, fish can experience seasonal variability to a much greater extent than the interannual variability particularly in mid-latitude regions. Second, why do anchovy flourish and sardine collapse or vice versa under the same ocean regime? Both anchovy and sardine experience the same ocean regime over large spatial and temporal scales, even though the environments which they encounter can differ because of their spatial and temporal differences in spawning and migration. Nonetheless, anchovy and sardine show contrasting outcomes of population dynamics under the same ocean regime. These issues are fundamental questions regarding the mechanisms of the species alternations, but the dramatic nature and different patterns of population dynamics of different species can be seen broadly for small pelagic fish worldwide (Peck et al. 2014).

This chapter reviews the biological mechanisms underlying climate impacts on the population dynamics of small pelagic fish, taking examples from species alternations between anchovy and sardine in the Kuroshio Current system. First, the chapter examines how environmental variability regulates the survival probability of small pelagic fish, highlighting the role of vital parameters such as growth rate as an amplifier linking subtle environmental variability to dramatic population dynamics. Then, the chapter introduces hypotheses for the biological mechanisms of species alternation, showing how environmental conditions differently affect the population dynamics of different small pelagic fish species. Lastly, recommendations for future research directions are presented. The concept of this review holds that differential responses of vital parameters to environmental factors constitute the key to understand the biological processes linking climate variability to the differences in population dynamics. Note that the term "climate variability" here denotes natural cyclical oscillations in ocean environments on multi-decadal time scales.

3.2 Climate Cascade

The process linking climate variability to population dynamics of small pelagic fish is here represented as an analogy of a cascade (Fig. 3.2). Climate variability induces ocean regime shift, which is an abrupt shift from one ocean

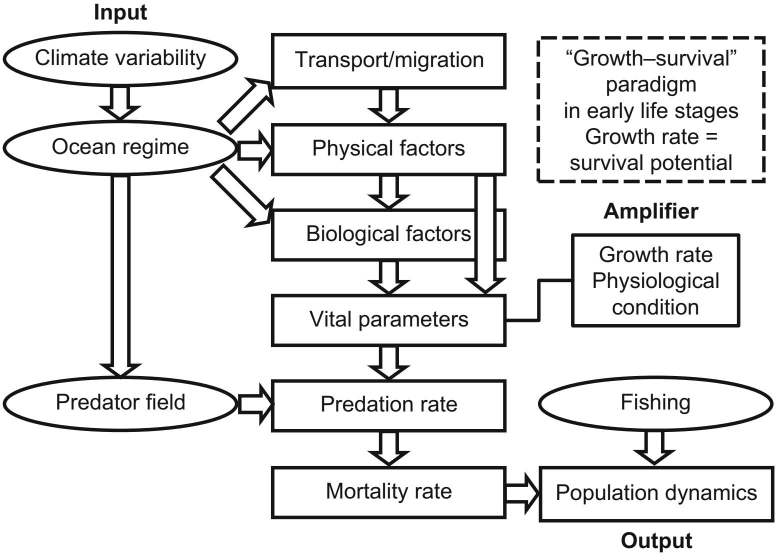

Fig. 3.2 Climate cascade model linking climate variability to population dynamics of small pelagic fish. Vital parameters function as an amplifier linking subtle environmental variability due to climate variability (input) to dramatic population dynamics (output)

environmental state to another (Hare and Mantua 2000). The ocean regime shift alters conditions of both physical and biological factors in the marine ecosystem (de Young et al. 2008). Depending on transport and migration, small pelagic fish encounter certain conditions of physical and biological factors, both of which determine their vital parameters such as growth rate and physiological condition. These vital parameters influence how vulnerable fish are to predation (i.e., predation rate). Predation rate also strongly depends on the predator field (i.e., predator abundance and composition), which is also subject to the ocean regime shift. As predation is the major and direct source of mortality of fish in general (Bailey and Houde 1989), the mortality rate is largely determined by a combination of the vital parameters and the predator field. Population dynamics is a phenomenon of changes in the number of recruits; therefore it is a function of the mortality rate of individual fish. Thus, such a process can be expressed as a "climate cascade" with climate variability as an input and population dynamics as an output.

Pörtner and Peck (2010) reviewed climate impacts on fish and fisheries from a viewpoint of the physiological responses of fish. (1) The observed effects of climate variability on fish at various levels (organismal, population, and community ecosystem) result from physiological changes at molecular, cellular, and whole organism levels. (2) The ultimate effects of climate variability at the ecosystem level will build on species-specific responses. (3) Such a cause-and-effect understanding is needed to reliably project the effects of climate variability on marine fish species. These lines of investigation emphasize the reasonability of considering vital parameters of fish as a central view in understanding the processes of climate impacts on population dynamics.

In the "climate cascade" model, vital parameters serve as an amplifier linking subtle environmental variability to dramatic population dynamics (see Sect. 3.3). Hence, none of the environmental factors influencing vital parameters should be ignored. Moreover, if there is any difference in the response of vital parameters to the environmental factors among different species, it could lead to dramatic differences in population dynamics among different species even under the same ocean regime.

3.3 Vital Parameters as an Amplifier

Why do even subtle environmental changes sometimes trigger dramatic alternations? In this section, a theoretical scenario of this process is introduced, focusing on the role of growth rate during the early life stages as an amplifier linking subtle environmental variability to dramatic population dynamics of fish.

3.3.1 Growth and Survival Mechanisms During Early Life Stages

Fish have high mortality rates during the early life stages, as the mortality rate follows an exponential decline with the somatic size and developmental stage (Bailey and Houde 1989). Growth rate is the dominant factor regulating the survival potential during the early life stages of fish (Anderson 1988). Larger and/or faster-growing individuals are more likely to survive than smaller and/or slower-growing conspecifics—this simple paradigm has received much attention in recruitment studies since the growth rate has been expected to be an effective predictor of recruitment success. The paradigm has been supported by numerous field studies (Hovenkamp 1992; Meekan and Fortier 1996; Hare and Cowen 1997; Sirois and Dodson 2000; Takasuka et al. 2003; Shoji and Tanaka 2006; Robert et al. 2007), although there have been some conflicting observations (Lankford et al. 2001; Munch and Conover 2003).

To date, three functional mechanisms have been proposed to explain the survival advantage of a higher growth rate (Takasuka et al. 2004a, 2017; Leggett and Frank 2008). The "bigger is better" mechanism (Miller et al. 1988) is a size-based concept which assumes survival advantages of larger somatic size of faster-growing individuals. The operational conditions of the mechanism are the positive relationship between the growth rate and somatic size at the population level and negative size-selective mortality. The "stage duration" mechanism (Chambers and Leggett 1987; Houde 1987) is a time-based concept which assumes that the mortality rate decreases markedly with the developmental stage. If a higher growth rate shortens the period until metamorphosis, faster-growing individuals will experience a lower cumulative mortality rate during the larval stage. The operational conditions of the mechanism are the larval stage characterized by a higher mortality rate and negative relationship between growth rate and stage duration. These two mechanisms link the growth rate to survival indirectly in the context of size and time (i.e., outcomes of growth rate). The "growth-selective predation" mechanism (Takasuka et al. 2003, 2007b) proposes that slower-growing individuals are more vulnerable to predation than their faster-growing conspecifics, even if they are of the same size. The operational conditions of the mechanism are that predation is the direct source of mortality and negative growth-selective mortality occurs at a given somatic size. This mechanism directly links the growth rate per se to predation mortality. It is useful to discriminate these mechanisms to understand the growth and survival processes theoretically, although in the natural environment, these cannot be separated. The following subsections are intended to explain in theory how environmental variability regulates the survival probability, using the "stage duration" and "growth-selective predation" mechanisms, as examples.

3.3.2 Consequence of Subtle Environmental Variability Through Stage Duration Mechanism

The “stage duration” mechanism is intuitive and suitable for simple simulations. A simulation study by Houde (1987) showed that more than a one hundredfold difference in larval survival can be derived from maximum growth variability through the “stage duration” mechanism. Now, a possible consequence of a 2 °C change in temperature in regulating survival probability is practically discussed based on data for Japanese anchovy larvae through the theory of the “stage duration” mechanism, as follows.

Growth rates of anchovy larvae followed a dome-shaped function of sea surface temperature, when recent 3-day mean growth rates examined through otolith microstructure analysis were pooled over various seasons and sea areas in the western North Pacific (Fig. 3.3). For example, a temperature decline of 2 °C from 18 °C to 16 °C can lead to a growth rate decline of 0.12 mm day^{-1} from 0.41 to 0.29 mm day^{-1}, based on the dome-shaped relationship of growth rate to temperature. This growth rate decline corresponds to an approximate 31% of the overall growth range.

Substantial variability in the timing of metamorphosis was shown by comparison of size-at-age between the metamorphosing larvae and non-metamorphosing larvae from a spring cohort in Sagami Bay in 2005 (Fig. 3.4). The difference was estimated as 21 days between the oldest non-metamorphosing larva and the youngest

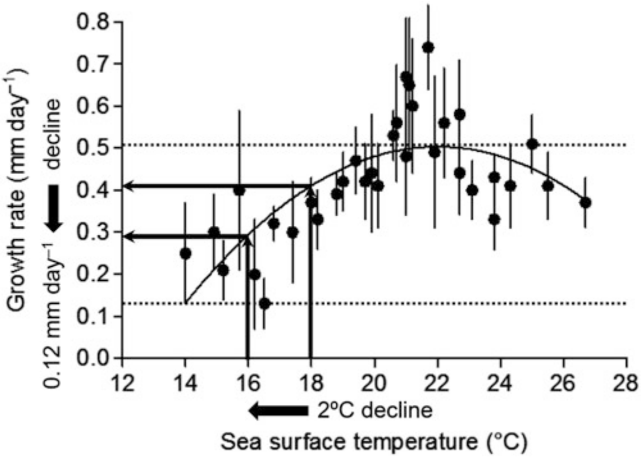

Fig. 3.3 Relationship of growth rate to sea surface temperature for Japanese anchovy *Engraulis japonicus* larvae in the western North Pacific. Mean ± standard deviation values of recent 3-day mean growth rate estimated through otolith microstructure analysis are shown at the sample level. A quadratic function was fitted to the mean values of growth rate against sea surface temperature ($y = -2.302 + 0.255x - 0.006x^2$; $n = 34$, $r^2 = 0.507$, $p < 0.001$). A temperature decline of 2 °C from 18 °C to 16 °C can lead to a growth rate decline of 0.12 mm day^{-1} (0.41 mm day^{-1} to 0.29 mm day^{-1}), which approximately corresponds to 31% of the growth range (Modified from Takasuka et al. 2007a)

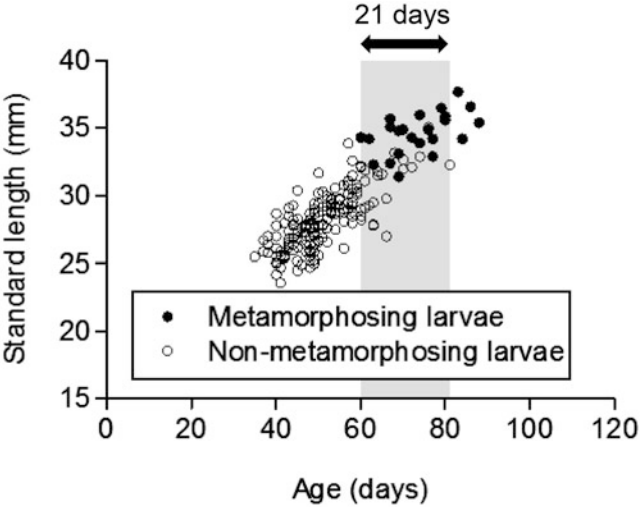

Fig. 3.4 Size-at-age of the metamorphosing larvae versus non-metamorphosing larvae of Japanese anchovy *Engraulis japonicus* from a spring cohort in Sagami Bay in 2005. The difference of 21 days was observed between the oldest non-metamorphosing larva and the youngest metamorphosing larva (Modified from Takasuka et al. 2017)

metamorphosing larva. In this cohort sample, the metamorphosing larvae had higher growth rates than the non-metamorphosing larvae. Hence, the difference of 21 days in the timing of metamorphosis is assumed to be due to growth variability. If so, a growth rate decline of 31% of the overall range corresponds to a 6.5-day delay of metamorphosis. Assuming that daily mortality rate is 30% as a realistic field value (Oozeki et al. 2009), that is, daily survival rate is 70%, the cumulative survival probability during the larval stage should be multiplied by 9.8%, as it is a power function of the survival rate ($0.70^{6.5} = 0.098$). This rough calculation means that, in theory, there can be approximately a ten times difference in the cumulative survival probability during the larval stage, as a consequence of a difference of 2 °C.

3.3.3 Consequence of Subtle Environmental Variability Through Growth-Selective Predation Mechanism

The “growth-selective predation” mechanism was proposed based on snapshot evidence of growth and predation relationship in field studies. Takasuka et al. (2003) compared the growth rates of Japanese anchovy larvae dissected from the stomach contents of predators (i.e., larvae that were actually ingested by predators: ingested larvae) and those of the larvae captured by the same trawl tows simultaneously with the predators (i.e., larvae from the original population: original larvae). The ingested larvae had lower growth rates than the original larvae, even if they were the same somatic size, at a given moment in the sea. However, the mechanism is predator-specific. Further tests of the mechanism for multiple predatory fish species revealed that small pelagic fish with filter and particulate feeding strategies were growth-selective predators, whereas piscivorous predators with raptorial feeding strategy were non-growth-selective predators (Takasuka et al. 2004b, 2007b; Robert et al. 2010). Now, possible effects of growth variability on the selective predation pressure are practically discussed based on data for Japanese anchovy larvae when they are attacked by growth-selective predators through the theory of the "growth-selective predation" mechanism, as follows.

The intensity of selective predation pressure was quantified using an index of relative predation mortality based on the frequency distributions of growth rate of the ingested larvae from the stomach contents of the growth-selective predators versus the original larvae (Takasuka et al. 2007b). In an example from an autumn cohort (Fig. 3.5), the difference in the mean value of growth rate seems small (0.03–0.04 mm day^{-1}, depending on the predatory species) between the ingested larvae and original larvae. However, the comparison of growth rate distributions between the ingested larvae and original larvae revealed an exponential decline of the index value of relative predation mortality. A growth rate decline from 0.50 to 0.30 mm day^{-1} corresponded to an increase in relative predation mortality from 0.50 to 2.49. That is, the probability of predation increases by approximately five times when larvae are attacked by growth-selective predators. Note that this calculation deals with an instantaneous mortality. Intuitively it is clear that the cumulative predation mortality could increase dramatically when larval populations are attacked repeatedly by growth-selective predators throughout their larval stage. Since the mechanism is predator-specific, the predator field would regulate the intensity of growth selection. Unfortunately it is difficult to quantify cumulative effects in the field. However, the above simple simulation indicates the potential for growth rate to exert a large effect on survival probability during the early life stages.

3.3.4 Vital Parameters and Species Alternations

The three functional mechanisms ("bigger is better," "stage duration," and "growth-selective predation") are theoretically independent of and synergistic with one another (Takasuka et al. 2003). That is, a single mechanism can operate independently of any other; however, all the mechanisms can exert synergistic effects on the survival probability. As such, growth rate potentially exerts a far greater impact on recruitment variability through synergistic effects of multiple mechanisms than previously expected. In theory, more than a thousandfold fluctuation could be expected when growth variability is maximized. In the climate cascade model, growth rate during the early life stages therefore serves as an amplifier linking subtle changes in environmental variables to dramatic changes in the population dynamics.

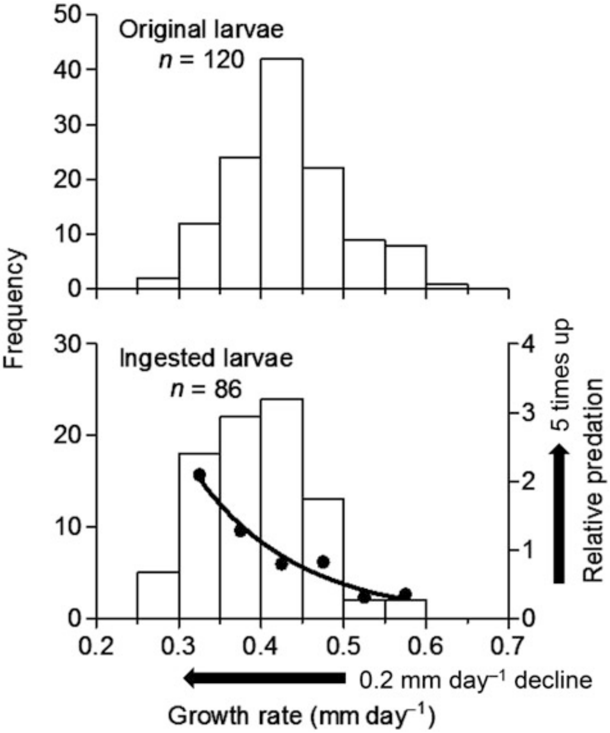

Fig. 3.5 Frequency distributions of growth rate compared between ingested larvae and original larvae in conjunction with an index of relative predation mortality for Japanese anchovy *Engraulis japonicus*. Recent 5-day mean growth rate was estimated through otolith microstructure analysis. The samples were from an autumn cohort in Sagami Bay in 2001. The ingested larvae were dissected from the stomach contents of Pacific round herring *Etrumeus teres* ($n = 15$) and Japanese jack mackerel *Trachurus japonicus* ($n = 6$). Relative predation mortality ratio (an index of intensity of relative predation mortality) was calculated as relative frequencies of each growth rate class (0.05 mm day^{-1}) of ingested larvae divided by those of original larvae (Hovenkamp 1992; Meekan and Fortier 1996). Function of single exponential decay was fitted to the index values ($y = 27.6e^{-8.0x}$, $r^2 = 0.962$, $p = 0.001$) (Reproduced from Takasuka et al. 2007b)

Why do anchovy flourish and sardine collapse or vice versa under the same ocean regime? Growth rates are determined mainly by external factors as well as internal factors. In particular, temperature and food are major environmental determinants of the growth rate (Heath 1992). Therefore, differential responses of vital parameters such as growth rate and physiological condition to environmental factors constitute a key to understand biological processes linking climate variability to differential population dynamics. The following sections will review hypotheses of mechanisms of species alternations based on differential responses to food and temperature between anchovy and sardine.

3.4 Food-Based Hypotheses for Species Alternations

Historically, studies on population dynamics of fish originated from the "critical period" hypothesis (Hjort 1914), which posits that year-class strength is determined by feeding success during the transition from endogenous to exogenous feeding right after hatching. This concept was then extended to the "match/mismatch" hypothesis (Cushing 1975), which focused on the match/mismatch in the seasonal timing of larval occurrence and the plankton bloom, and the "ocean stability" hypothesis (Lasker 1975), which relates to the importance of stability of the water column for providing food for larval fish. These lines of inquiry have led to further hypotheses based on the food availability through bottom-up processes, including prevailing food-based hypotheses for biological mechanisms of species alternations.

3.4.1 Optimal Environmental Window Hypothesis

The "optimal environmental window" hypothesis (Cury and Roy 1989) was proposed to explain recruitment dynamics based on bottom-up processes in upwelling systems (Fig. 3.6). This hypothesis does not deal with species alternations but has been a notable contribution to recruitment studies of small pelagic fish in upwelling systems. As well known, wind-induced upwelling entrains nutrients to the surface layer. The nutrient supply enhances plankton production and thus increases food availability for small pelagic fish. However, excessive turbulence can disturb their feeding success. As a result, recruitment follows a dome-shaped curve against wind

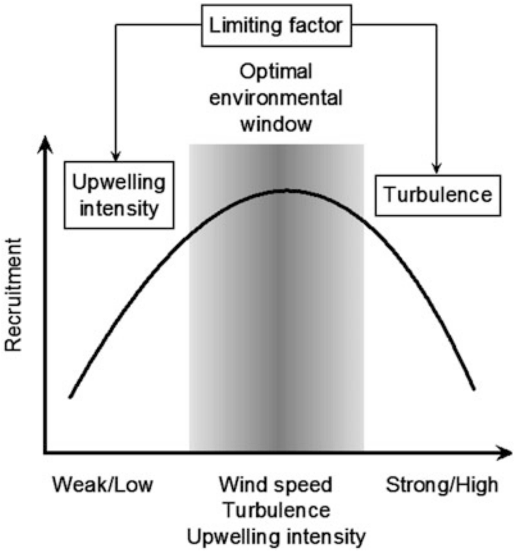

Fig. 3.6 Conceptual framework of the "optimal environmental window" hypothesis based on small pelagic fish recruitment in relation to food supply due to upwelling intensity and feeding success due to turbulence in upwelling ecosystems (Modified from Cury and Roy 1989)

speed, turbulence, and upwelling intensity. That is, moderate upwelling provides the optimal environmental window to maximize the probability of recruitment success. This hypothesis has several advantages. First, the mechanism links physical to biological processes. Second, it has generality and applicability. Third, it can be extended to multiple factors and species. The concept fits well the framework of climate cascade and has led to several hypotheses based on bottom-up processes, including biological mechanisms of species alternations.

3.4.2 Trophic Dissimilarity Hypothesis for Upwelling Systems

The "trophic dissimilarity" hypothesis (van der Lingen et al. 2006a, 2009) was proposed based on the differential feeding strategies between anchovy *E. encrasicolus* and sardine *S. sagax* under shifting intensity of upwelling in the Benguela Current system (Fig. 3.7). Basically, both anchovy and sardine are plankton feeders which are able to opportunistically switch between filter and particulate feeding strategies. However, the mean size of prey copepod was larger in the diets of anchovy than in the diets of sardine from mixed shoals of both species in the Benguela Current system (Louw et al. 1998). Similarly, there are differences in gill raker morphology between these two species (van der Lingen et al. 2006a, 2009). Overall, anchovy have coarser gill rakers and thus are considered to be more adapted to a particulate feeding strategy, whereas sardine have finer gill rakers and thus are considered to be more adapted to a filter feeding strategy.

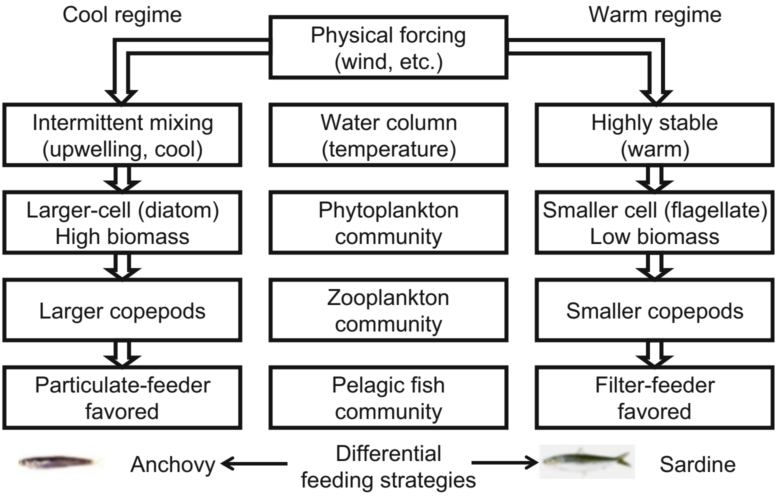

Fig. 3.7 Conceptual framework of the "trophic dissimilarity" hypothesis based on differential feeding strategies between anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax* in the Benguela Current system (Modified from van der Lingen et al. 2006a)

In the context of climate cascade, ocean regime shift occurs between warm and cool regimes due to physical forcing such as wind speed. When intermittent mixing due to upwelling occurs and the sea surface becomes cooler, the enhanced nutrient supply supports the production of larger-sized phytoplankton (e.g., diatoms) at a higher biomass level. Such a phytoplankton community supports the production of larger copepods in the zooplankton community. This cool regime enhances the availability of larger prey items for the pelagic fish community and therefore favors particulate feeders, that is, anchovy. In contrast, when the water column is highly stable without upwelling mixing and sea surface becomes warmer, nutrient supply is not sufficient to support larger phytoplankton and zooplankton and supports smaller-sized phytoplankton (e.g., flagellates) at a low-biomass level. Such a phytoplankton community leads to a zooplankton community with smaller copepods. This warm regime provides smaller prey items for the pelagic fish community and therefore favors filter feeders, that is, sardine.

The “trophic dissimilarity” hypothesis has been one of the most accepted ideas as a biological mechanism of species alternations in general. In the California Current system, zooplankton size was positively related to the upwelling velocity, and small pelagic fish production was related to the level of wind-stress curl (Rykaczewski and Checkley 2008). The mechanism explained that alongshore equatorward wind stress results in coastal upwelling, which supports the production of larger phytoplankton and zooplankton, and that cyclonic wind-stress curl results in curl-driven upwelling enabling production of smaller phytoplankton and zooplankton between the coast and the wind-stress maximum. Rykaczewski and Checkley (2008) hypothesized that anchovy *E. mordax* preferring larger prey items are favored by coastal upwelling inshore, whereas sardine *S. sagax* preferring smaller prey items are favored by wind-stress curl offshore in the California Current system.

The differences in trophic ecology between anchovy and sardine seem to be rather consistent among various ecosystems (van der Lingen et al. 2009). Recently, several studies have compared trophic ecology between European anchovy *E. encrasicolus* and European sardine *Sardina pilchardus*. In the Bay of Biscay, anchovy and sardine both feed on small- to medium-sized copepods, but anchovy have a higher trophic plasticity than sardine, suggesting some trophic segregation between the two species (Chouvelon et al. 2014). Similarly, substantial dietary differences were reported for anchovy and sardine juveniles from the Gulf of Lions in the Mediterranean (Costalago et al. 2014), although prey size partitioning was not unequivocally supported by another study on the trophic ecology of anchovy and sardine in the eastern Mediterranean (Nikolioudakis et al. 2014).

However, the “trophic dissimilarity” hypothesis cannot be applied to anchovy and sardine in the Kuroshio Current system for two main reasons. First, anchovy *E. japonicus* populations flourish during warm regimes, and sardine *S. melanostictus* populations flourish during cool regimes in this western boundary current system. This regime and fish relationship is in marked contrast to the cases in the upwelling ecosystems. Second, trophic dissimilarity is unclear. It is true that characteristics of feeding apparatus also differ between anchovy (coarser gill rakers) and sardine (finer gill rakers) in the Kuroshio Current system; however, there are only minimal differences in gill raker morphology between the two species during the early life stages, that is, high-mortality stages, since the difference becomes larger with development, in the Kuroshio Current system (Tanaka et al. 2006, van der Lingen et al. 2009). If a similar phenomenon is observed in other systems, it may be a weak point of the "trophic dissimilarity" hypothesis. Moreover, recent comparative studies on diets of anchovy and sardine during their larval stage in the Kii Channel, Japan, showed that prey items of these two species have a high degree of overlap (Yasue et al. 2011). Further, using a stable isotope approach, trophic similarity was observed between anchovy and sardine throughout their life stages (Yasue et al. 2014). Overall, their interspecific differences were much less than their intraspecific differences such as effects of seasonal changes. So far, these studies on the trophic ecology of anchovy and sardine in the Kuroshio Current system concluded that they are ecologically directly competing species, probably throughout their life stages, in terms of their trophic positions in the pelagic ecosystem.

3.4.3 Trophodynamics Hypothesis for the Kuroshio Current System

In the Kuroshio Current system, earlier studies on population dynamics tended to focus on sardine rather than anchovy, because of their commercial importance and their sharp population decline during the 1990s which received much attention from fisheries biologists. Noto and Yasuda (1999) found a close relationship between the mortality coefficient anomaly from postlarva to age 1 sardine and the February sea surface temperature anomaly in the Kuroshio Extension and its southern recirculation area, which is an important nursery ground of sardine after transport and migration from the coastal spawning grounds. In short, cooler sea surface temperatures in the nursery ground in winter are linked to sardine recruitment success. This finding formed the basis for the bottom-up hypothesis of the sardine population dynamics. The bottom-up background for the relationship of mortality coefficient anomaly to sea surface temperature anomaly was provided by further oceanographic studies in the Kuroshio Extension region. Spring phytoplankton density is related to the winter mixed layer depth, indicating that deeper winter mixed layer leads to enhanced phytoplankton growth and blooms in spring, in the nursery ground (Nishikawa and Yasuda 2008; Nishikawa et al. 2011, 2013).

Based on these findings, a "trophodynamics" hypothesis can be structured for the species alternations in the Kuroshio Current system, as follows (Fig. 3.8). This hypothesis is mainly formed by a combination of the previous studies on bottom-up processes for the sardine population dynamics and is supplemented by the author's perspectives particularly on the anchovy population dynamics. In the Kuroshio Current system, the ocean regime shifts between warm and cool regimes due to physical forcing similar to upwelling regions. When the mixed layer becomes deeper and the sea surface becomes cooler in winter, the richer nutrient supply

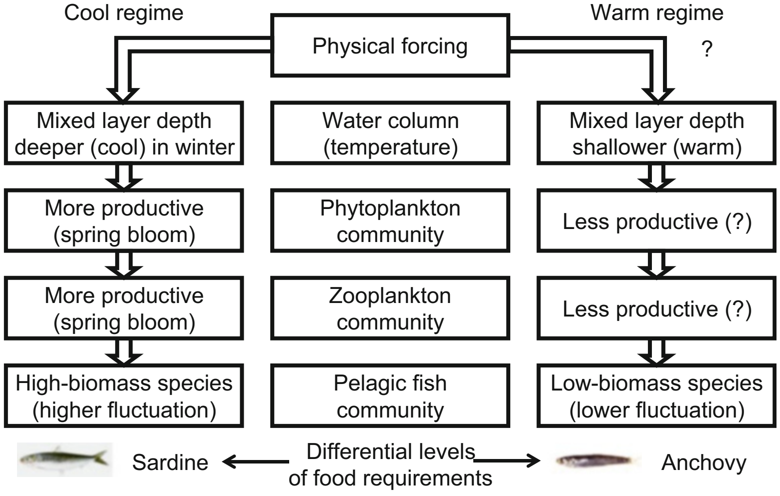

Fig. 3.8 Conceptual framework of the "trophodynamics" hypothesis based on winter mixed layer depth and spring plankton bloom in the nursery grounds for anchovy *Engraulis japonicus* and sardine *Sardinops melanostictus* in the Kuroshio Current system

supports the spring phytoplankton bloom. Such a phytoplankton community supports production of the zooplankton community. This cool regime enhances the food availability in the nursery ground for sardine. In contrast, when the mixed layer is shallower and sea surface becomes warmer, less nutrient supply is available for production of phytoplankton and zooplankton, decreasing the food availability for sardine. Accordingly, this process well explains how sardine populations flourish during cool regimes and collapse during warm regimes. On the contrary, this scenario assumes that warm regimes characterized by shallower mixed layer depth favor anchovy populations. However, it is still unknown why anchovy populations do well under the less productive conditions of phytoplankton and zooplankton during warm regimes.

There could be two possible explanations to support this assumption. First, there is a marked difference in the maximum biomass level between anchovy and sardine. As mentioned above, the maximum biomass level for sardine was approximately one order higher than for anchovy in the Kuroshio Current system (Fig. 3.1). Hence, anchovy may be able to sustain their population level under less productive conditions, although sardine may require more productive conditions to increase populations. Second, there is a difference in the spawning season between the two species (Takasuka et al. 2008c). The spawning season of sardine is limited to a relatively short period from late winter to early spring with the peak in February to March. In contrast, the spawning season of anchovy extends almost throughout the year with the peak in June to July. Hence, survival of sardine larvae would strongly depend on the food availability during a relatively limited period from winter to spring, whereas survival of anchovy larvae would not be so strongly linked to food availability for any one limited larval period. Therefore, the hypothesis assumes that the more productive condition during cool regimes favors sardine by satisfying their higher food requirement during the limited period of larval occurrence and that the less productive condition during warm regimes still allows anchovy populations to increase in place of sardine probably because anchovy have a longer period of larval occurrence (Fig. 3.8). That is, the species alternations could be attributed to differential levels of food requirements between a high-biomass species with a higher extent of fluctuation and a low-biomass species with a lower extent of fluctuation. To test this hypothesis, future studies will need to quantify food requirements and the carrying capacity for both species.

3.5 Temperature-Based Hypotheses for Species Alternations

Temperature-based hypotheses function as an alternative and complementary approach to the food-based hypotheses. In the climate cascade model, physical factors directly influence vital parameters as well as biological factors (Fig. 3.2). In the food-based hypotheses, only indirect effects of temperature by way of food availability have been considered. Obviously, however, temperature directly affects vital parameters. Indeed, temperature and food are two major determinants of the growth rate during the early life stages. Reproductive parameters are also affected by physiological processes (temperature) as well as energy gain processes (food).

3.5.1 Optimal Growth Temperature Hypothesis

The “optimal growth temperature” hypothesis (Takasuka et al. 2007a) was proposed based on differential optimal temperatures for growth rates during the early life stages between anchovy *E. japonicus* and sardine *S. melanostictus* in the Kuroshio Current system. In that study, the recent growth rates of anchovy and sardine larvae were estimated through otolith microstructure analysis, using samples of larvae collected broadly from different regions in various seasons in the Kuroshio Current system. Dome-shaped relationships were detected between the growth rate and the sea surface temperature for both anchovy and sardine larvae when the data were analyzed over various regions and seasons, indicating the existence of optimal temperatures for larval growth rates within the large spatial and temporal scales in the field (Fig. 3.9). The optimal growth rate for anchovy larvae occurs at 22.0 °C, whereas that for sardine larvae occurs at 16.2 °C.

In the Kuroshio Current system, anchovy and sardine populations have flourished during warm and cool regimes, respectively. If both species experience similar conditions, the differential optimal temperatures for larval growth rates would

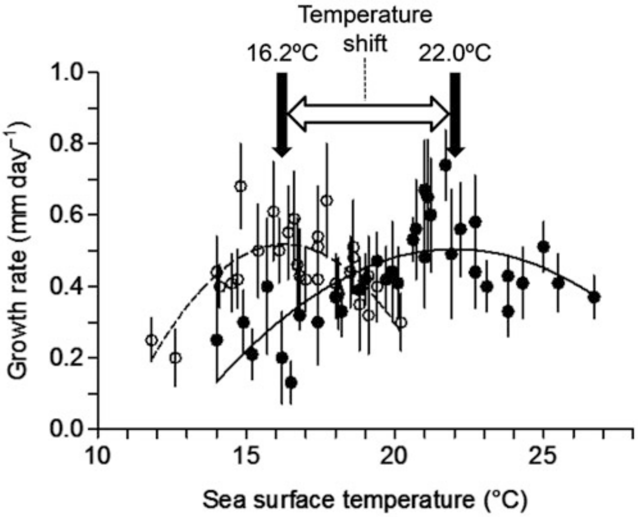

Fig. 3.9 Conceptual framework of the "optimal growth temperature" hypothesis based on differential optimal temperatures for larval growth rate between anchovy *Engraulis japonicus* and sardine *Sardinops melanostictus* in the Kuroshio Current system. Mean ± standard deviation values of recent 3-day mean growth rate estimated through otolith microstructure analysis are shown at the sample level. Quadratic functions were fitted to the mean values of growth rate against sea surface temperature for anchovy ($y = -2.302 + 0.255x - 0.006x^2$; $n = 34$, $r^2 = 0.507$, $p < 0.001$) and sardine ($y = -3.742 + 0.523x - 0.016x^2$; $n = 30$, $r^2 = 0.526$, $p < 0.001$). Optimal temperatures were estimated as 22.0 °C and 16.2 °C for anchovy and sardine, respectively (Modified from Takasuka et al. 2007a)

provide a simple mechanistic explanation of shifts in favorable conditions between the two species. That is, when the temperature is around 22 °C, the growth rates of anchovy larvae will be at the maximum level, while those of sardine larvae will be at a low level. In this case, anchovy will flourish and simultaneously sardine will collapse, since higher growth rate would enhance survival probability. As the temperature declines owing to an ocean regime shift, the growth rates of anchovy larvae will decrease gradually, while the growth rates of sardine larvae will increase rapidly. When the temperature reaches around 16 °C, anchovy will collapse and simultaneously sardine will flourish. If temperature turns back owing to another ocean regime shift, the dominant species will also turn back from sardine to anchovy. Hence, temperature shifts between these optima could lead to contrasting fluctuations in growth rates during early life stages between the two species. This simple framework of the "optimal growth temperature" hypothesis provides a possible biological mechanism leading to the out-of-phase oscillations between anchovy during warm regimes and sardine during cool regimes. The dramatically contrasting consequences between the two species can be predicted by a simulation of potential effects of growth rates on survival probability through the "stage duration" mechanism similar to Figs. 3.3 and 3.4. By this simulation, the cumulative survival probability during the larval stage was theoretically predicted to differ by 66 times for sardine and 4 times for anchovy in the opposite directions in the case of temperature shift between 18 °C and 20 °C. This result also explains why sardine populations respond to environmental changes more dramatically than anchovy populations. This anchovy and sardine relationship in terms of temperature preference was also true for the juvenile growth rates of anchovy and sardine in the offshore nursery grounds of the Kuroshio Current system (Takahashi et al. 2009).

In reality, however, anchovy and sardine do not always experience the same environmental conditions even under the same ocean regimes, mainly because of their different spawning seasons. Numerical particle-tracking experiments as part of the models revealed differences in the ambient temperatures which anchovy and sardine larvae experience during transport from the inshore spawning to the offshore nursery grounds (Itoh et al. 2009, 2011). Overall, anchovy larvae experience higher temperatures than sardine larvae. However, a retrospective analysis on the historical temperature shifts in their spawning grounds still showed that the ambient temperatures for larvae of both species fluctuated mainly between their optimal growth temperatures (Takasuka et al. 2007a). Therefore, such temperature shifts could lead to contrasting consequences in growth rates between the two species. A retrospective analysis also showed that the time-series trend of growth rates reconstructed from the growth and temperature relationships and the estimated ambient temperatures corresponded to that of recruitment per spawning biomass (an index of recruitment success) of sardine (Takasuka et al. 2007a). At the same time, however, the analysis also revealed some discrepancies among the time-series of reconstructed growth rates, recruitment per spawning biomass, and population dynamics. For example, the higher values of reconstructed growth rates and recruitment per spawning during the mid-1990s did not allow sardine populations to recover. Also, the linkage between the reconstructed growth rates and recruitment per spawning biomass was ambiguous for anchovy during some periods. These aspects which are not in agreement with the theory of the "optimal growth temperature" hypothesis suggested potential synergistic effects of other factors such as trophic interactions and fishing pressure. In other words, the temperature shifts might provide the necessary conditions rather than the sufficient conditions to drive the species alternations.

3.5.2 *Optimal Spawning Temperature*

The differential temperature optima between anchovy and sardine were also confirmed for the spawning temperature (Takasuka et al. 2008a). In addition, the concept was extended to multi-species pelagic fish in the Kuroshio Current system (Takasuka et al. 2008a). The spawning temperature optima were determined based on the occurrence of eggs and early larvae in relation to sea surface temperature, using a long-term data set of egg and larval surveys off the Pacific coast of Japan since 1978 (Oozeki et al. 2007; Takasuka et al. 2008c). Spawning temperature index was calculated by a quotient analysis on relative frequencies of positive samples in which eggs are observed versus all samples representing the sampling efforts of plankton net vertical tows (Fig. 3.10). Anchovy exhibited a broad plateau-like spawning temperature pattern with a midpoint of optimal range at approximately 22 °C. In contrast, sardine exhibited a more steeply peaked pattern with a marked peak at approximately 16 °C. These optimal spawning temperatures exactly match the optimal growth temperatures during early life stages. That is, anchovy is considered in comparison as a “warm” and “eurythermal” species, whereas sardine is considered as a “cool” and “stenothermal” species. Mackerel also exhibited a steeply peaked pattern, but the peak was observed at approximately 18 °C. On the contrary, jack mackerel showed a very similar spawning temperature pattern to anchovy. These temperature optima are consistent with the timing of their populations flourishing and collapsing in their long-term population dynamics. The peak of population dynamics of mackerel was between those of anchovy and sardine, and the population dynamics pattern of jack mackerel was similar to that of anchovy. Further, the steepness of the optima was consistent with the extent of population fluctuations. Sardine and mackerel with stenothermal spawning patterns showed dramatic fluctuations relative to anchovy and jack mackerel with more eurythermal features. In these comparisons, similarities and differences in spawning temperature optima have reflected those in the long-term population dynamics of the small pelagic fish community in the Kuroshio Current system (Fig. 3.10). This concept can also be applied to the apparent relationship of these four species to another important fisheries resource, Japanese common squid *Todarodes pacificus*, which have also shown a cyclic pattern of population dynamics, being largely synchronized with anchovy and jack mackerel (Sakurai et al. 2013). The ranges of normal and optimal temperatures for active swimming behavior of their paralarvae (Yamamoto et al. 2012) showed similar characteristics as anchovy and jack mackerel, even though the data for common squid paralarvae were obtained from a laboratory experiment.

The “optimal growth temperature” hypothesis cannot be applied directly to the species alternations in other ecosystems of the world because of the differences in relationships of the dominant species to temperature regimes (Fig. 3.1). That is, the responses of species to temperature regimes are different among different ecosystems. Yet, the concept of such a temperature-based idea itself has potential for extrapolation to other ecosystems, when species-specific responses are considered. The observed relationships in optimal spawning temperatures between anchovy *E. japonicus* and sardine *S. melanostictus* in the Kuroshio Current system show a marked contrast to those between anchovy *E. mordax* and sardine *S. sagax* in the California Current system (Lluch-Belda et al. 1991; Takasuka et al. 2008b). In the California Current system, anchovy exhibit a “cool” and “stenothermal” pattern, while sardine exhibit a “warm” and “eurythermal” pattern in terms of spawning temperature. The spawning temperature pattern of anchovy *E. mordax* in the California Current system was indeed very similar to that of sardine *S. melanostictus* in the Kuroshio Current system. The spawning temperature optima are species-specific rather than genus-specific. Accordingly, the reversed species-specific temperature optima of anchovy and sardine under the reversed temperature regimes could provide a possible theoretical solution to the synchronous species alternations

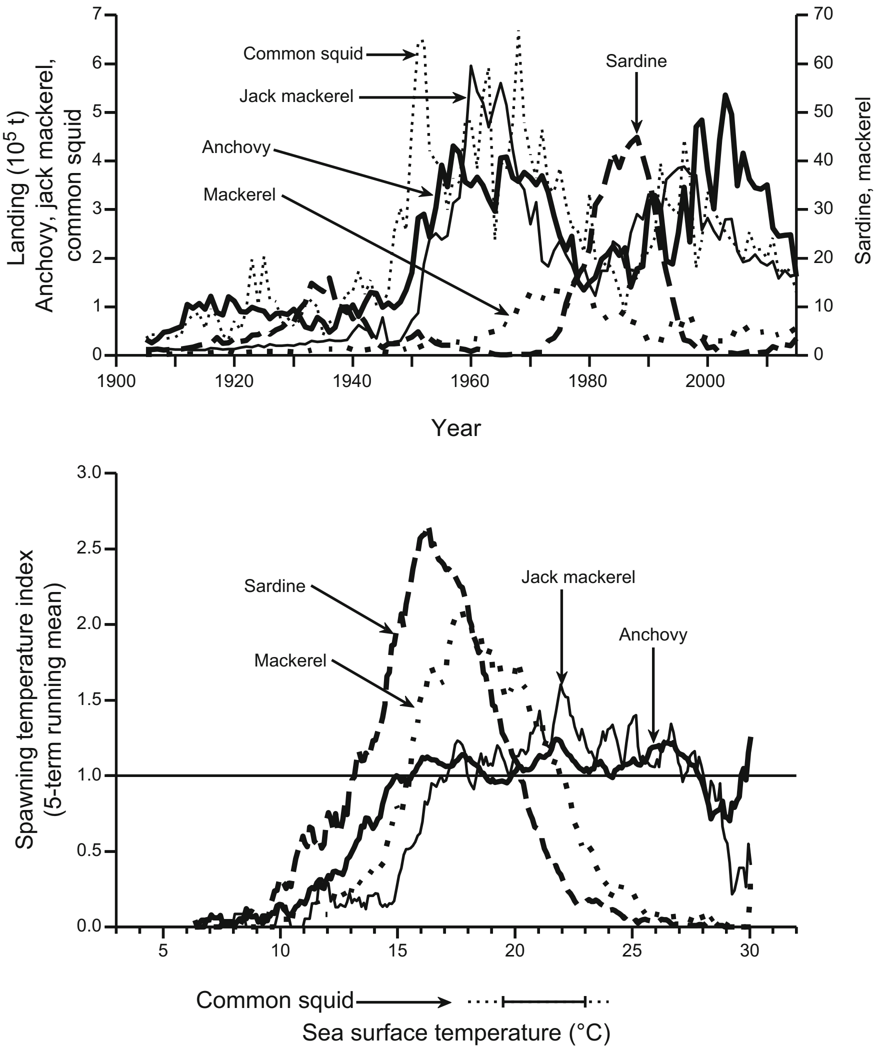

Fig. 3.10 Similarities and differences in spawning occurrence to sea surface temperature among anchovy *Engraulis japonicus*, sardine *Sardinops melanostictus*, mackerels *Scomber japonicus* and *S. australasicus*, and jack mackerel *Trachurus japonicus* in relation to those in their population dynamics on multi-decadal time scales in the Kuroshio Current system. Landing histories are shown for anchovy, sardine, mackerels, and jack mackerel in the Kuroshio Current system (upper panel). The landing data were compiled and updated from Yatsu et al. (2005) and Takasuka et al. (2008a, b). Spawning temperature index (lower panel) was calculated as relative frequencies of each temperature class (0.1 °C) of positive samples in which eggs are observed divided by those of all samples representing sampling efforts of plankton net vertical tows, using a long-term data set of egg and larval surveys off the Pacific coast of Japan. Occurrence of eggs was analyzed for anchovy, sardine, and mackerels; occurrence of larvae was analyzed for jack mackerel. The 0.1 °C data series were smoothed by five-term running means. The horizontal line indicates the baseline of optima, above which temperature interval was assumed to be preferred for spawning (Lluch-Belda et al. 1991) (Modified from Takasuka et al. 2008a). Landing history of Japanese common squid *Todarodes pacificus* is also shown in the upper panel; normal and optimal temperature ranges for active swimming behavior of Japanese common squid paralarvae (Yamamoto et al. 2012) are shown under *x*-axis in the lower panel (dotted and solid horizontal lines, respectively)

between the opposite sides of the North Pacific (Takasuka et al. 2008b). However, these results do not mean that direct temperature effects constitute a single major mechanism driving species alternations but that such a pathway exists as one of the mechanisms driving species alternations under temperature shifts.

3.6 Other Hypotheses

Undoubtedly, no single factor or mechanism can sufficiently explain everything to do with the species alternations in light of the complexity of marine ecosystems (Duffy-Anderson et al. 2005). For example, a combination of temperature and food availability determined growth rates of anchovy larvae in the nursery ground (Takahashi and Watanabe 2005). The food- and temperature-based hypotheses and some other hypotheses are theoretically independent of and synergistic with one another, as in the growth and survival mechanisms during the early life stages. As well as food and temperature, intraspecific and interspecific interactions, fishing pressure, etc. could be potentially influential and promote or mitigate the processes of species alternations.

3.6.1 Intraspecific Interactions

As one of the possible intraspecific interactions, density-dependent processes are important components in understanding population dynamics of organisms. Kawasaki and Omori (1995) discussed the roles of density-dependent versus density-independent processes in the population dynamics of sardine in the Kuroshio Current system. They hypothesized that the start of the population collapse of sardine was caused by recruitment failure of over-dispersed offspring produced from parents with a low lipid content. Long-term biological data set has shown that the gonadal somatic index in spawning season and the size at age 1 of sardine declined during their high-biomass period in Korean waters (Kim et al. 2006). As above, density-dependent process would be influential in the population dynamics of sardine. On the contrary, possibilities of density-dependent effects are less known for anchovy populations.

Although the roles of density-dependent processes in anchovy and sardine in the Kuroshio Current system are still under debate, density-dependent effects on biological parameters such as growth and fecundity have been well documented for marine fish in general. The effects are known to be compensatory such that higher growth and fecundity are achieved at lower densities and potentially facilitate population recovery (Rose et al. 2001; Nash et al. 2009). For example, the nutritional condition and gonad mass per body weight were higher, and the length at maturity was lower during the lower biomass periods in sardine *S. sagax* in the southern Benguela (van der Lingen et al. 2006b). Such changes in the conditions of females could exert considerable effects on the reproductive success of females and survival success of offspring through maternal effects on quantitative and qualitative aspects of the produced eggs (Green 2008).

3.6.2 Interspecific Interactions

The roles of interspecific interactions such as food competition between anchovy and sardine as well as prey–predator interactions have not been well understood in the Kuroshio Current system. In general, interspecific interactions have various possibilities and pathways of their influences on population dynamics. Some studies have emphasized the effects of interspecific interactions on the species alternations (Bakun and Cury 1999; Bakun and Broad 2003; Alheit and Niquen 2004).

As a unique idea, the "school trap" hypothesis (Bakun and Cury 1999) focuses on the disadvantages of the minor species in mixed-species schools. In this hypothesis, the mixed-species schools (anchovy and sardine) migrate to the nursery, feeding, and spawning grounds with favorable conditions for the major species, in which the minor species is affected by unfavorable conditions. But the minor species remain in the schools because schooling is an essential antipredator behavior. Note that this hypothesis was not intended to explain the alternating phase, but it was proposed as a mechanism promoting the species dominance after one species becomes more dominant than the other.

Food competition between anchovy and sardine may also be a possible mechanism. However, as in the "trophic dissimilarity" hypothesis, anchovy and sardine are assumed to be segregated more or less in utilizing food resources in upwelling systems. In contrast, they are concluded to be ecologically directly competing species in terms of their trophic positions in the Kuroshio Current system (Yasue et al. 2011, 2014). To test the concept of food competition between anchovy and sardine, further studies will be needed to obtain quantitative estimates of daily rations and prey availability at fine scales.

Prey–predator interactions definitely constitute key processes in the population dynamics of small pelagic fish as in the climate cascade model (Fig. 3.2). Top-down controls have been reported in some marine ecosystems (Frank et al. 2005). Even under bottom-up (Ware and Thomson 2005) and wasp-waist controls (Cury et al. 2000), predation plays a role in determining the population dynamics of fish, since predation is the major and direct source of mortality of fish (Bailey and Houde 1989). Indeed, the growth and survival mechanisms are predator-specific, and therefore the predator field would regulate characteristics of the survivors as well as predation mortality (Takasuka et al. 2007b). Nonetheless, the effects of predator fields on species alternations remain unclear, mainly because time-series data of predator fields are lacking for the Kuroshio Current system and for many other current systems. Predator fields vary with the developmental stage while being transported and migrating from spawning to feeding grounds. In most current studies, discussions on biological mechanisms of species alternations inherently assume constant predation pressure. This issue needs to be clarified based on field studies.

3.6.3 Fishing Pressure

Fishing pressure has not been regarded as a major factor causing species alternations; however, it should not be ignored as a potential factor influencing the population dynamics of anchovy and sardine. In general, it is difficult to discriminate the effects of fishing and environmental factors on fish population dynamics, although it was for the first time achieved by Hsieh et al. (2006). Indeed, the effects of fishing on sardine population dynamics have been a central issue in fisheries biology and management in Japan (Katsukawa 2007). A simulation study using an individual-based life cycle model concluded that low fishing mortality was required to allow sardine stock to recover in the Kuroshio Current system (Suda et al. 2005). The effects of fishing pressure have been given more attention for sardine than for anchovy, since the population dynamics shows more dramatic fluctuations in sardine than in anchovy in the Kuroshio Current system (Takasuka et al. 2008a).

Of particular concern is the population dynamics during the low-biomass periods in general, since the populations could be at risk of extinction (Myers et al. 1995; Hutchings 2014). Fishing pressure could accelerate the collapse or prevent the recovery of the stocks particularly during the low-biomass periods (Shelton et al. 2006). This issue is strongly related to compensation due to density-dependent effects which could promote population recovery during the low-biomass periods. However, the effects of fishing could be more critical if depensation (also known as Allee effect), that is, inverse density-dependent effects, occurs under high fishing pressure (Dulvy et al. 2003; Nash et al. 2009; Hutchings 2014). Further, fishing may also affect the age structure of fish populations which is indicative of potential of productivity and stability of the populations (Brunel and Piet 2013; Hixon et al. 2014).

3.7 Future Recommendations

International activities of studies on climate impacts on population dynamics of small pelagic fish were led by the Small Pelagic Fish and Climate Change (SPACC), which was a regional program of the Global Ocean Ecosystem Dynamics (GLOBEC) International Program, since it was launched in 1994 with a workshop in La Paz, Mexico. The SPACC program aimed to understand and predict climate-induced dynamics of production of small pelagic fish in relation to physical and biological processes in marine ecosystems and included several major themes: long-term changes in ecosystems, retrospective analyses, comparative population dynamics, reproductive habitat dynamics, and economic implications of climate variability. The SPACC program culminated in 2010 with the publication of its review book (Checkley et al. 2009). Currently, the activities are continuing in working groups of some international organizations such as the International Council for the Exploration of the Sea (ICES) (Alheit 2010) and the North Pacific Marine Science Organization (PICES), but no international program specific to small pelagic fish (like the SPACC program) is ongoing. In the following subsections, some personal perspectives are presented as future recommendations: synthesis of different hypotheses, synthesis among different ecosystems, and multidisciplinary approaches.

3.7.1 Synthesis of Different Hypotheses

Reviewing hypotheses of species alternations, each hypothesis is at least theoretically reasonable in addressing how differently environmental conditions could affect the population dynamics of different species. However, each hypothesis has both advantages and disadvantages in its explanatory power. Overall, different hypotheses focus on different factors and processes. For example, food-based hypotheses do not consider direct temperature effects; temperature-based hypotheses do not consider food availability. These hypotheses and processes should be integrated into a larger framework, at least for assessing species alternations within specific ecosystems, in the future. Note that the different mechanisms are not necessarily exclusive to one another. Moreover, there are still some controversies in the application of any hypothesis proposed from one ecosystem to another ecosystem. Such an inability to apply hypotheses suggests that the relative contributions of mechanisms and dominant factors driving the species alternations may substantially differ among different ecosystems (e.g., upwelling versus non-upwelling western boundary current systems).

3.7.2 Synthesis Among Different Ecosystems

Synthesis among different ecosystems has been a goal of international activities such as the SPACC program. The author proposes three recommendations toward a breakthrough of synthesis among different ecosystems. First, extracting species-specific responses to multiple environmental factors throughout the life history is an essential step. Second, interspecific and intersystem comparisons should be done in a uniform approach within the same study framework. Previous trials of synthesis have spent substantial efforts gathering and reviewing the results of analyses by different study groups from different ecosystems. However, due to methodological differences among studies, bottlenecks in the synthesis frequently occur. Barange et al. (2009) examined habitat expansion and contraction of anchovy and sardine in the Kuroshio, California, Humboldt, and Benguela Current systems. In their study, the relationships between stock biomass, distribution area, and mean density of sardine and anchovy populations were compared among these different current systems using a uniform approach. Lastly, synthesis needs multidisciplinary approaches as discussed below.

3.7.3 Multidisciplinary Approaches

Multidisciplinary approaches are required to realize such syntheses. For example, field, laboratory, and model studies need to be tightly integrated in order to test hypotheses of mechanisms regulating population dynamics. Field and laboratory studies provide complimentary approaches to each other: some hypotheses should be tested in the field to ensure biological parameters are realistic, but other hypotheses can only be tested under laboratory conditions. In any case, the information on biological parameters obtained from field and laboratory studies should be incorporated into predictive models eventually, since predicting future trends is an ultimate goal of studies on population dynamics of small pelagic fish.

Recent developments of physical–biological individual-based models (IBMs) have contributed to understanding survival processes under environmental variability by expressing spatial and temporal variability of mortality rates of fish particularly during the early life stages (Hufnagl and Peck 2011; Peck and Hufnagl 2012). For the IBMs to work as a powerful tool, physiological parameters need to be assessed (Pörtner and Peck 2010).

For the species alternations, a bioenergetics model is now being developed. A lower trophic level ecosystem model, North Pacific Ecosystem Model for Understanding Regional Oceanography (NEMURO), was extended to NEMURO.FISH (NEMURO For Including Saury and Herring), which is a bioenergetics model of fish growth and population dynamics, by the PICES Model Task Team (Ito et al. 2004; Kishi et al. 2007; Werner et al. 2007). NEMURO.FISH is being developed to NEMURO.SAN (Sardine and ANchovy) to further examine the species alternations (Ito et al. 2006, 2010; Werner et al. 2007). In the Kuroshio Current system, growth and migration of sardine have been modeled (Okunishi et al. 2009, 2012a, b). Such bioenergetics models are intended to contribute to the prediction of future trends of population dynamics. Moreover, the models are expected to be powerful tools for testing different hypotheses, clarifying the relative importance of each factor, and synthesizing them among different ecosystems.

Finally, links of biological studies to management and economics would be an essential goal of future international activities. After the SPACC program finished, a workshop on future plans was held in La Paz, Mexico, in February 2010 (van der Lingen et al. 2010). In this workshop, a framework of task teams was structured as a proposal, which comprises four themes: hypotheses, climate, models, and management. First, the "hypotheses" task aims to explicitly test hypotheses of mechanisms of population dynamics of small pelagic fish. Second, the "climate" task aims to review potential effects of climate variability on their population dynamics. Third, "models" task aims to develop coupled physical–biological models for simulating and predicting their population dynamics under climate variability. Lastly, "management" task aims to make these activities relevant to and useful for management and economics. In particular, "management" is an update from the previous SPACC program. A multidisciplinary approach linking biological studies to fisheries management and economics is a current issue among research scientists who are interested in the population dynamics of small pelagic fish (e.g., ICES/PICES Symposium on Forage Fish Interactions: Creating the tools for ecosystem-based management of marine resources, Nantes, France, November 12–14, 2012; Peck et al. 2014; ICES/PICES Symposium on "Drivers of dynamics of small pelagic fish resources," Victoria, Canada, March 6–11, 2017).

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Chapter 4
Population Dynamics of Demersal Fish Focusing on Walleye Pollock (*Gadus chalcogrammus*)

Tetsuichiro Funamoto

Abstract Demersal fishes constitute a high trophic level in marine ecosystems. They have relatively long lifespans, and because their biomass does not easily recover after collapse, they are considered more vulnerable to overfishing than pelagic fishes. Like pelagic fishes, the population dynamics of demersal fishes are closely linked to environmental changes. Therefore, their stock management must consider their biological characteristics in relation to environmental factors. This chapter reviews the relationships of demersal fish recruitment with various environmental factors, focusing on walleye pollock (*Gadus chalcogrammus*) as an example of an important demersal fish resource. In addition, the incorporation of recruitment studies with stock assessment works is discussed. Finally, recommendations for future fisheries management strategies based on interdisciplinary research are also provided.

Keyword Demersal fish · Integrated management · Population dynamics · Recruitment mechanism · Recruitment model · Stock assessment · Walleye pollock

4.1 Advantages and Disadvantages of Living Near the Sea Bottom

While pelagic fishes live away from the sea bottom, demersal fishes basically live near the sea bottom. Living near the sea bottom has some advantages. One of them is hiding places; fish can take refuge among structures such as rocks, corals, and seaweeds as well as burrow into the sea bottom. Some fishes can also mimic those structures and the sea bottom. These escape and mimic behaviors can decrease mortalities of demersal fishes. In addition, fishes living on the sea bottom do not need to swim to maintain a stable posture in the water, resulting in a reduced energy expenditure.

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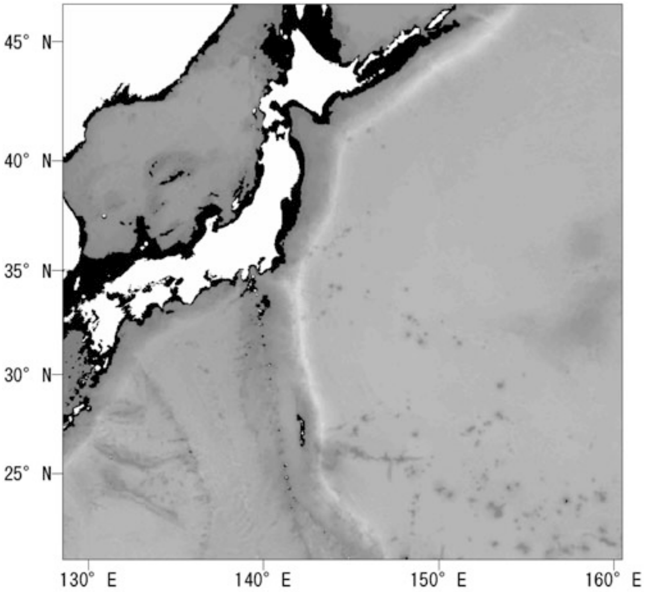


Fig. 4.1 Sea area around Japan. Black indicates the sea area with a bottom depth from 0 to 500 m. Land is shown in white

On the other hand, living near the sea bottom has some disadvantages including horizontal and vertical distribution restrictions. Figure 4.1 shows the sea area around Japan. In this sea area, demersal fishes which can use the sea bottom from 0–500 m depth can reside in the black area if conditions other than bottom depth are ignored. In contrast, pelagic fishes can use all sea surface layers in black and gray areas. Therefore, the habitat capacity of demersal fishes is significantly small if compared to that of pelagic fishes. This small habitat capacity can limit the maximum biomass and recruitment. Demersal fishes which are ranked in the world's top 20 catch (mt) in 2011 included only walleye pollock (*Gadus chalcogrammus*, hereafter as pollock), largehead hairtail (*Trichiurus lepturus*), and Atlantic cod (*Gadus morhua*) (FAO 2013). Moreover, these demersal fishes live not only near the sea bottom but in mid-depth layers as well, especially at night (e.g., Munekiyo 1990; Engas and Soldal 1992; Bailey et al. 1999). In 2011, the largest catch among the demersal fishes always living near the sea bottom was produced by Pacific cod (*Gadus macrocephalus*); however, this catch was the 25th among all the fish species, implying that the maximum biomass of demersal fish is restricted by the habitat capacity.

The second disadvantage of living near the sea bottom is that fishes are exposed to strong predation. Many demersal fishes are piscivorous and at a high trophic level in marine ecosystems (e.g., Pihl 1994; Fujita et al. 1995). The four previously mentioned demersal fishes with large catches are all piscivorous (e.g., Fujita et al. 1995; Bailey et al. 1999; Link and Garrison 2002; Martins et al. 2005). At the early life stage, most demersal fishes settle to the sea bottom where many of these piscivorous fishes live. Hence, settlement is equivalent to movement into places where predators are waiting. This means that predation after settlement can play a significant role in the process of recruitment determination of demersal fishes. For pollock in the eastern Bering Sea, at least one-third of the variability in spawner-to-recruit survival can be accounted for by predation mortality after settlement (Mueter et al. 2006). Furthermore, for some demersal fishes with a large biomass, such as pollock and Atlantic cod, cannibalism after settlement can be an important mortality factor (e.g., Bjørnstad et al. 1999; Wespestad et al. 2000).

4.2 Characteristics of Demersal Fish

One characteristic of demersal fish is a long lifespan (e.g., Kawasaki 1980; King and McFarlane 2003). Some demersal fishes such as sablefish (*Anoplopoma fimbria*) and Patagonian toothfish (*Dissostichus eleginoides*) live >50 years (Kimura et al. 1998; Collins et al. 2010). Among six fish species for which a total allowable catch (TAC) is set in Japan (i.e., Japanese sardine [*Sardinops melanostictus*], Japanese jack mackerel [*Trachurus japonicus*], chub mackerel [*Scomber japonicus*], blue mackerel [*Scomber australasicus*], Pacific saury [*Cololabis saira*], and pollock), only pollock is a demersal fish and has the longest lifespan (Table 4.1). Because a long lifespan is related to a low natural mortality coefficient (M), pollock has the lowest M among these six species.

Long lifespan (or low M) has some advantages. First, long lifespan enhances the efficacy of cutting down on catch, because survival rate of uncaught fish to the next year is high. Hence, relatively long-term management plans can be formulated for each year class of demersal fish. In contrast, the efficacy of reducing catch is low for cohort management of pelagic fishes with short lifespans; even if good recruitment occurs and fishing pressure is low, the number of fish can decease dramatically within 1 year due to the high M.

In the field of fisheries, two types of recruitment are defined: biological recruitment and fishery recruitment (e.g., Caley et al. 1996). Biological recruitment indicates the number of individuals entering some life history stage such as settlement or maturity. On the other hand, fishery recruitment indicates the number of individuals entering the exploitable stock. Although the term “recruitment” in this chapter may refer to biological recruitment (e.g., Sect. 4.1) or fishery recruitment (e.g., Sect. 4.5), this term is always used as a synonym for year-class strength. That is, the term “recruitment” in this chapter implies the number of fish entering the life stage (or reaching the size/age) at which natural mortality stabilizes near-adult levels (e.g., Ludsin et al. 2014).

Long lifespan is usually associated with an old age at maturity. Among TAC fish species in Japan, pollock has the highest age at maturity (Table 4.1), which has some disadvantages. For example, if a management plan regulates that fishes are not caught before their first spawning, an older age at maturity leads to an older age at

Table 4.1 Lifespan, natural mortality coefficient (M), age at maturity, and average and standard deviation (SD) of recruitment per spawning (RPS) for six fish species for which the total allowable catch is set in Japan

Main distribution	Species	Stock name	Lifespan (years)	*M*	Age at maturity[a] (years old)	RPS[b] (n/kg)	SD of RPS (n/kg)
Pacific Ocean	Japanese sardine (*Sardinops melanostictus*)	Pacific	7	0.40	2	26	20
	Japanese jack mackerel (*Trachurus japonicus*)	Pacific	5	0.50	2	29	9
	Chub mackerel (*Scomber japonicus*)	Pacific	8	0.40	3	10	12
	Blue mackerel (*Scomber australasicus*)	Pacific	6	0.40	2	11	11
	Pacific saury (*Cololabis saira*)	Northwestern Pacific	2	1.25	1	41	22
	Walleye pollock (*Gadus chalcogrammus*)	Japanese Pacific	>10	0.25[c]	5	10	8
Sea of Japan	Japanese sardine	Tsushima current	7	0.40	2	39	34
	Japanese jack mackerel	Tsushima current	5	0.50	2	28	14
	Chub mackerel	Tsushima current	6	0.40	2	6	2
	Blue mackerel	Tsushima current	6	0.40	2	6	2
	Walleye pollock	Japan Sea	>10	0.25[c]	6	3	2

Modified from Fisheries Agency and Fisheries Research Agency (2014)

[a] Age at >90% maturity, [b] average for about10–30 years, [c] M for age 3 and older

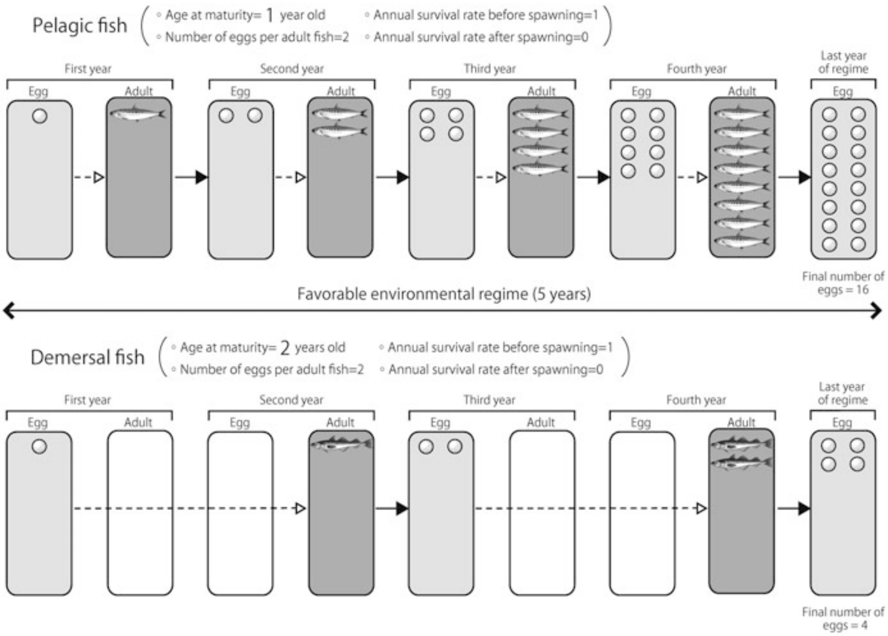


Fig. 4.2 Schematic depicting the stock resilience of pelagic and demersal fishes. Age at maturity is assumed to be 1 and 2 years for pelagic and demersal fishes, respectively. Dotted and solid arrows indicate maturity and spawning, respectively. One egg in the first year results in 16 and 4 eggs in the fifth year for pelagic and demersal fishes, respectively

first exploitation. Thus, even if there is a good recruitment, a long period is needed before it is initially exploited. In addition, an old age at maturity is thought to restrict stock resilience (i.e., recovery speed). For pelagic fishes with a young age at maturity, if the effects of density dependence and fishery are ignored, good recruitment owing to a favorable environmental regime rapidly results in a large spawning stock biomass (SSB). Large SSB produces better recruitment, which quickly leads to larger SSB, which in turn produces a much better recruitment. This positive feedback will continue until the end of the favorable regime (Fig. 4.2). That is, a multiplier effect of favorable environmental conditions and increased SSB on recruitment can occur for pelagic fishes with a young age at maturity. However, this multiplier effect cannot be expected for demersal fishes with an old age at maturity, because a relatively long time is required before a good recruitment results in a large SSB.

Another characteristic of demersal fishes is the low recruitment per spawning (RPS), and one reason for this low RPS is probably small habitat capacity (see Sect. 4.1). Among TAC fish species in Japan, RPS is lowest for pollock (Table 4.1). Because low RPS indicates low stock resilience, if the biomass of a demersal fish species declines to a low level, a longer time is theoretically required to recover than for a pelagic fish species. Furthermore, low RPS is usually associated

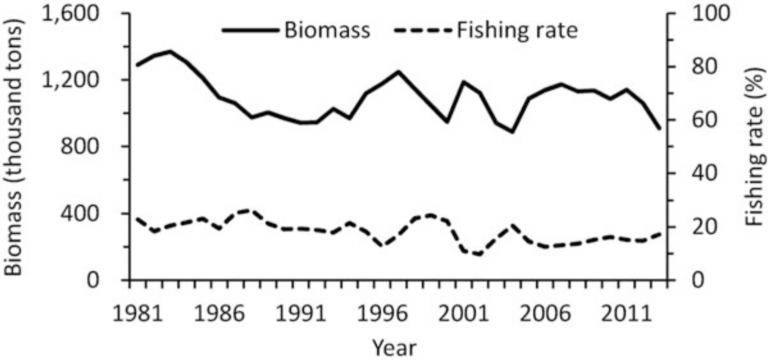


Fig. 4.3 Biomass and fishing rate of walleye pollock (*G. chalcogrammus*) off the Pacific coast of northern Japan (Modified from Funamoto et al. 2015)

with a small standard deviation (SD) of RPS. Among TAC fish species in Japan, the SD of RPS is smallest for pollock (Table 4.1). This implies that the fluctuation range of biomass is usually less for demersal fishes than for pelagic fishes if the effect of the fishery is removed. For example, the biomass of pollock off the Pacific coast of northern Japan has been surprisingly stable after 1981 under a stable fishing rate (Fig. 4.3).

4.3 Factors Affecting Demersal Fish Recruitment

As mentioned in Chap. 3, recruitment of pelagic fishes is strongly affected by the environmental conditions which mainly affect survival during the early life stages. Because demersal fishes also have egg, larval, and juvenile stages that are vulnerable to unfavorable environments, their recruitment is also affected by the environmental conditions. For example, water temperature influences the hatching rate of eggs and growth rate of larvae for demersal fishes (e.g., Nakatani 1988; Yamashita et al. 2001; Buckley et al. 2004). In addition, because most demersal fishes have a pelagic phase, their recruitment is influenced by transport (e.g., Wespestad et al. 2000; Churchill et al. 2011). Transport is especially important for demersal fishes which must be transported into appropriate sea areas for settlement. The abundance of predators around the sea bottom can also significantly affect the recruitment of demersal fishes for which predation after settlement plays an important role in recruitment processes (e.g., Bailey 2000; Funamoto et al. 2013).

In addition to the environmental conditions, the recruitment of commercial demersal fishes can be directly affected by the fishery through decreased SSB. The recruitment of noncommercial demersal fishes is also influenced by the fishery if discards lead to death. The effect of decreased SSB depends on the shape of the stock–recruitment relationship. For example, if the stock–recruitment relationship is a Ricker type (i.e., dome-shaped), a decrease in SSB leads to decreased recruitment at lower SSB than the vertex of the parabolic curve. In contrast, decreased SSB leads to increased recruitment at higher SSB than the vertex of the parabolic curve. Moreover, demersal fishes including commercial and noncommercial fishes are vulnerable to changes in bottom topography caused by bottom trawling (i.e., indirect effects of fishery) (e.g., Turner et al. 1999; Thrush and Dayton 2002).

4.4 Recruitment Mechanism of Pollock

Numerous studies have been conducted to understand the processes controlling the recruitment of demersal fish. Especially, extensive knowledge and hypotheses exist for pollock, because the world total catch of this fish exceeded 3 million tons in 2011, which is second only to Peruvian anchoveta (*Engraulis ringens*) (FAO 2013).

Pollock is widely distributed in the North Pacific Ocean from Puget Sound to off northern Japan (Bailey et al. 1999). This species is an important component of the North Pacific ecosystem not only as a prey, predator, and competitor of other fishes but also as a prey item for seabirds and marine mammals. Although pollock is semi-pelagic in some areas, they are basically dependent on the sea bottom in regions shallower than about 200 m depth, so pollock can be regarded as a demersal fish. The scientific name of pollock was recently changed from *Theragra chalcogramma* to *Gadus chalcogrammus* based on extensive genetic studies (e.g., Coulson et al. 2006; Carr and Marshall 2008). These studies indicate that pollock is closely related to the Atlantic cod. Reproductive traits of these two species have a number of features in common, such as single-pair, ventral mounting, multiple spawning over a period of several days, and pelagic eggs (e.g., Brawn 1961; Sakurai 1989).

Existing knowledge and hypotheses about the recruitment fluctuation mechanism of four pollock stocks worldwide—in the eastern Bering Sea, Gulf of Alaska, off the Pacific coast of northern Japan, and the Sea of Japan off northern Japan—are summarized below.

4.4.1 Eastern Bering Sea

Pollock in the eastern Bering Sea (hereafter, EBS pollock) is one of the largest pollock stocks worldwide; in 2013 its biomass (total weight of individuals aged $\geq$3 years) was estimated at 8,261,000 tons (Ianelli et al. 2013). Pollock represents a major biological component of the Bering Sea ecosystem (Bailey et al. 1999).

There are several hypotheses about the recruitment mechanism of EBS pollock, such as the cold-pool hypothesis (Wyllie-Echeverria and Wooster 1998), larval transport hypothesis (Wespestad et al. 2000), and oscillating control hypothesis (OCH) (Hunt et al. 2002). Of these, the OCH focuses on the shift between bottom-up and top-down

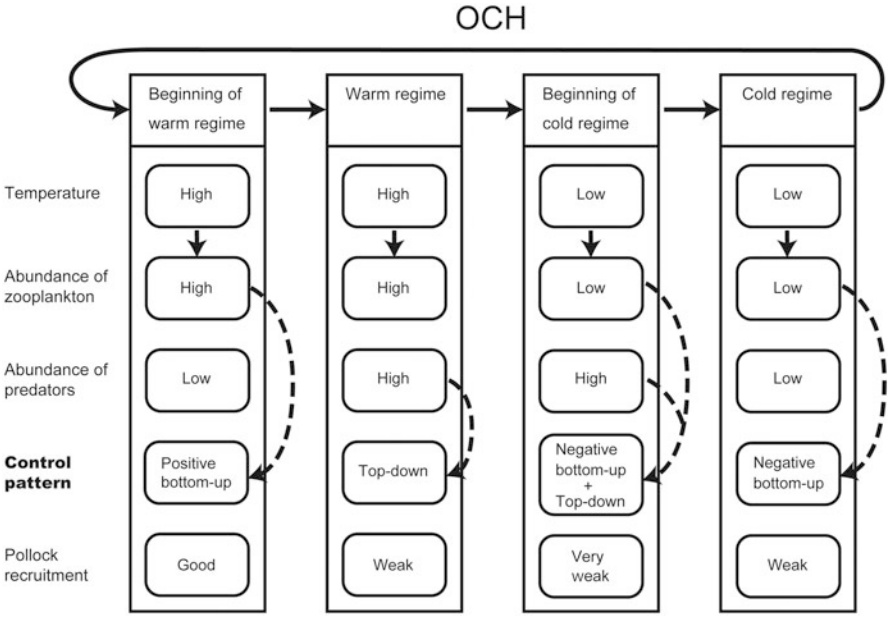


Fig. 4.4 Oscillating control hypothesis (OCH) for recruitment mechanism of eastern Bering Sea walleye pollock (*G. chalcogrammus*) (Modified from Hunt et al. 2002)

control (Fig. 4.4). At the beginning of a warm regime, the recruitment of pollock and some other demersal fishes increases because of abundant zooplankton (i.e., under positive bottom-up control). However, as this good recruitment grows, the control of pollock recruitment becomes top-down through cannibalism and predation by other demersal fishes, resulting in weak pollock recruitment. After a cold regime begins, pollock recruitment becomes weaker because of the reduced zooplankton biomass and abundant predators (i.e., under negative bottom-up and top-down control). If these weak recruitments lead to poor predators, top-down control is weakened, and pollock recruitment increases slightly. Furthermore, after a warm regime resumes, zooplankton become abundant, and pollock recruitment is enhanced again. The OCH proposed that recruitment of EBS pollock is regulated by this oscillating control system.

An important criterion of the OCH is that if the effects of predation are ignored, recruitment is high in warm years, because early ice retreat and late bloom enhance zooplankton abundance (Hunt et al. 2002). However, in recent years, the recruitment of EBS pollock has tended to be low in years with high water temperature and vice versa (Ianelli et al. 2013). On the basis of this new trend, the OCH was revised such that temperature conditions are divided into two seasons (Hunt et al. 2011) (Fig. 4.5). The new OCH indicates spring temperature affects the abundance of small zooplankton which are important food for early larval-stage pollock, whereas summer temperature affects the abundance of large zooplankton which are important food for

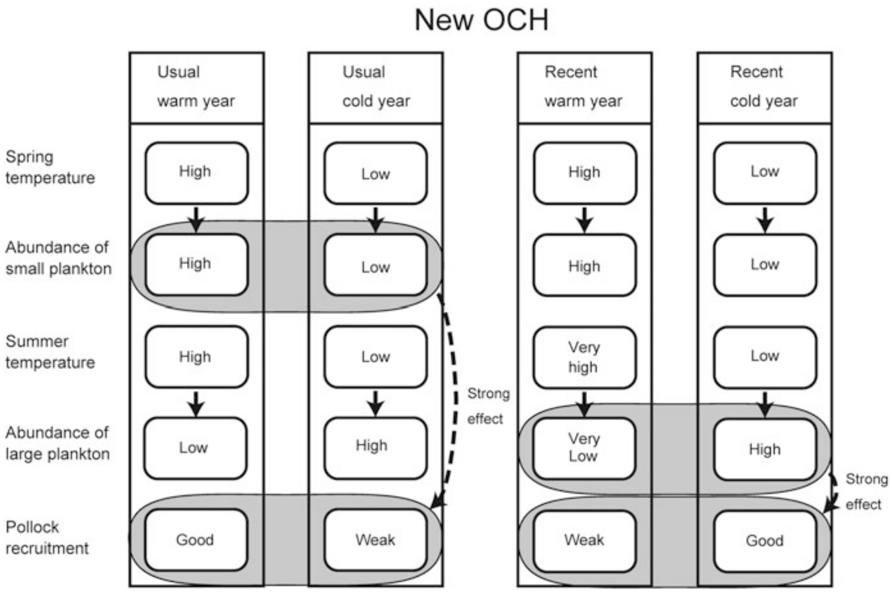


Fig. 4.5 Bottom-up regulation in the new oscillating control hypothesis (OCH) for eastern Bering Sea walleye pollock (*G. chalcogrammus*) (Modified from Hunt et al. 2011)

late larval-stage pollock. In addition, high spring temperatures lead to an increase in small zooplankton, while high summer temperatures a decrease in large zooplankton. In recent years with high temperatures, small zooplankton have been abundant because of high spring temperatures; meanwhile, large zooplankton have been very scarce because of very high summer temperatures. Therefore, larvae had low energy densities in autumn and experienced low overwinter survival. In contrast, in recent years with low temperatures, small zooplankton have been scarce because of low spring temperatures, whereas low summer temperatures led to an increase in large zooplankton, resulting in pollock larvae with high levels of energy reserves in autumn and high overwinter survival. These low and high overwinter survival rates produce poor and good recruitments, respectively. Therefore, the new OCH indicates that a low summer temperature is important for recent good recruitment of EBS pollock through favorable feeding conditions at the late larval stage.

Interestingly, the OCH focuses on the effect of water temperature on the larval feeding condition, although temperature also affects pollock growth in the early life stages (e.g., Hamai et al. 1971; Kooka et al. 2007). Moreover, because pollock is the most abundant fish species in the Bering Sea, cannibalism is an important component for its recruitment dynamics (Mueter et al. 2006). This strong effect of cannibalism on recruitment is probably the main reason for the Ricker-type stock–recruitment relationship being detected for EBS pollock (Wespestad and Quinn 1996).

4.4.2 Gulf of Alaska

Pollock in Gulf of Alaska (hereafter, GOA pollock) is a smaller stock than EBS pollock, and in 2013 its biomass (total weight of individuals aged ≥ 3 years) was estimated at 1,074,000 tons (Dorn et al. 2013). However, GOA pollock has served as a model stock for research on recruitment dynamics, because the spawning season is short and early life stages tend to aggregate in small areas (e.g., Bailey et al. 1996).

Regarding the recruitment of GOA pollock, Bailey et al. (2005) advocated the complex system hypothesis (Fig. 4.6). This hypothesis divides recruitment-

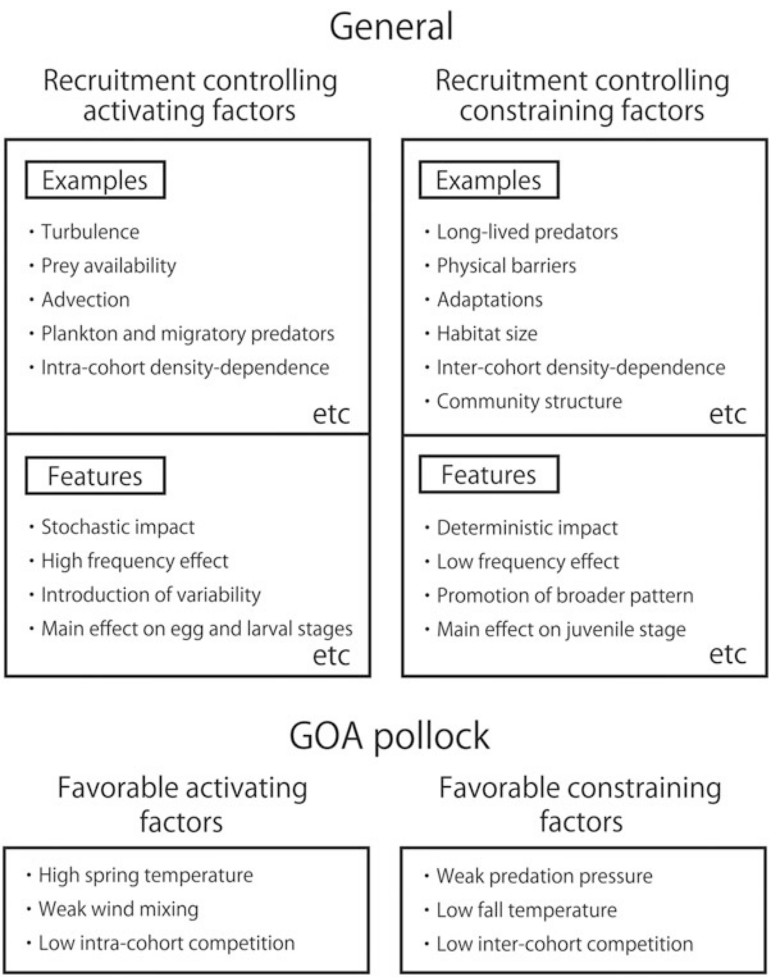


Fig. 4.6 Recruitment-controlling factors in complex system hypothesis for general marine fishes and Gulf of Alaska (GOA) walleye pollock (*G. chalcogrammus*) (Modified from Bailey et al. 2005)

controlling factors into activating and constraining factors. Activating factors are high-frequency events during the egg and larval stages, which introduce variability to the population dynamics. In contrast, constraining factors are lower-frequency events and tend to promote broader patterns. Important activating factors of GOA pollock are spring temperature and wind mixing, and low spring temperature and strong wind mixing tend to result in high larval mortality. Although interpreting the effects of spring temperature and wind mixing on larval survival is not straightforward, these factors have been considered to affect larval food availability (Ciannelli et al. 2004). For example, high water column turbulence (i.e., strong wind mixing) may reduce the foraging success of young larvae. On the other hand, important constraining factors are fall temperature and predation, and high fall temperature and strong predation pressure (mainly by arrowtooth flounder [*Atheresthes stomias*]) tend to lead to low juvenile survival. High fall temperature is thought to increase metabolic demands and/or limit the habitat capacity of juvenile pollock. In addition to these factors, intra- and inter-cohort density dependences also strongly affect GOA pollock recruitment (Bailey et al. 2005). Although density-dependent processes are difficult to categorize as activating or constraining, intra- and inter-cohort density dependences are usually considered as activating and constraining, respectively.

A noteworthy product of research on the recruitment mechanism of GOA pollock is their life table which has enabled the determination of when each year-class strength was established. The abundance index at each developmental stage from egg to recruitment has been estimated for GOA pollock (Bailey and Spring 1992; Bailey 2000). The resultant life table clarified that the critical stage of GOA pollock shifted from the larval stage to the juvenile stage after a major environmental regime shift in the late 1970s (Bailey 2000).

4.4.3 Pacific Coast of Northern Japan

As pollock off the Pacific coast of northern Japan are usually called the Japanese Pacific stock, they will be referred to as Japanese Pacific (JP) pollock in the following. The biomass (total weight of individuals aged $\geq$0 years) of JP pollock in 2013 was 910,000 tons, which is similar to that of GOA pollock (Dorn et al. 2013; Funamoto et al. 2015). The life history traits of JP pollock are described in Kendall and Nakatani (1992), Sakurai (2007), and Funamoto et al. (2014).

The recruitment of JP pollock is influenced by winter temperature, and high winter temperature tends to result in good recruitment (Funamoto 2007; Funamoto et al. 2013). How water temperature affects the recruitment of JP pollock is discussed in Sect. 4.4.4. Egg and larval transports, which are controlled by ocean currents, wind conditions, and the vertical position of eggs and larvae, are also important for recruitment of JP pollock (Shimizu and Isoda 1997; Kuroda et al. 2014). Good recruitment is likely to occur when eggs and larvae are successfully transported and retained to larval nursery grounds. In addition to temperature and transport, which affect survival before settlement, predation including cannibalism significantly impacts juvenile survival after settlement (Funamoto et al. 2013, 2014).

For JP pollock, an otolith analysis indicates that a strong year class is characterized by early-hatching individuals (i.e., individuals hatching in January and February) (Shida and Nishimura 2002; Nishimura et al. 2007). This is probably because of the high abundance and large body size of early-hatching individuals (Funamoto et al. 2013, 2014). Namely, the abundance of late-hatching individuals is likely to be too low to produce a strong year class. Moreover, larger juveniles are generally better able to escape from predators (e.g., Sogard 1997), probably resulting in low predation mortality of early-hatching individuals with large body sizes. In fact, after the 2005 year class, all year classes with a low abundance and small size at larval stage have resulted in a weak year class (T. Funamoto, unpublished data).

Taken together, high winter temperature, successful egg/larval transport, and low predation pressure appear to favor the recruitment of JP pollock through enhancement of the survival of early-hatching individuals (Fig. 4.7).

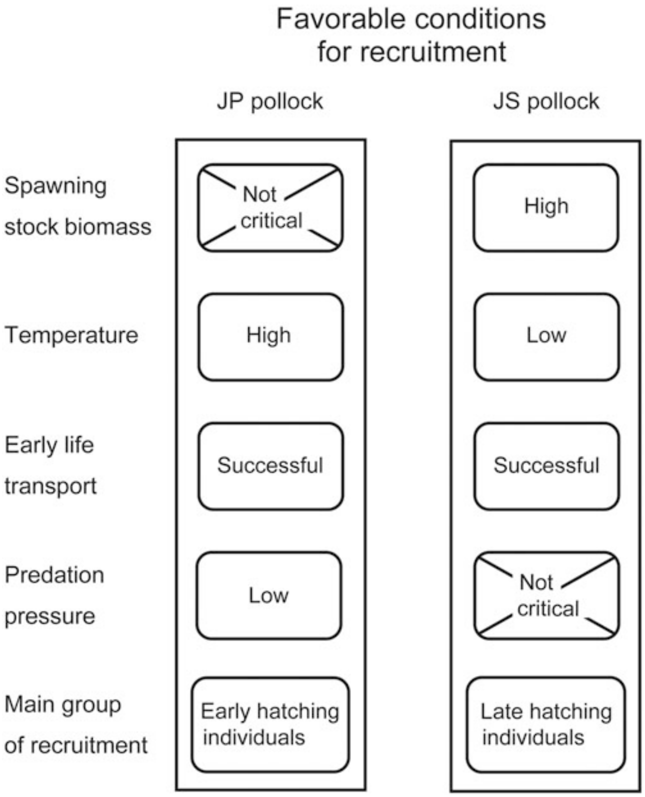


Fig. 4.7 Favorable conditions for the recruitment of Japanese Pacific (JP) and Japan Sea (JS) walleye pollock (*G. chalcogrammus*)

4.4.4 Sea of Japan off Northern Japan

Pollock in the Sea of Japan off northern Japan are usually referred to as the northern Japan Sea stock. Hence, in this book, they are referred to as the Japan Sea (JS) pollock. The biomass (total weight of individuals aged ≥2 years) of this stock was 96,000 tons in 2013, down from 868,000 tons in 1990 (Chimura et al. 2015). This critical situation of JS pollock warrants the necessity of appropriate stock management. The life history traits of JS pollock are described in Kooka (2012) and Funamoto et al. (2014).

It is likely that winter and spring temperatures regulate the recruitment of JS pollock and that low temperature is suitable for good recruitment (Funamoto 2011; Funamoto et al. 2014). If the temperature–RPS relationships of JP and JS pollock are combined, a dome-shaped relationship occurs with the RPS peak at about 5–6 °C (Fig. 4.8). Although the reason for this dome-shaped relationship remains unclear, two possibilities are presented here. One possibility is that the interaction of growth and metabolism produces an optimum survival temperature (OST) for pollock larvae (Fig. 4.9). Hamai et al. (1971) examined the growth of pollock larvae at 2 °C, 6 °C, and 10 °C in the laboratory and found that growth was faster at higher temperatures; however, the difference in growth between 6 °C and 10 °C was quite small. On the other hand, metabolism is usually higher at higher temperatures. Hence, if the growth rate is similar,

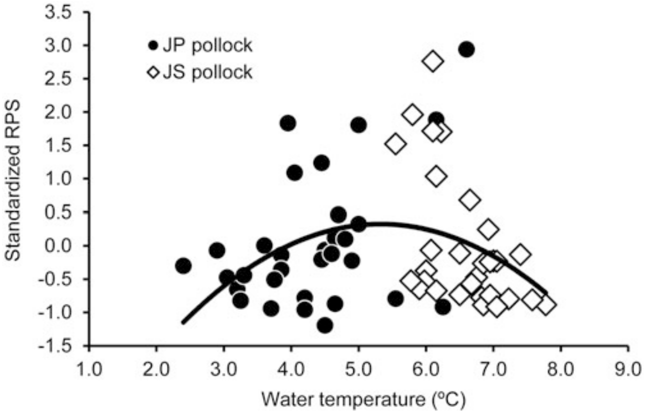


Fig. 4.8 Relationship between recruitment per spawning (RPS) and water temperature for Japanese Pacific (JP) and Japan Sea (JS) walleye pollock (*G. chalcogrammus*). RPS is standardized for each stock. The water temperatures of each stock are averages in nursery grounds during the critical larval period (February for JP pollock and April for JS pollock). The solid line indicates a quadratic function fitted to the combined data of both stocks ($y = -4.57 + 1.84x - 0.17x^2$). In this function, RPS is highest at approximately 5–6 °C. Water temperature data are from the Japan Meteorological Agency website (http://goos.kishou.go.jp/rrtdb/database.html), and RPS data are from Chimura et al. (2015) and Funamoto et al. (2015)

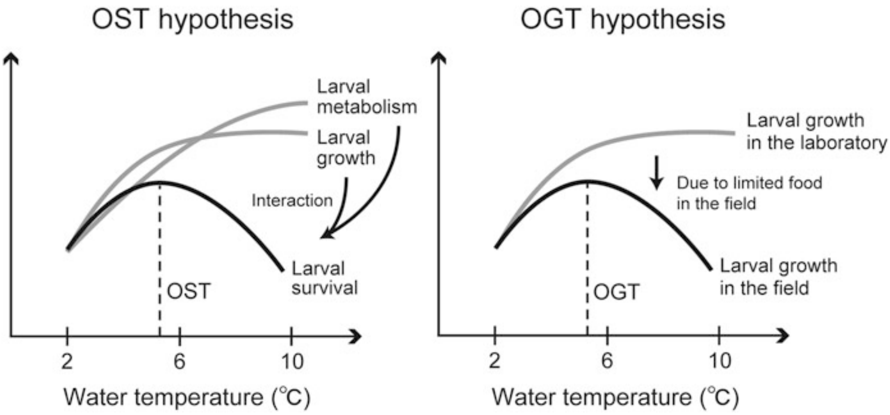


Fig. 4.9 Effects of water temperature on growth, metabolism, and survival of walleye pollock (*G. chalcogrammus*) larvae. In the optimum survival temperature (OST) hypothesis, the interaction between larval growth and metabolism produces an OST at approximately 5–6 °C. In the optimum growth temperature (OGT) hypothesis, larval growth in the field is highest at an OGT of approximately 5–6 °C, because limited food conditions in the field diminish larval growth at high temperature

pollock larval survival is expected to be higher at 6 °C than 10 °C, because metabolism is lower at 6 °C. That is, pollock larvae have an OST at approximately 5–6 °C, which can explain the dome-shaped relationship between temperature and pollock RPS.

Another possibility is that an optimum growth temperature (OGT) exists for pollock larvae (Funamoto et al. 2013, 2014) (Fig. 4.9). As mentioned above, the growth of pollock larvae in the laboratory is better at higher temperatures from 2 to 10 °C but similar at 6 °C and 10 °C (Hamai et al. 1971). On the other hand, larval food availability in the field is probably lower than that in the laboratory. Under the limited food availability in the field, larval growth may be lower at 10 °C than 6 °C owing to the higher metabolism at 10 °C. In other words, food conditions in the field are insufficient to support the metabolic requirements for rapid larval growth at 10 °C, resulting in an OGT of around 5–6 °C. This OGT of pollock larvae can also explain the dome-shaped relationship between temperature and pollock RPS.

Besides temperature, successful transport of early life stages into juvenile nursery grounds, which is mainly governed by ocean currents, is also considered to be important for the recruitment of JS pollock (Funamoto 2011; Funamoto et al. 2014). Additionally, the strong correlation between juvenile abundance before settlement and recruitment implies that predation after settlement does not strongly affect JS pollock recruitment (Funamoto et al. 2014). This is probably attributable to warm temperatures in the Sea of Japan. Juvenile pollock (potential prey) are usually distributed over continental shelves (<200 m depth) at temperatures <16 °C, whereas adult pollock (potential main predator) are mainly found over the continental shelf and in deeper waters with temperature <6 °C (Miyake et al. 1996; Honda et al. 2004;

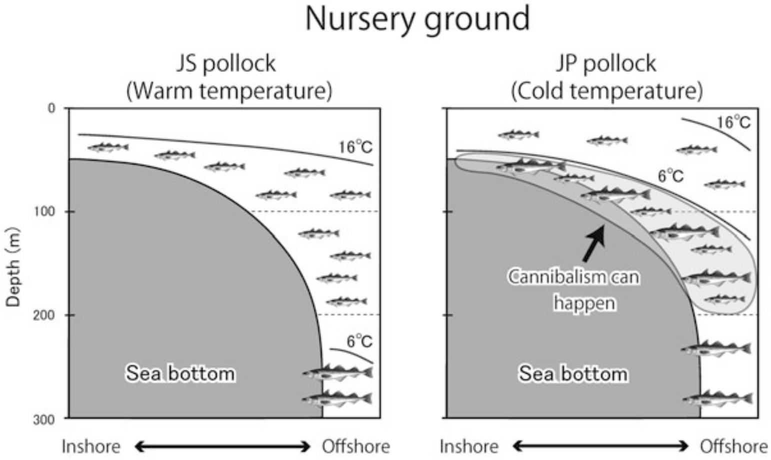


Fig. 4.10 Schematic depicting the distributions of water temperature and walleye pollock (*G. chalcogrammus*) in the nursery grounds of Japan Sea (JS) and Japanese Pacific (JP) pollock. Small and large pollock indicate juvenile (potential prey) and adult (potential predator) pollock, respectively. In the nursery grounds of JS pollock, warm temperatures prevent cannibalism by segregating juveniles from adults. Meanwhile, in the nursery grounds of JP pollock, cold temperatures enable contact between juveniles and adults, resulting in strong cannibalism

Miyashita et al. 2004). Therefore, warm temperatures in the nursery grounds of JS pollock lead to segregation of juvenile and adult habitats because of the vertical and horizontal distribution limits of adult pollock, resulting in a low frequency of cannibalism (Fig. 4.10). The density-independent stock–recruitment relationship detected for JS pollock confirms the small influence of cannibalism on recruitment (Funamoto 2007, 2011). From the viewpoint of stock management, this stock–recruitment relationship indicates that a significant recovery of SSB is urgently needed for the JS pollock, because increased SSB directly leads to better recruitment for this stock.

Otolith analysis shows that strong year classes of JS pollock are largely comprised of late-hatching individuals (i.e., individuals hatching in late February and March) (Natsume and Sasaki 1995; Funamoto et al. 2014). Although the significance of these late-hatching individuals remains unclear, one possibility is the large abundance of late-hatching individuals (Funamoto et al. 2014). In contrast to JP pollock, the abundance of early-hatching individuals may be too low to produce a strong year class for JS pollock. In addition, because the impact of predation on recruitment is not strong for JS pollock, large body size due to early-hatching appears to be not essential for good recruitments of this stock. In summary, JS pollock recruitment is favorable when abundant late-hatching individuals produced by large SSB experience low temperature and are successfully transported to the juvenile nursery grounds (Fig. 4.7).

4.4.5 Other Sea Areas

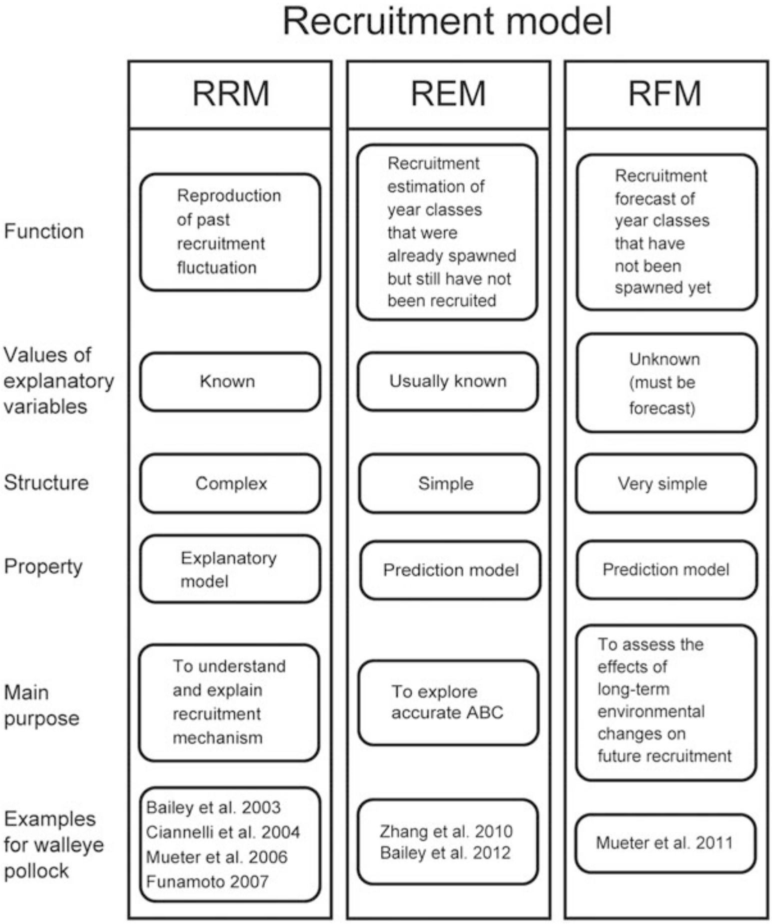
Pollock is an important fisheries resource also in other sea areas such as the western Bering Sea and the Sea of Okhotsk. Recent annual catches are around 400,000 tons in the western Bering Sea and around 1 million tons in the Sea of Okhotsk (Kim 2013; Bulatov 2014). Although information on the recruitment mechanism in these sea areas is restricted, water temperature and solar activity are likely to affect pollock recruitment in the western Bering Sea (Bulatov 1995, 2014). In addition, a positive correlation with Pacific Decadal Oscillation (PDO) is observed for the pollock biomass in the Sea of Okhotsk (Bulatov 2014).

4.4.6 Summary of Pollock Recruitment Mechanism

Important factors affecting pollock recruitments are likely to include water temperature, food availability, transport, and cannibalism. Of these, how water temperature affects pollock recruitment is still unclear, but it is possible that water temperature strongly affect larval growth and/or food availability (e.g., Hamai et al. 1971, Hunt et al. 2011). For pollock, strong density dependency is thought to be mainly caused by cannibalism (e.g., Wespestad and Quinn 1996). Because the shape of stock–recruitment relationship depends on the intensity of density effects, cannibalism is important from a viewpoint of stock assessment and management. On the other hand, although the effects of age/size structure of spawners on recruitment have been intensively studied for some demersal fishes such as Atlantic cod (e.g., Cardinale and Arrhenius 2000; Marteinsdottir and Begg 2002), these effects have rarely been studied for pollock. There is a concern that reduced size/age distribution can cause low recruitment through reduced reproductive potential. This indicates that the effects of demographic structure of stocks on recruitment should also be investigated for pollock.

4.5 Recruitment Modeling

Recruitment modeling enables the simulation of past, recent, and future biomass fluctuations, enabling proposals for appropriate management measures through management strategy evaluation. In addition, accurate simulation of the future biomass generated by recruitment modeling can result in highly reliable estimations of the allowable biological catch (ABC). Hence, recruitment modeling is vital for sound stock management of fisheries resources (e.g., Needle 2001). This means that an important output of studies on recruitment mechanisms is the contribution to recruitment modeling.



Recruitment model

	RRM	REM	RFM
Function	Reproduction of past recruitment fluctuation	Recruitment estimation of year classes that were already spawned but still have not been recruited	Recruitment forecast of year classes that have not been spawned yet
Values of explanatory variables	Known	Usually known	Unknown (must be forecast)
Structure	Complex	Simple	Very simple
Property	Explanatory model	Prediction model	Prediction model
Main purpose	To understand and explain recruitment mechanism	To explore accurate ABC	To assess the effects of long-term environmental changes on future recruitment
Examples for walleye pollock	Bailey et al. 2003 Ciannelli et al. 2004 Mueter et al. 2006 Funamoto 2007	Zhang et al. 2010 Bailey et al. 2012	Mueter et al. 2011

Fig. 4.11 Three types of recruitment models. *RRM* recruitment reproduction model, *REM* recruitment estimation model, *RFM* recruitment forecast model

There are basically three types of recruitment models (Fig. 4.11). The first is a recruitment reproduction model (RRM), which reproduces past recruitment fluctuations. This model is mainly developed to understand and explain recruitment mechanisms, and many recruitment models are classified as this type of model. The second is a recruitment estimation model (REM), which estimates the recruitment of recent year classes that were already spawned but still have not recruited to the stock. In most cases, the values of explanatory variables are known for this model. The third is a recruitment forecast model (RFM), which forecasts the recruitment of future year classes that have not yet been spawned. From the viewpoint of the properties of the models, REMs and RFMs are prediction models, whereas RRMs are explanatory models. In general, RRMs are more complex and use more explanatory variables than REMs and RFMs; this is because the prediction accuracy of more complex models using more explanatory variables tends to be low (e.g., Pace 2003, Adkison 2009). In addition, for RFMs, the values of explanatory variables also must be forecasted. Therefore, the explanatory variables of this model are restricted to those for which future values can be rationally forecasted, such as water temperature and predator abundance (e.g., Mueter et al. 2011).

4.6 Recruitment Models for Pollock

Many recruitment models have been developed for pollock (Fig. 4.11). However, most of them are RRMs, which have greatly contributed to obtaining and the verification of the concepts about pollock recruitment mechanisms presented in Sect. 4.4. For example, Funamoto (2007) revealed the relationship of water temperature and SSB with recruitment for JP and JS pollock by using simple RRMs. In addition, Mueter et al. (2006) used nonlinear RRMs to test the leading hypotheses about the recruitment mechanism of EBS pollock, including the OCH. In contrast, there are few REMs and RFMs that aim to estimate or forecast pollock recruitment.

In recent years, REMs were constructed for GOA pollock. Zhang et al. (2010) created an REM incorporating the abundance of juvenile pollock and predators as explanatory variables. Bailey et al. (2012) proposed another REM, which includes larval pollock abundance, predator biomass, wind speed, and water temperature as explanatory variables. In both models, pollock abundance estimated by monitoring survey was adopted as the explanatory variable. Therefore, environmental explanatory variables only need to account for variability in pollock survival after the monitoring survey, resulting in only one environmental variable (i.e., predator abundance) in the REM created by Zhang et al. (2010). Moreover, because there is a 5-year dynamic cycle in GOA pollock recruitment, an autocorrelative structure is incorporated into both models (Zhang et al. 2010; Bailey et al. 2012). Although the underlying cause of this autocorrelation is presently unknown, it may be due to inter-cohort competition, maternal contributions, cannibalism, or a combination thereof.

For EBS pollock, an RFM was developed by Mueter et al. (2011). Explanatory variables of this model include water temperature, SSB, and a predation index. Of these explanatory variables, future temperature was forecasted by a statistical downscaling approach using IPCC climate model output. Meanwhile, future SSB was forecasted by a population dynamics model, and future arrowtooth flounder biomass (a major component of the predation index) was assumed to be constant or linearly increasing. This model forecasts EBS pollock recruitment will decline through 2050 under the forecast values for the explanatory variables.

4.7 Stock Assessment and Recruitment Prediction of Demersal Fishes

Demersal fishes which have a long lifespan are suitable for biomass estimations using virtual population analysis (VPA) and age-structured models. In these models, a longer lifespan results in more accumulated information, which subsequently improves the accuracy of the biomass estimation (e.g., Megrey 1989; Hilborn and Walters 1992). Hence, the biomasses of EBS and GOA pollock have been estimated by age-structured models, and those of JP and JS pollock have been estimated by VPA (Dorn et al. 2013; Ianelli et al. 2013; Chimura et al. 2015; Funamoto et al. 2015).

On the other hand, for demersal fishes with long lifespans, precise recruitment estimation is necessary to explore the appropriate ABC. If the lifespan is long, small errors in the recruitment estimation are increasingly amplified with age, resulting in large errors in the future predicted biomass and the ABC. For example, the 2014 ABC of JP pollock increased from 157,000 tons (estimated in 2013) to 210,000 tons (estimated in 2014), mainly because the recruitment of the 2009 year class was underestimated in the 2013 stock assessment (Funamoto et al. 2015). In contrast, the 2010 ABC of EBS pollock decreased from 1,233,000 tons (estimated in 2008) to 813,000 tons (estimated in 2009) mainly because of an overestimation of the 2006 year class in the 2008 stock assessment (Ianelli et al. 2009). These examples highlight the importance of precise recruitment estimation of already spawned year classes for accurate ABC calculations for demersal fishes. Because making precise recruitment forecasts of year classes that have not been spawned yet is extremely difficult, the accuracy of the ABC largely depends on the accuracy of the recruitment estimation (Fig. 4.11). If long lifespan leads to old age at exploitation, demersal fishes are suitable for recruitment estimation, because there is a long time from birth to recruitment. Representative recruitment estimations use the results from pre-recruitment abundance survey and/or REM, which are both useful for recruitment estimations. Therefore, hybrid REM incorporating the result from a pre-recruitment abundance survey as an explanatory variable may become the main recruitment estimation method as carried out in the case for GOA pollock (Zhang et al. 2010; Bailey et al. 2012).

RFMs are required to assess the effects of long-term environmental changes such as regime shift and global warming on future recruitments (Fig. 4.11). Furthermore, if a population dynamics model incorporating an RFM can be developed, it will be possible to evaluate the performance of each management strategy under various environmental conditions, enabling appropriate long-term strategic management proposals. As described in Sect. 4.8, demersal fishes are suitable for stock management. Therefore, population dynamics models incorporating RFMs should be constructed for demersal fishes to develop appropriate management strategies.

4.8 Stock Management Strategies for Demersal Fishes

As mentioned in Sect. 4.2, the stock resilience of demersal fishes with low RPS and/or old age at maturity is low. Hence, if the biomass of these demersal fishes decreases to a low level, they will theoretically require more time to recover than pelagic fishes with high RPS and young age at maturity. This highlights the importance of managing demersal fishes such that they do not decrease to undesirably low levels (Fig. 4.12). For example, the biomass of some Atlantic cod stocks in Canada decreased dramatically in the 1990s and has not recovered yet (e.g., DFO 2012). The pollock stock in the Donut Hole also collapsed in the 1990s and still has not recovered (Ianelli et al. 2013). On the other hand, reduction of catch is highly effective for demersal fishes with long lifespans (see Sect. 4.2). In addition, fluctuations in the biomass of demersal fish are usually small owing to the small SD of RPS. Therefore, demersal fishes are suitable for stock management, and great efforts should be made for. In other words, although recovery from management failure (i.e., decreased biomass) is difficult, appropriate management can yield successful biomass control for demersal fishes. In contrast, the efficacy of cutting down on catch is low for pelagic fishes with short lifespans. Moreover, a large SD of RPS usually leads to wide fluctuations in the biomass of pelagic fishes, implying stock

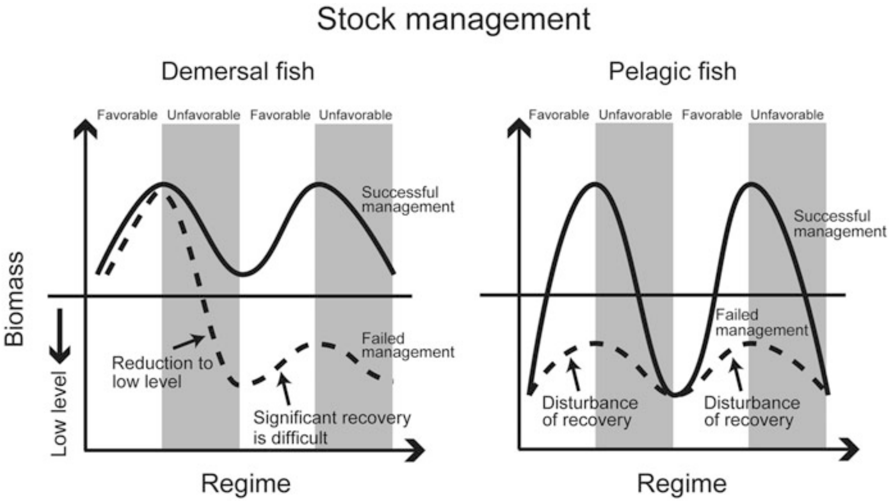


Fig. 4.12 Examples of successful and failed stock management for demersal and pelagic fishes. Demersal fishes should be managed such that they do not decrease to undesirably low levels, because recovery to desirable levels becomes difficult even under favorable environments owing to the low recruitment per spawning (RPS) and/or old age at maturity. On the other hand, pelagic fishes should be managed so as not to negatively affect recovery under favorable environments; this is because stock management that does not reduce biomass to undesirably low levels is difficult owing to the large standard deviation of RPS, whereas the high RPS and young age at maturity enable recovery to desirable levels

management, which does not reduce biomass to undesirably low levels, is difficult for pelagic fishes. On the other hand, the stock resilience of pelagic fishes with high RPS and/or young age at maturity is high. Therefore, pelagic fishes should be managed so as not to negatively affect their recovery in favorable environments (Fig. 4.12).

In addition to stock conservation (i.e., stock management), future fisheries management should consider the following five aspects: (1) conservation of resources and environments, (2) guarantee of human food supplies, (3) sound development of industry, (4) contribution to local community, and (5) promotion of culture (Fisheries Research Agency 2009) (Fig. 4.13). For example, the impacts of fisheries not only on target resources but also on nontarget resources and environments should be assessed to protect marine ecosystems. Regarding the contribution to local communities, total job creation by fishing, which includes employment in fisheries, processing, transport, and retailing in the whole local community, should be taken into account. Future fisheries management should shift toward integrated management that aims to enhance the total contribution of fisheries in these five aspects. Fisheries targeting demersal fishes are expected to be a good model for such integrated management as demersal fishes are at least suitable for stock management (i.e., stock conservation). On the other hand, integrated management requires integrated research, which is defined as "interdisciplinary research for society and human well-being which deals with the sustainability of dynamic fisheries systems, taking various knowledge,

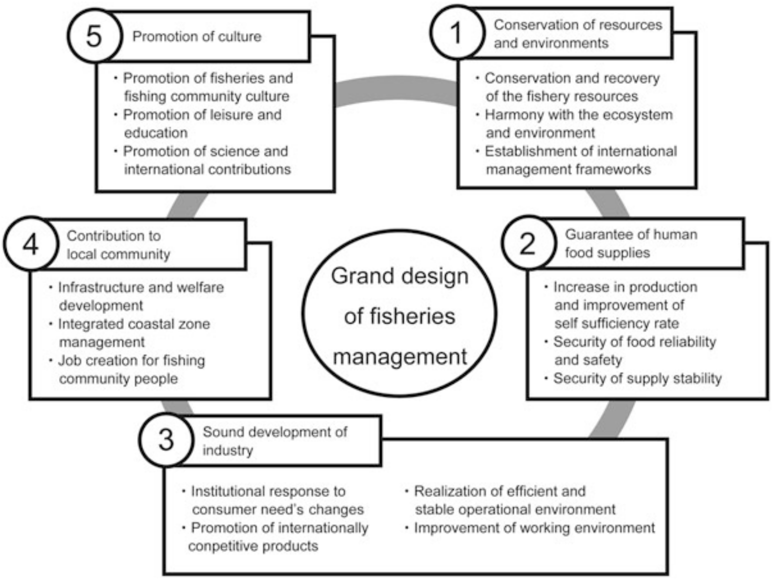


Fig. 4.13 Grand design of future fisheries management (Modified from Fisheries Research Agency 2009)

values, and needs into account" (Makino and Sakurai 2014). To implement this integrated research, researchers from multiple disciplines including biology, oceanography, stock dynamics, chemistry, economics, and business management should cooperate and provide broad perspectives.

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Chapter 5
Significance of Sex-Specific Ecological and Life History Traits on the Sustainable Exploitation of Sharks

Yasuko Semba

Abstract Sharks, which maintain the role of top predator in aquatic ecosystems, have a reproductive system and life history traits that are quite different from those of most teleosts, including internal fertilization, slow growth, high age at maturity, and the live birth of only a few well-formed offspring. Although shark species show diversity in many traits such as body size, morphology, diet, habitat (vertically, horizontally, and latitudinally), and reproductive system (ovoviviparous and viviparous), sexual difference in various phenotypic traits is one of their major characteristics. Sex-specific phenotypic traits such as life history parameters and sexual segregation are illustrated, focusing on shortfin mako and other species. A survey of the literature on growth suggests that slow growth and large body size in females are a major trend in sharks with significant intersexual difference in growth. Sexual segregation of sharks is reported with varying degrees of resolution, but its pattern is variable depending on the species, and the underlying mechanisms are largely unclear. The implication of intersexual difference in life history and behavioral traits is discussed from both evolutional and practical points of view. Existing studies that have evaluated the effect of sexual difference suggest the importance of including sex-specific traits in stock assessment and management, especially for species with marked sexual difference. Given its significance, both the study of sexual difference in the biological characteristics and the collection of sex-specific information on fishery statistics are important for understanding population dynamics and the sustainable exploitation of shark species.

Keywords Behavioral traits · Life history traits · Mating system · Sharks · Sexual difference · Sexual segregation · Sustainable use

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5.1 Biological Characteristics of Sharks

5.1.1 Difference Between Teleost Fishes and Sharks

Predatory fish, such as tunas, billfish, and sharks, occupy a high trophic level in the marine ecosystem. They have a significant impact on the population dynamics of the lower trophic level components discussed in the previous chapters. Among predatory fish, this chapter focuses on sharks because of their many unique aspects that differentiate them from teleost species.

Sharks belong to the group Elasmobranchii, which includes sharks and rays (Nelson 2006). More than 500 species of sharks are suggested based on a DNA sequence analysis (Naylor et al. 2012).

With a few exceptions of planktivorous species, sharks occupy a high trophic level in the aquatic ecosystem (Wetherbee and Cortés 2004). One of the most prominent characteristics common to sharks is that they reproduce through internal fertilization by copulation. Their reproductive patterns are divided into oviparous or viviparous (Wourms 1977), with the latter accounting for 70% of all shark species (Wourms and Demski 1993). Litter sizes in viviparous species range from 2 to 300 (Cortés 2000), and the number of eggs deposited in one spawning is reported to be 2 for oviparous species in general. The gestation period for viviparous species ranges from 1 to 2 years, and a resting period between pregnancies is suggested in some species. The reproductive cycle of the viviparous shark is estimated to be between 1 and 3.5 years (Carrier et al. 2004). Thus, the fecundity of sharks is generally believed to be smaller than that of teleost fishes. However, the large size of the neonate, coupled with the predatory activity immediately after birth or hatch in sharks, suggests that their mortality at early stage is smaller than that of teleost fishes. In this context, the relationship between spawning biomass and recruitment and that between litter size and recruitment in shark is suggested to be stronger than in teleost fishes (Holden 1973; Holden 1977).

In terms of life history traits, sharks have a long life span, high age at maturity, and small litter size with well-formed neonates compared with the majority of teleost fishes. Although the possibility of large fluctuations of biomass caused by changes in the environment is suggested to be low, sharks are relatively susceptible to the effects of large perturbations such as overexploitation and, in such cases, their population requires time to recover to the original status.

5.1.2 Sexual Specificity in Sharks

Although intraspecific variations in morphology, life history, and ecological aspects are widely observed in nature on various scales, sex is the most fundamental attribute in this issue, because sex affects a wide range of traits in animals, from anatomy to physiology and behavior. Such differences are often most apparent during

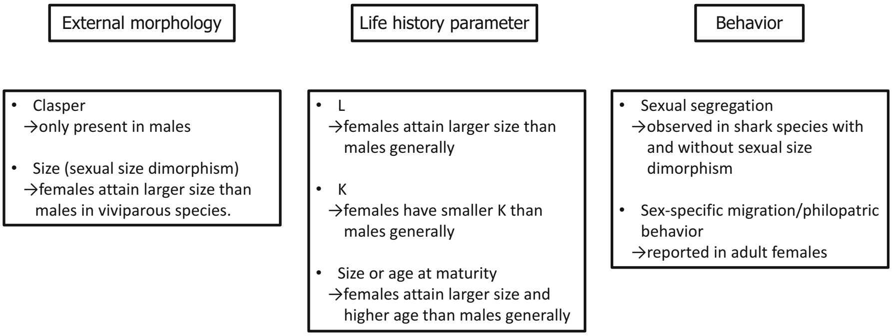


Fig. 5.1 Schematic diagram of sexual differences in sharks

reproduction, but they can also occur at other stages of life (Magurran and Garcia 2000). Sexual difference in various phenotypic traits is one of the major characteristics observed in sharks (Fig. 5.1), and the two prominent aspects of sexual difference in sharks are focused on in this chapter: sexual size dimorphism and sexual segregation.

Sexual size dimorphism (SSD) is observed in many species of shark. A comparative study on SSD in sharks indicated that, in live-bearing species, females are 10 and 16% larger than conspecific males in viviparous and ovoviviparous species, respectively, whereas in egg-laying species, females are 1% larger than conspecific males (Sims 2005).

Considering the dominance of viviparous species in all shark species (Wourms and Demski 1993), SSD is suggested to be one of the most common forms of sexual dimorphism in sharks. As discussed later, SSD in sharks is suggested to be associated with intersexual differences in life history traits such as growth parameter and age at maturity. Thus, sexual difference in life history traits, especially for the growth parameter, of sharks is the focus of the following section.

Sexual segregation, the phenomenon that males and females live apart for most of the year and only gather for mating, is a universal phenomenon in sharks (Strasburg 1958; Springer 1967; Sims 2005). Sexual segregation is a part of social segregation (Conradt 2005), and this behavior is observed in shark species both with and without SSD.

In general, several hypotheses have been formulated to explain sexual segregation in sharks (Sims 2005): (1) the sexual dimorphism–body size hypothesis (also called the forage-selection hypothesis), which suggests that different physiological (such as thermal preference) and/or energy requirements between the sexes are largely responsible for sexual segregation; (2) the reproductive strategy hypothesis (predation risk hypothesis), which suggests that females choose habitats in which their reproductive success would be maximized, such as areas where they are safe from predators or where offspring survival would be maximized; (3) the activity budget hypothesis, which suggests that sexual differences in activity budgets and movement rates may lead to sexual segregation; and (4) the social factor hypothesis, which suggests that aggression of one sex toward the other (i.e., sexual harassment by males of females) causes sexual segregation.

Exploitation of sharks has been discussed mainly from the perspective of their life history strategy (i.e., long life span, high age at maturity, and low fecundity), which suggests their vulnerability to overfishing. However, given the sexual differences reviewed in this chapter, the intersexual differences in various phenotypes, including life history and behavioral traits, have equal significance for reliable stock assessment and effective conservation of this group.

5.2 Case Study of Shortfin Mako

5.2.1 Biological Background

An illustration of sex-specific traits in life history and of behavioral traits is discussed using the example of the shortfin mako (*Isurus oxyrinchus*) and extant knowledge of other species.

Shortfin mako is a large species of pelagic shark belonging to Lamnidae that is distributed widely from the tropical to the temperate pelagic oceans throughout the world (Compagno 2001). It shows prominent female-biased SSD (Stevens 1983; Francis and Duffy 2005; Joung and Hsu 2005), and the occurrence of sexual or ontogenetic segregation has been noted (Mucientes et al. 2009), which is suggested by the fact that, unlike the juveniles and the adult males, adult females are rarely observed (Mollet et al. 2000). These characteristics imply differences in both the life history traits and the behavior of the sexes in this species. Shortfin mako have been caught mainly as a bycatch in pelagic longline and drift net fisheries, and the susceptibility to disturbance is of concern, because of their demographic features (Cortés et al. 2010) as well as because of their behavioral features (i.e., sexual segregation: Mucientes et al. 2009).

Progress in understanding both sex-specific life history and behavior is thus imperative for sustainable exploitation of this species.

5.2.2 Life History Traits

Prominent sexual differences in life history traits are apparent in shortfin mako. In the western and central North Pacific Ocean (Semba et al. 2009), males and females grow at similar rates until approximately 7 years of age; after this age, the growth rate of males slows in comparison to that of females (Fig. 5.2). In terms of the size and age at maturity (i.e., 50% size and age at maturity), males and females mature with a precaudal length (PCL) of approximately 156 and 256 cm, respectively, corresponding to an age of 5.2 years in males and 17.2 years in females (Semba

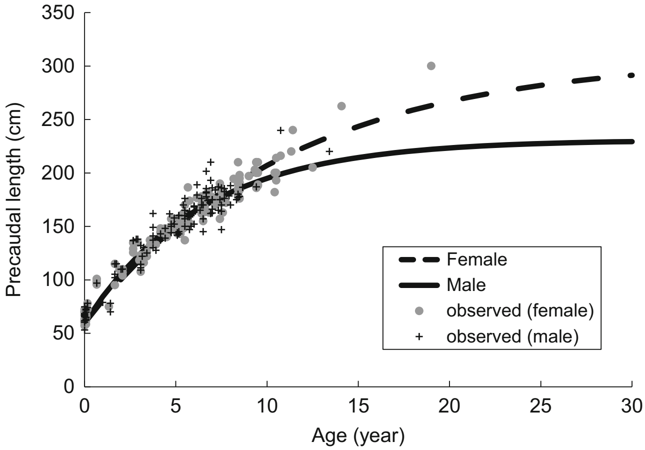
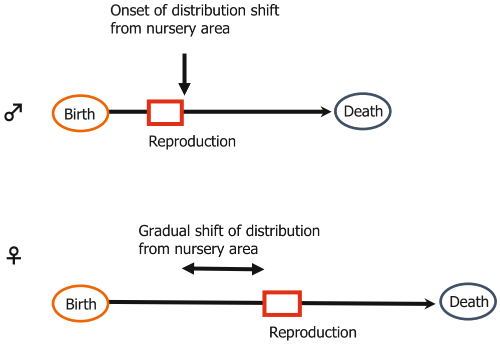


Fig. 5.2 Estimated von Bertalanffy growth curves for shortfin mako in the western and central North Pacific Ocean

Fig. 5.3 Schematic diagram of sexual differences in life history and behavioral traits of shortfin mako



et al. 2011). The same trend was found in studies worldwide on this species for both growth trajectory (Pratt Jr. and Casey 1983; Bishop et al. 2006; Natanson et al. 2006; Cerna and Licandeo 2009) and size at maturity (Stevens 1983; Francis and Duffy 2005; Joung and Hsu 2005; Maia et al. 2007). The results of a series of studies support the conclusion that bimaturism occurs in which females can delay maturity and grow larger compared with males for this species. The apparent slowdown of growth in males at their size at maturity suggests that males invest resources in reproduction earlier than females (Fig. 5.3).

Sexual differences in growth trajectory have been indicated in many species. Among 30 species for which sexual difference in the growth trajectory was statistically significant (with no conflicting results among corresponding references), the growth coefficient (K in the von Bertalanffy growth equation) of females is smaller, and the theoretical maximum length (L_∞ in the von Bertalanffy growth equation) of females is larger than those of males in 22 species, with an adverse trend (larger K and smaller L_∞ in females) estimated for 5 species (Table 5.1). In the remaining

Table 5.1 Sex-specific parameters on von Bertalanffy growth equation cited from studies with statistical evaluation of sexual difference in growth trajectory

Species	L_∞		K		t_0		Reference and statistical significance
	Female	Male	Female	Male	Female	Male	
Heterodontiformes							
Heterodontus portusjacksoni	133.7 cm TL	112.5 cm TL	0.059	0.075	−5.294	−4.944	**1)**
Orectolobiformes							
Orectolobus hutchinsi	149.45 cm TL		0.117		n.a.		2)
Orectolobus halei	163.0 cm TL		0.09		n.a.		3)
Orectolobus maculatus	212.8 cm TL		0.2		n.a.		3)
Orectolobus ornatus	99.9 cm TL		0.19		n.a.		3)
Lamniformes							
Carcharias taurus	295.8 cm TL	249.5 cm TL	0.11	0.16	−4.2	−3.4	**4)**
Alopias superciliosus	293 cm FL	206 cm FL	0.06	0.18	n.a.		**5)**
Alopias vulpinus	274.5 cm FL	225.4 cm FL	0.09	0.17	−4.82	n.a.	**6)**
Isurus oxyrinchus	325.29 cm TL	296.6 cm TL	0.076	0.087	−3.18	−3.58	**7)**
	308.6 cm PCL	231.3 cm PCL	0.09	0.156	n.a.		**8)**
Lamna ditropis	207.4 cm PCL	182.8 cm PCL	0.17	0.23	−2.3	−1.9	**9)**

Lamna nasus	233 cm FL	182.2 cm FL	0.06	0.112	−6.86	−4.75	**10)**
Carcharhiniformes							
Galeus sauteri	48.3 cm TL	44.3 cm TL	0.374	0.392	n.a.		**11)**
Scyliorhinus canicula	75.14 cm TL	87.42 cm TL	0.15	0.118	−0.96	−1.09	**12)**
Mustelus antarcticus	201.9 cm TL	141.7 cm TL	0.086	0.17	−3.01	−2.08	**13)**
Mustelus californicus	142.4 cm TL	101.8 cm TL	0.218	0.35	−1.032	−1.002	**14)**
Mustelus canis	123.6 cm TL	105.2 cm TL	0.292	0.439	−1.94	−1.52	15)
Mustelus henlei	97.7 cm TL		0.244		−1.271		14)
Mustelus lenticulatus	147.2 cm TL		0.119		−2.35		16)
Mustelus manazo	111.0 to 135.2 cm TL	83.0 to 109.6 cm TL	0.113 to 0.161	0.155 to 0.28	−3.02 to −2.51	−2.64 to −2.16	**17)***
Mustelus mustelus	205.0 cm TL	145.1 cm TL	0.06	0.12	3.55	−2.14	**18)**
Triakis semifasciata	153.6 cm TL		0.082		−2.31		19)
Triakis megalopterus	171.1 cm TL		0.11		−2.43		20)
Furgaleus macki	118.1 cm FL		0.42		−0.491		21)
Galeorhinus galeus	182.9 cm TL		0.124		−1.29		13)
Carcharhinus acronotus	113.7 to 165.0 cm FL	80.1 to 188.7 cm FL	0.138 to 0.352	0.117 to 0.771	−2.68 to −1.2	−2.01 to −0.8	**22)**
	113.5 cm FL	105.8 cm FL	0.18	0.21	−4.07	−3.9	**23)**
	129.34 cm TL		0.24		n.a.		24)
Carcharhinus amboinensis	289.5 cm TL	279.4 cm TL	0.085	0.091	−3.125	−2.794	25)
Carcharhinus brevipinna	232.8 cm PCL	196.3 cm PCL	0.1	0.146	−2.9	−2.3	**26)**
Carcharhinus cautus	123.8 cm TL	110.5 cm TL	0.198	0.287	−2.52	−1.75	**27)**
Carcharhinus falciformis	311.0 cm TL		0.101		−2.718		28)
	216.4 cm PCL		0.148		−1.76		29)

(continued)

Table 5.1 (continued)

Species	L_∞		K		t_0		Reference and statistical significance
	Female	Male	Female	Male	Female	Male	
	332.0 cm TL		0.0838		−2.761		30)
	299.4 cm TL		0.066		n.a.		31)
Carcharhinus isodon	155.9 cm TL	133.8 cm TL	0.244	0.412	−2.07	−1.39	**32)**
Carcharhinus leucas	262.1 cm TL	248.4 cm TL	0.1235	0.1692	−2.44	−1.03	**33)**
	230.0 cm PCL		0.071		−5.12		34)
	228.9 cm FL		0.089		n.a.		35)
Carcharhinus limbatus	195.0 cm TL	166.5 cm TL	0.197	0.276	−1.15	−0.88	**36)**
	141.6 to 158.5 cm FL	126 to 147.4 cm FL	0.16 to 0.24	0.21 to 0.27	−3.43 to −2.18	−2.58 to −2.21	**37)**
Carcharhinus longimanus	284.9 cm TL		0.996		−3.391		38)
Carcharhinus obscurus	349 cm FL	373 cm FL	0.039	0.038	−7.04	−6.28	**39)**
	142 cm FL	195 cm FL	0.187	0.092	n.a.	n.a.	**40)**
Carcharhinus plumbeus	165 to 197 cm TL	166 to 184 cm TL	0.059 to 0.086	0.059 to 0.087	−4.8 to −3	−5.4 to −3.8	**41)***
	210.0 cm TL		0.17		−2.3		42)
	152.8 cm PCL	138.5 cm PCL	0.1	0.12	n.a.	n.a.	**43)**
	239.6 cm FL		0.04		n.a.		44)
Carcharhinus porosus	136.4 cm TL		0.077		−3.27		45)
Carcharhinus sorrah	123.9 cm TL	98.4 cm TL	0.34	1.17	−1.9	−0.6	**46)**

Carcharhinus signatus	270 cm TL		0.11		−2.71		47)
Carcharhinus tilstoni	194.2 cm TL	165.4 cm TL	0.14	0.19	−2.8	−2.6	**46)**
Galeocerdo cuvier	365 cm PCL		0.117		−2.34		48)
Isogomphodon oxyrhynchus	169.72 cm TL	166.68 cm TL	0.118	0.11	−2.419	−2.608	**49)****
Loxodon macrorhinus	89.5 cm TL	83.2 cm TL	0.18	0.44	−6.3	−2.6	**50)**
Negaprion brevirostris	399.9 cm TL		0.077		−2.16		51)
Prionace glauca	352.1 cm TL		0.157		−1.01		52)
	237.5 cm TL	299.85 cm TL	0.15	0.1	−2.15	−2.44	**53)**
	311.6 cm TL		0.12		−1.66		54)
Rhizoprionodon terraenovae	94.02 cm TL		0.73		−0.88		55)
	74.8 cm PCL		0.5		−0.92		56)
Sphyrna lewini	353.3 cm TL	336.4 cm TL	0.153	0.131	−0.633	−1.09	**57)**
	233.1 cm FL	214.8 cm FL	0.09	0.13	−2.22	−1.62	**58)**
	376 cm TL	364 cm TL	0.1	0.123	−1.16	−1.18	**59)**
Sphyrna mokarran	307.8 cm FL	264.2 cm FL	0.11	0.16	−2.86	−1.99	**60)**
Sphyrna tiburo	93.9 to 139.8 cm TL	85.8 to 100.7 cm TL	0.16 to 0.29	0.25 to 0.44	−2.39 to −0.93	−2.66 to −0.31	**61)**
Sphyrna zygaena	285 cm FL	272 cm FL	0.07	0.06	n.a.		**62)**
Hexanchiformes							
Notorynchus cepedianus	189 cm TL	229 cm TL	0.295	0.22	n.a.		**63)**

(continued)

Table 5.1 (continued)

Species	L_∞		K		t_0		Reference and statistical significance
	Female	Male	Female	Male	Female	Male	
Squaliformes							
Squalus acanthias	100.76 cm TL	94.23 cm TL	0.12	0.11	n.a.		**64)**
Squalus megalops	93.2 cm TL	52.6 cm TL	0.033	0.089	−8.12	−6.94	**65)**
	75.6 cm TL	45.5 cm TL	0.042	0.158	n.a.		**66)**
	94.4 cm TL	72.6 cm TL	0.04	0.053	−8.48	−8.76	**67)**
Etmopterus baxteri	68.13 to 69.25 cm TL	59.55 to 60.59 cm TL	0.04 to 0.116	0.082 to 0.163	−4.51 to −1.56	−2.00 to −1.43	**68)**
Etmopterus pusillus	49.01 cm TL	54.04 cm TL	0.17	0.13	n.a.		**69)**
Etmopterus spinax	55.84 cm TL	57.96 cm TL	0.12	0.09	n.a.		**70)**
Squatina californica	125.2 to 127.0 cm TL		0.101 to 0.146		n.a.		71)

L_∞, K, and t_0 denote asymptotic length, von Bertalanffy growth coefficient, and theoretical age at which the organism was 0 length, respectively. TL, FL, and PCL denote total length, fork length, and precaudal length, respectively

References in bold and in normal type denote those with statistically significant and insignificant difference in growth parameters, respectively. Those with * include estimates of growth parameters for several group (e.g., different populations in time and space) with both statistically significant and insignificant difference

Reference with ** means statistical significance is variable depending on the kind of statistical test. References cited in Table 5.1 are provided below

Detailed information on references with * are noted in those for the text

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The sexual differences discussed above indicate that life history strategies differ between the sexes, especially in species with marked sexual difference. Early maturity in males may suggest that they invest their resources in reproduction at an earlier age than females to increase their chance of mating, whereas late maturity in females may suggest that they invest their resources in growth rather than in reproduction, to attain a large body size, which is associated with the increase of litter size. The large female adult size would be accompanied by a longer period of growth with slow growth rate or larger asymptotic size (Karkach 2006) compared with males.

5.2.3 Distribution and Behavior

In the case of shortfin mako, the occurrence of sexual segregation was suggested to occur in the southeast Pacific (Mucientes et al. 2009). Population structuring was suggested in the area (20–40°S, 100–140°W) where males predominated in the west and females were found mainly in the east (Fig. 1a in Mucientes et al. 2009). However, sexual differences in nutritional (i.e., prey items) and habitat requirements (i.e., sea-surface temperature or primary productivity) were not supported as an explanation in this study.

Semba (2011) further investigated the population distribution pattern including sexual segregation for the population in the North Pacific Ocean (6–43°N, 132°E–140°W), taking into account the ontogenetic stage, based on wide-ranging fishery and research data. In this study, the occurrence ratio of each component of population (i.e., juvenile males, juvenile females, adult males, subadult females, adult females, etc.) on a grid of 1° (latitude) by 1° (longitude) per month was estimated based on a logistic regression model. The results showed clear ontogenetic segregation between juveniles (<150 cm PCL) and adults ($\geq$150 cm PCL for males and 250 cm PCL for females). Regarding the occurrence ratio of juvenile males and females in all components of the population, juvenile females and males were estimated to occur in high ratio in the nursery ground with female-biased occurrence ratio to some degree (Fig. 5.4a, b). The area where subadult females (150 cm $\leq$ PCL $<$ 250 cm) occur in high ratio moved to the south and east (Fig. 5.5), while adult males dominated in more southern and eastern areas where adult females are known to occur in the mating season, with some latitudinal and seasonal expansion of distribution estimated (Fig. 5.6). Whereas the pattern of sexual segregation between adult males and females was not clarified because of the paucity of data for adult females, the behavior of adult females is suggested to be different from other components of the population, given that specific migration patterns associated with the stage of pregnancy are proposed based on the spatio-temporal pattern of occurrence of pregnant females (Semba 2011).

Sex-specific migration or philopatric behavior has been suggested in adult females of white shark (*Carcharodon carcharias*) and gray nurse shark (*Carcharias taurus*) (Bansemer and Bennett 2009; Pardini et al. 2001). Thus, it is suggested that ontogenetic segregation occurs and that sexual segregation may become increasingly prominent according to growth in shortfin mako. Compared with females, which change the distribution gradually, males are suggested to show a drastic change of distribution according to growth. This difference may be related to the shift of resources allocation from growth to reproduction (Fig. 5.3).

Other than shortfin mako, patterns of sexual segregation have been reported in many species of shark including the white shark, small-spotted (lesser spotted) catshark (*Scyliorhinus canicula*), blue shark (*Prionace glauca*), scalloped hammerhead shark (*Sphyrna lewini*), and spiny dogfish (*Squalus acanthias*). Quantitative analysis suggested the following variables as factors that contribute to the sexual segregation of sharks (Table 5.2): environmental factors such as sea-surface temperature for white shark (Robbins 2007), salinity and ambient water temperature for small-spotted catshark (Rodríguez-Cabello et al. 2007), habitat such as depth for spiny dogfish (Dell'Apa et al. 2014) and lesser spotted dogfish (Sims et al. 2001), diet preference for scalloped hammerhead (Klimley 1987), and avoidance of harassment by males for small-spotted catshark (Wearmouth et al. 2012).

There are common trends that can be found for the correlations between the variables and sex in some species, but these are not observed in other species. For example, whereas small-spotted catshark and blue shark males show preference for warm waters, white shark males prefer lower temperature compared with females. Intersexual differences in diet have been indicated in scalloped hammerhead shark, but not in shortfin mako (Table 5.2). It is suggested that some or all of the aforementioned hypotheses may contribute to sexual segregation in sharks (Sims 2005) and that the mechanism of sexual segregation in each shark species remains largely unclear. It is also suggested that a difference in the requirements for resources between the sexes and/or sexual conflict (e.g., increased rates of survival for females and their offspring versus the chance of mating for males) underlies sexual segregation in sharks.

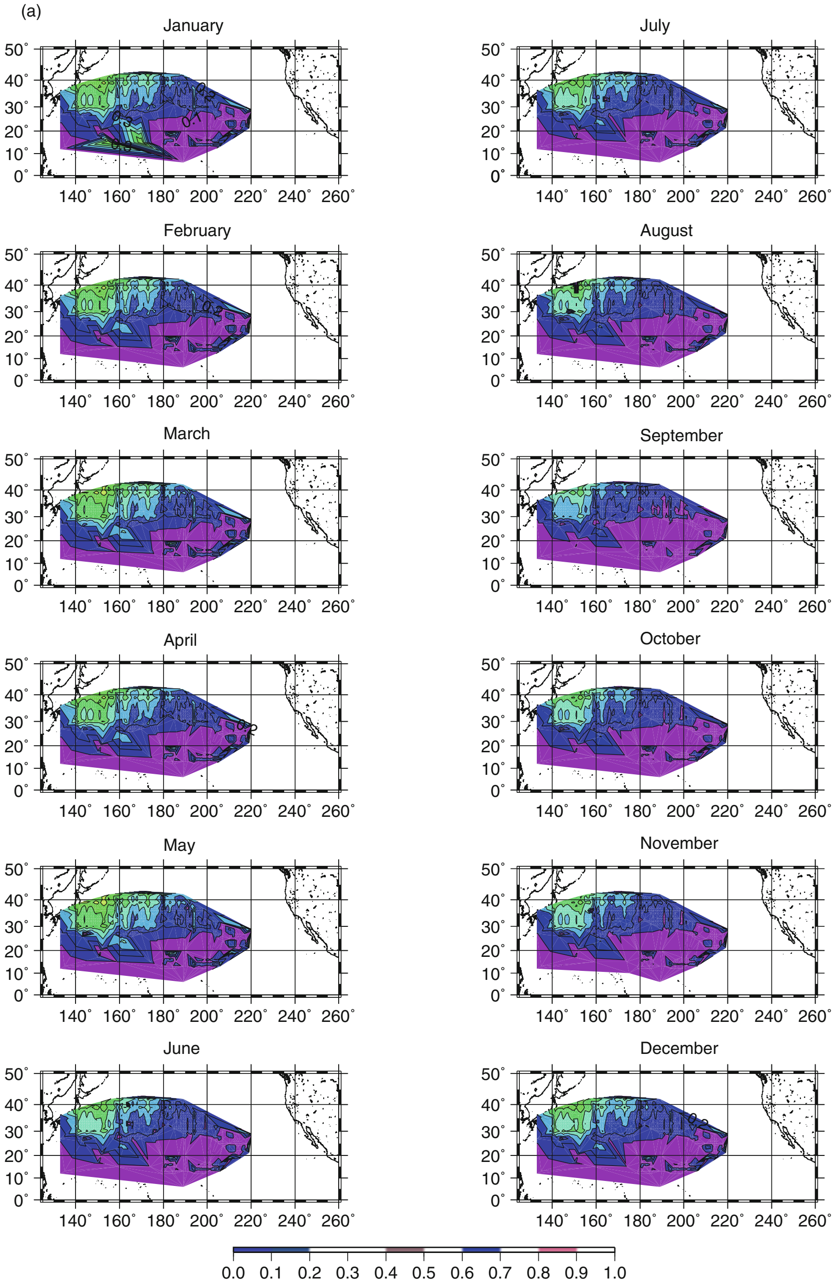

Fig. 5.4 Geographical and temporal changes of the occurrence ratio of (**a**) juvenile female and (**b**) juvenile male shortfin mako estimated from research and commercial data obtained between 2006 and 2008. The scale indicates the occurrence ratio of juvenile males or females on the grid of 1° (latitude) × 1° (longitude) per month. The ratio ranges from 0 (the lowest occurrence, the darkest color) to 1 (the highest occurrence, the brightest color)

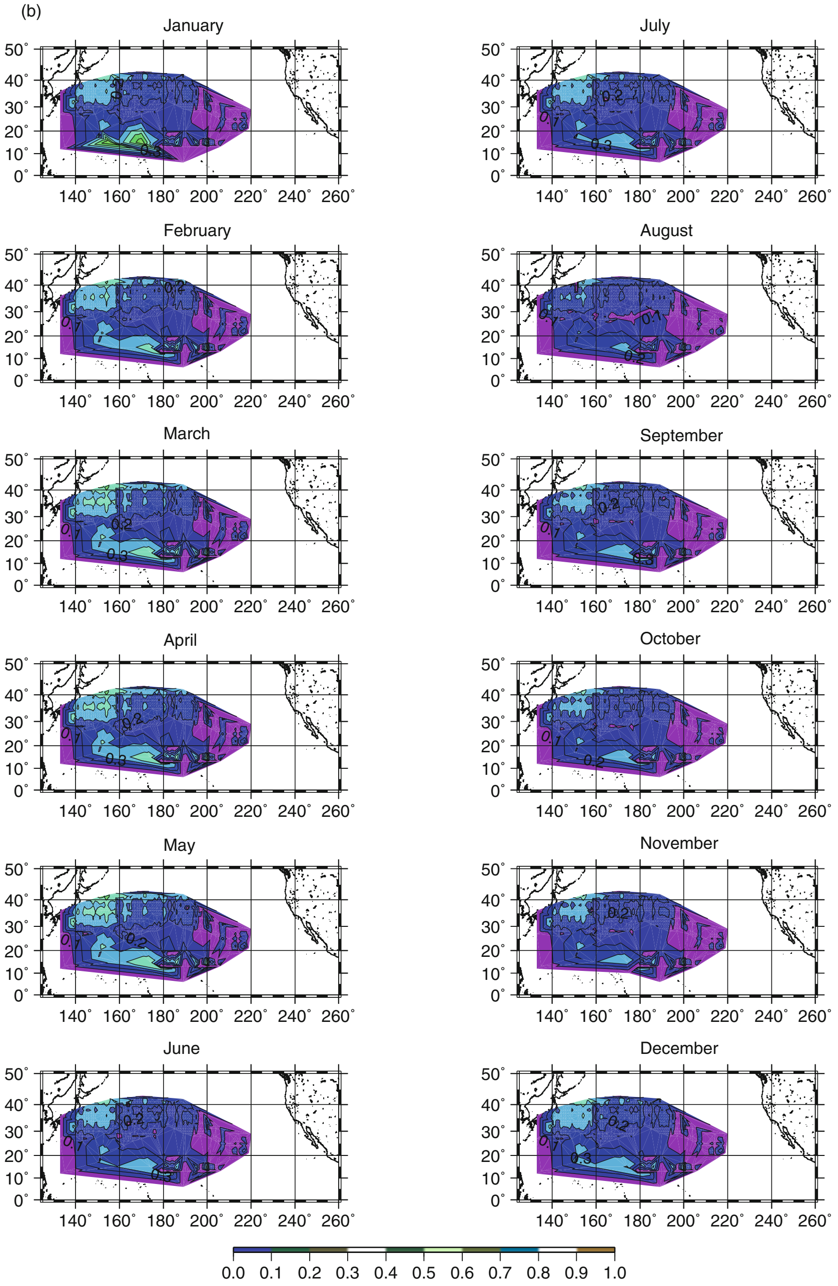

Fig. 5.4 (continued)

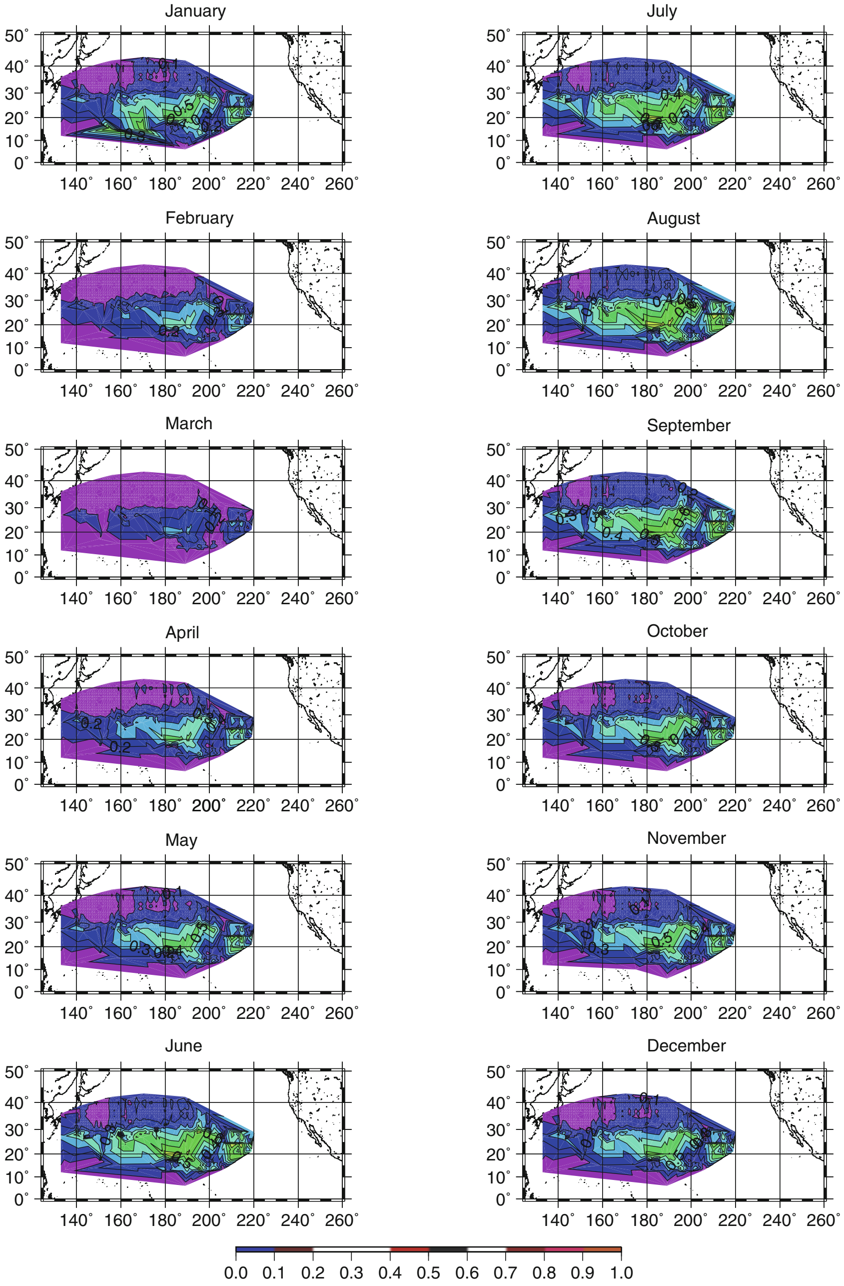

Fig. 5.5 Geographical and temporal changes of the occurrence ratio of subadult female shortfin mako estimated from research and commercial data obtained between 2006 and 2008. The scale indicates the occurrence ratio of subadult female on the grid of 1° (latitude) × 1° (longitude) per month. The ratio ranges from 0 (the lowest occurrence, the darkest color) to 1 (the highest occurrence, the brightest color)

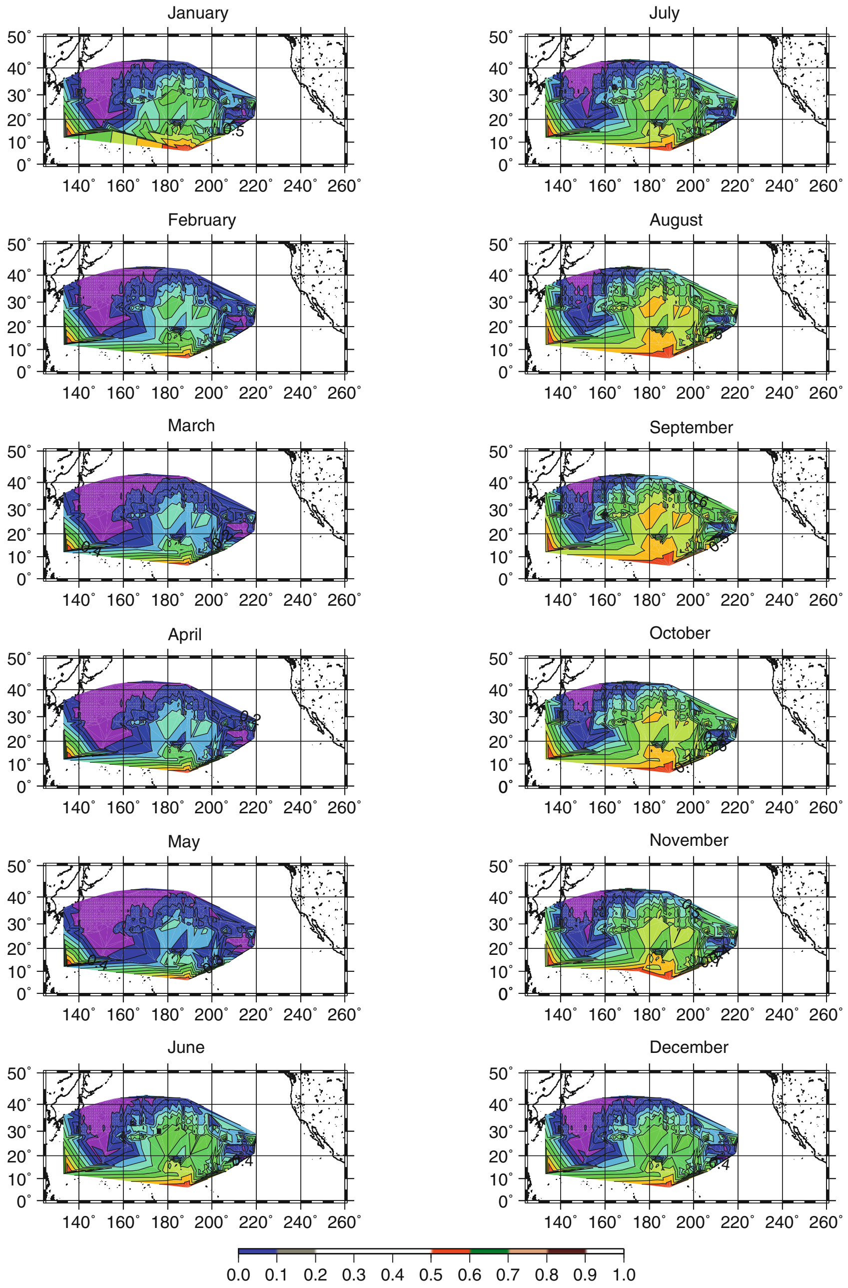

Fig. 5.6 Geographical and temporal changes of the occurrence ratio of adult male shortfin mako estimated from research and commercial data obtained between 2006 and 2008. The scale indicates the occurrence ratio of adult males on the grid of 1° (latitude) × 1° (longitude) per month. The ratio ranges from 0 (the lowest occurrence, the darkest color) to 1 (the highest occurrence, the brightest color)

Table 5.2 Summary of reported sexual segregation in sharks in relation to possible factors

Species	Type of resource with sexual difference			Social factor	References
	Diet	Environment	Habitat		
Carcharodon carcharias	n.a.	*Females* occur in higher temperature and less abundant in waters with low tidal height, while *males* occur in lower temperature and abundant in waters with low tidal height (1)	n.a.	n.a.	Robbins (2007)
Carcharodon carcharias	n.a.	n.a.	*Females* frequently occur in inshore areas in spring and summer, while *males* seldom occur in inshore areas in spring and summer (3)	n.a.	Kock et al. (2013)
Isurus oxyrinchus	No significant differences in the diet composition were found between the sexes (2)	No correlation between male catch number and SST and between male or female catch number and chlorophyll a. Negative correlation between female catch number and SST is inconclusive (3)	*Females* are predominant in east of survey area, while *males* are predominant in west of survey area (20–40°S, 100–140°W) (1)	n.a.	Mucientes et al. (2009)

(continued)

Table 5.2 (continued)

Species	Type of resource with sexual difference			Social factor	References
	Diet	Environment	Habitat		
Scyliorhinus canicula	n.a.	n.a.	*Females* stay in shallow (day) and in deep (night) area, while *males* stay in deep (day) and shallow (night) area (3)	Females spend more time in suboptimal thermal habitats with male presence (1)	Sims et al. (2001) and Wearmouth et al. (2012)
Scyliorhinus canicula	Males (adult) prey on greater number of prey taxa than females (adult) (2)	*Females* (adult) show more affinity for high salinity than males, and *males* (adult) show preference for shallow and warm waters (3)	n.a.	n.a.	Rodríguez-Cabello et al. (2007)
Prionace glauca	n.a.	*Females* (>90 cm PCL) are caught in 8–21 °C, while *males* (>90 cm PCL) are caught in 14–21 °C (3)	*Females* (subadult) appear in the area between 40 and 50°N, while *males* (subadult) appear in the area between 30 and 40°N (3)	n.a.	Nakano (1994) and Nakano and Nagasawa (1996)
Sphyrna lewini	*Females* (≤160 cm) consume pelagic prey, while *males* (≤160 cm) consume benthic prey predominantly (3)	n.a.	*Females* move to offshore area at smaller size than males and are caught in deeper area, while *males* stay in coastal area for longer period and are caught in shallower area (1)	n.a.	Klimley (1987)

(continued)

Table 5.2 (continued)

Species	Type of resource with sexual difference			Social factor	References
	Diet	Environment	Habitat		
Squalus acanthias	n.a.	n.a.	*Females* prefer deep area and occur in high ratio in late morning or night (south of 42°N), while *males* prefer shallow area and occur in high ratio early in the day (south of 42°N) (3)	n.a.	Dell'Apa et al. (2014)

Sexual difference in resource requirement such as diet, environmental factors, and habitat with empirical evidence for social factors is summarized

PCL denotes precaudal length

(1), (2), and (3) indicate statistically significant difference, statistically insignificant difference between the sexes, and no statistical test, respectively

5.3 Implications of the Sexual Difference in Life History and Behavior on the Sustainable Use of Sharks

5.3.1 Ecological Perspective

As discussed above, there are marked differences in the life history traits and behavior between males and females in some species of sharks; therefore, sex is an important variable in the intraspecific variation of sharks. Such differences in the phenotypic traits are suggested to be closely associated with the reproductive strategy of each sex (Fig. 5.7). Reproduction includes conflict of interest between the sexes over the maximization of its own success at propagating genes (Krebs and Davis 1993). The elucidation of the mating system is suggested to provide insights into the inference of intersexual relationship, which leads to understanding the mechanism by which sex-specific phenotypic traits are maintained. Regarding the SSD and sexual bimaturism, they are influenced by the mating system of the species as follows: males tend to delay maturity and grow larger in polygynous species where males compete directly with one another for females, whereas the opposite would be expected in species with promiscuous mating, external fertilization, and indeterminate growth where males do not control access to females (Stearns 1992). Although sharks do not adopt external fertilization, it is suggested that they grow indeterminately and that males do not control access to females; thus, the latter regime is suggested to be the case in sharks. In sharks, direct observation of reproductive events such as mating behavior, including mate selection, is generally difficult, except for some tractable species that are small and accessible.

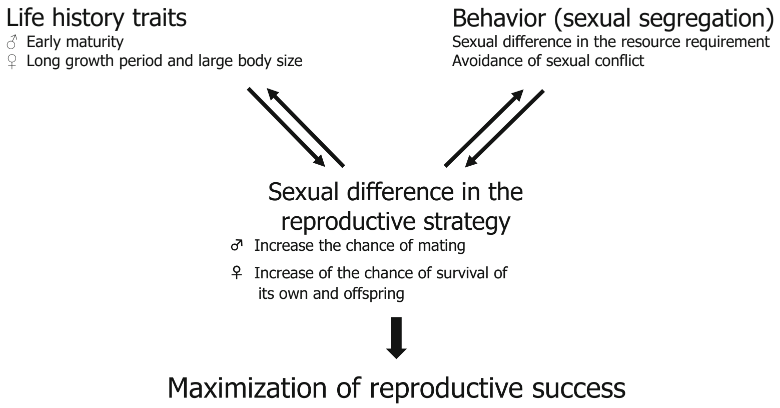

Fig. 5.7 Conceptual framework of sexual difference in the life history traits and behavior of sharks in relation to the reproductive strategy of each sex

Recent studies with a range of molecular techniques revealed the genetic mating system in lemon shark (*Negaprion brevirostris*, Feldheim et al. 2001a, b), hammerhead shark (*Sphyrna tiburo*, Chapman et al. 2004), bignose shark (*Carcharhinus altimus*, Daly-Engel et al. 2006), sandbar shark (*Carcharhinus plumbeus*, Daly-Engel et al. 2006, 2007, Portnoy et al. 2007), spiny dogfish (Lage et al. 2008; Veríssimo et al. 2011), small-spotted catshark (Griffiths et al. 2012), nurse shark (*Ginglymostoma cirratum*, Saville et al. 2002, Heist et al. 2011), shortspine spurdog (*Squalus mitsukurii*, Daly-Engel et al. 2010), brown smoothhound shark (*Mustelus henlei*, Byrne and Avise 2012, Chabot and Haggin 2014), bluntnose sixgill shark (*Hexanchus griseus*, Larson et al. 2011), leopard shark (*Triakis semifasciata*, Nosal et al. 2013), gummy shark (*Mustelus antarcticus*) and rig (*Mustelus lenticulatus*, Boomer et al. 2013), sand tiger shark (*Carcharias taurus*, Chapman et al. 2013), shortfin mako (Corrigan et al. 2015), starry smoothhound shark (*Mustelus asterias*, Farrell et al. 2014), and whale shark (*Rhincodon typus*, Schmidt et al. 2010). Genetic polyandry (i.e., multiple paternities in females) was detected in these studies, but the percentage of litters with multiple sires differs greatly among species from 11% in shortspine spurdog to 93% in brown smoothhound shark within the species for which more than two litters were investigated (Table 5.3). In sandbar shark, the ratio of females with multiple sires is estimated to differ depending on the populations (Daly-Engel et al. 2007; Portnoy et al. 2007), and the difference in the population structure such as operational sex ratio and subsequent encounter rate is suggested to partly explain the variety. Both spatial and interannual variability in the percentage of litters with multiple paternities are reported in brown smoothhound shark (Bryne and Abise 2012, Chabot and Haggin 2014).

The prevalence of genetic polyandry suggests the occurrence of male–male competition for copulation with females. In sharks, females are a scarce resource for which males compete (Krebs and Davis 1993), given that they invest much effort to develop embryos (i.e., gestation), while males make little parental investment. If males tend to maximize the number of mating attempts to increase the number of

Table 5.3 Summary table of paternity analysis for sharks

Species	No. of litters examined	Percentage of litter with multiple paternities (%)	Number of sires	References
Ginglymostoma cirratum	1	100	4	Saville et al. (2002)
Rhincodon typus	<1	100	1	Schmidt et al. (2010)
Carcharias taurus	15	40	2	Chapman et al. (2013)
Isurus oxyrinchus	1	100	2	Corrigan et al. (2015)
Scyliorhinus canicula	13	92	1–4	Griffiths et al. (2012)
Mustelus antarcticus	29	24	1–4	Boomer et al. (2013)
Mustelus asterias	12	58	1–3	Farrell et al. (2014)
Mustelus henlei	14	93	1–3	Byrne and Avise (2012)
Mustelus henlei	18	22	1–2	Chabot and Haggin (2014)
Mustelus lenticulatus	19	13	1–3	Boomer et al. (2013)
Triakis semifasciata	22	36.4	1–2	Nosal et al. (2013)
Carcharhinus altimus	1	100	2	Daly-Engel et al. (2006)
Carcharhinus plumbeus	1	100	2	Daly-Engel et al. (2006)
Carcharhinus plumbeus	20	40	1–2	Daly-Engel et al. (2007)
Carcharhinus plumbeus	20	85	1–5	Portnoy et al. (2007)
Negaprion brevirostris	1	100	3	Feldheim et al. (2001a)
Negaprion brevirostris	63	81	1–4	Dibattista et al. (2008a)
Sphyrna tiburo	22	18.8	1–3	Chapman et al. (2004)
Hexanchus griseus	1	100	9	Larson et al. (2011)
Squalus acanthias	10	30	1–2	Lage et al. (2008)
Squalus acanthias	29	17	1–2	Veríssimo et al. (2011)
Squalus mitsukurii	27	11	1–2	Daly-Engel et al. (2010)

their own offspring, a long reproductive lifetime or early maturity may benefit this strategy. From the perspective of the females, a correlation between the number of mating events and the number of offspring is suggested to be less strong than for males because of the physiological limitations (i.e., volume of body cavity in females) and because increasing the chance of offspring survival may take precedence. Therefore, the large body size of females would be favored because both litter size and/or body size at birth are suggested to increase in proportion to the female body size, within the limit of the body cavity and energetic restrictions of the female. However, the benefit of multiple mating for females is unclear in the case of sharks (Portnoy et al. 2007; DiBattista et al. 2008b), especially in relation to female body size. In sharks, there is evidence indicating costly aspects for multiple mating in females, and thus it was suggested that forced polyandry occurs in some cases (DiBattista et al. 2008b). Further study is necessary to understand the mechanisms underlying the mating system and the significance this has on the shark population.

5.3.2 A Practical Perspective on the Effective Management of Sharks

From the perspective of sustainable exploitation of resources, the sexual differences discussed in this chapter need to be considered in the assessment of the impact of exploitation on the population and in the construction of management measures, especially for species with marked sexual dimorphism in life history and behavioral traits.

There are a limited number of studies that have evaluated quantitatively the effect of sexual difference in life history and behavioral traits on the result of stock assessment or management for fishery resources. Okamura et al. (2014) investigated the impacts of sex- and age-/depth-specific seasonal migration on the MSY-based reference points for lingcod (*Ophiodon elongatus*) stocks in British Columbia. They indicated that the estimated MSY, B_{MSY}, and $\%SPR_{MSY}$ changed markedly and nonlinearly when sex-specific seasonal migrations and different seasonal and depth-specific fishing practices were modeled. They concluded that consideration of the sexual difference in the seasonal distribution enables better management of this stock.

The effect of sexual dimorphism has been evaluated (SU et al. 2011) and taken into consideration in the stock assessment of blue marlin (*Makaira nigricans*) in the Pacific Ocean (Lee et al. 2014). Based on a simulation study for the age-structured population dynamics model, SU et al. (2011) suggested that estimates of spawning biomass are negatively biased and fishing intensity (F_{2006}) is positively biased when sexual dimorphism (i.e., growth parameter and length–weight relationship) is ignored. Lee et al. (2014) incorporated sex structure in the stock synthesis (SS) and reported that the consideration of sex-specific life history (i.e., natural mortality, growth parameter) and length–weight relationship in the model improved model performance.

From the demographic perspective, it is suggested that developing management strategies by using single-sex models could underestimate the probability of population decline risk for shortfin mako (Tsai et al. 2014). Given that sexual dimorphism in vital rates such as survival rates and longevity may produce distinctly different dynamics from those predicted by single-sex models (Gerber and White 2014), the vital rates of both sexes are better to be considered in the analysis of population dynamics.

In relation to management and conservation, concern over the exploitation of species with sexual segregation is particularly heightened when one of the sexes of the target animals is exploited to a different extent because of spatially focused fisheries, which can lead to population structure deterioration (Wearmouth and Sims 2008).

Female-biased exploitation would lead to a pronounced decrease in the reproductive potential of the population because it would reduce the number of fertile females, which may lead to a decrease in the number of offspring. Selective harvesting of large males leads to female-biased sex ratios and is suggested to negatively affect the abundance and stability of the resources through sperm limitation and subsequent decrease of female reproductive output in large decapods crustacean resources (Sato 2012). However, it does not necessarily lead to a reduction in fecundity rate of resources if harvested species show polygynous mating systems in which a single mature male is capable of inseminating many females (Milner et al. 2007). When male-biased exploitation leads to a change in the operational sex ratio, the mating system of the population and genetic diversity of a litter may be affected.

Given that there are clear differences between monogamous and polygynous mating systems with respect to the ratio of adult males to females necessary for all females to be mated (Milner et al. 2007), knowledge of the patterns and processes of mating systems is important in understanding how fishery activities can affect the resistance of commercially exploited marine fish to catastrophic decline and their resilience thereafter (Rowe and Hutchings 2003; Tsai et al. 2014).

5.4 Future Directions

In this chapter, the concept of sex-specificity (i.e., sexual difference) was introduced into the discussion on the sustainable exploitation and conservation of sharks. Investigations on the mechanism underlying various sexual differences are expected to provide solid ground to achieve this aim.

Practically, information on the size and sex of individuals caught in the fishery is crucial for the reliable assessment and conservation of stock. Although the natural mortality (M) and the life span of sharks with respect to their sex were not discussed in this chapter, such issues deserve to be pursued, considering that it has been reported in teleosts (Wilderbuer and Turnock 2009) and marine mammals (Ramp et al. 2010). In the case of blue shark in the North Pacific Ocean, stock assessment by using the SS model, in which sex-specific growth trajectory and M as well as detailed fishery statistical and biological input data were considered, has been conducted (Rice et al. 2014). The need for sex-specific information on biological characteristics such as growth, longevity, and M as well as on fishery statistics such as catch number and size of fish caught is becoming increasingly important for the study and management of various species of shark.

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Part II
Monitoring Systems

Chapter 6
Part II Description

Ichiro Aoki

For sustainable fisheries in the context of ecosystem-based management, it is essential to collect, process, and integrate a broad range of data on various ecosystem components as well as data specifically related to fishery-targeted species. Monitoring datasets enable ecosystem assessment and adaptive management in response to changes occurring within the ecosystem. Also, systematic and high-resolution data that can observe the dynamic processes of marine ecosystems facilitate the understanding of relationships between the dynamics of fisheries resources and the ocean environment.

Various observation tools have been used to monitor the status and change in fisheries resources and the ocean environment including biological components. Chapters in this part of the book describe three representative methods for fishery and ecosystem monitoring: biological sampling, hydroacoustics, and catch-based stock assessment, which are commonly used methods worldwide in fisheries science. Other promising techniques that are currently being developed such as satellite remote sensing, electronic tagging, genomics, and cabled observatory have shown significant progress as follows.

Application of satellite remote sensing is extensively prevailing today in fisheries as a useful tool for environmental monitoring and assessment. For jack mackerel (*Trachurus murphyi*) in the South-East Pacific Ocean, satellite remote sensing data, including sea surface temperature (SST), sea surface height, and sea surface chlorophyll-a (Chl-a) concentration, combined with fisheries data are used to identify suitable environmental conditions and predict potential fishing grounds (Li et al. 2016). Integration of ichthyoplankton survey data with remote sensing data such as SST, Chl, ocean current, and ocean wind enabled the clarification of the effect of

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hydrodynamic processes on European anchovy (*Engraulis encrasicolus*) eggs and larvae distribution and transport in the Mediterranean Sea (Falcini et al. 2015).

Recent developments of electronic tagging techniques have enabled the potential to observe the in situ behaviors, physiology, and ecology of marine animals. There are four varieties of electronic tags: implantable archival tags, pop-up satellite archival tags, satellite-linked radio tags, and acoustic tags (Sippel et al. 2015). The data are obtained through fishery recapture or acoustic/satellite telemetry, providing biological information and ambient physical parameters simultaneously. Hussey et al. (2015) describe a wide variety of aquatic telemetry studies. Typically, electronic tagging experiments have been used to reveal seasonal horizontal migration and diel vertical migration of highly migratory pelagic predators such as tunas and sharks in relation to the ocean environment. Sippel et al. (2015) note that the inclusion of electronic tagging data in stock assessment models requires to consider various factors, while electronic tags are one of the most informative data sources for stock assessment.

New genetic monitoring techniques are rapidly developing. Quantification of environmental DNA, which refers to genetic material from organisms in the environment, can be a promising tool for population or ecosystem assessment and management (Kelly et al. 2014). Yamamoto et al. (2016), for example, suggested that spatial variation in the species-specific environmental DNA concentration could reflect the distribution and biomass of a fish species and that the environmental DNA method would allow quick surveillance of fish population in the sea.

In general, drifting and moored buoys have been used as observation platforms that complement ship-based surveys that are inherently limited in time and space and provide time series data collection over long periods of time. Likewise, the recent development of multidisciplinary cabled observatory technology is promising for remote, long-term, and continuous monitoring of marine ecosystems and environments. The observatory system is deployed on the seafloor and connected to the shore by cables, allowing unlimited electric power and real-time communication to a suite of instruments and sensors (Aguzzi et al. 2015). Worldwide cabled observatories are being operated in several areas in different oceans to explore the relationship between biological communities and environmental changes (Aguzzi et al. 2015).

The capability to collect a broad array of data using various platforms and instruments for sampling and observing marine organisms and their environments is currently progressing to encompass a range of temporal and spatial scales. These data assemblages can potentially be utilized as “big data.” Applications of artificial intelligence and machine learning can contribute to enhance analysis and decision making in fisheries management systems.

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Chapter 7
Biological Monitoring: Fish Eggs, Fish Larvae, and Zooplankton

Yoshioki Oozeki

Abstract To understand the processes linking environmental variability to fish population dynamics in marine ecosystems, the dynamics of lower trophic levels including zooplankton as fish prey resources needs to be studied. Furthermore, the spawning habitat is the place connecting the life history of spawning adults and offspring and thus reflects the physiological characteristics and stock conditions of the fish resource. The survival rate of fish larvae and juveniles transported from the spawning grounds eventually determines the recruitment success. A long-term monitoring system based on fishery-independent biological sampling is therefore essential to clarify mechanisms of dynamics of the lower trophic organisms and fish spawning habitats. This chapter introduces the technological advances and data applications of fishery-independent monitoring surveys, after briefly reviewing their history and current status in Japan and also worldwide. These reviews include (1) long-term zooplankton monitoring, (2) long-term fish egg and larval surveys and spawning monitoring, and (3) sampling of fish larvae and juveniles (pre-recruit stages). Moreover, the chapter provides recommendations for monitoring systems and perspectives on future directions toward continuity of long-term monitoring.

Keywords Acoustic devices · Biological monitoring · Data integration · Fish egg · Fish larva · Net system · Optical devices · Zooplankton

7.1 Introduction

Biological monitoring of marine organisms is one of the crucial components for assessing the status of marine ecosystems (Hays et al. 2005). Biological monitoring for detecting changes in fisheries resources and marine ecosystems is composed of two approaches, fishery-dependent and fishery-independent (Gunderson 1993;

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Rotherham et al. 2007). For the purpose of sustainable use of fisheries resources, fishery-dependent monitoring of catch effort and landings by fisheries should form the base information. However, several management strategies are widely adopted to maintain fisheries resources for avoiding overfishing. These fisheries management strategies include effort controls, e.g., limiting the number of vessels, day closures, area closures, and/or harvest controls by setting total allowable catch (TAC), individual quota (IQ), and so on (e.g., Melnychuk et al. 2013). Under these management strategies, landing data obtained from fisheries are not effective indices of the actual abundance and distribution of fisheries resources because of both spatiotemporal restrictions of the fishery and size selection at the time of catch. Therefore, biological samplings independent from fishing data gain importance especially for highly managed fishing resources.

Maintaining the marine ecosystem itself is imperative for the sustainable use of fisheries resources. Processes linking environmental variability to fish population dynamics in marine ecosystems should be well known. Dynamics of lower trophic levels including zooplankton as fish prey resources need to be studied with consideration of competitive processes including non-fisheries species. Also the spawning habitat is the place connecting the life history stages of spawning adults and offspring and thus could reflect the physiological characteristics and stock conditions of fish resources. Survival rate of fish larvae and juveniles transported from the spawning grounds will determine the recruitment success. Thus, the target species for biological monitoring include not only certain fisheries resources in the market size class but also a variety of species from lower trophic to higher predatory species and a variety of life stages from egg to spawners.

It is well documented that the marine ecosystems including fisheries resources are highly affected by global climate change and the effects of global warming (e.g., Chavez et al. 2003; Hinder et al. 2012a). A long-term biological monitoring system based on fishery-independent sampling is therefore essential to clarify the changes of marine ecosystem and to understand the dynamics of the lower trophic organisms and fish spawning habitats. Recent developments of advanced technology have been prominently introduced into sampling systems and analyzing procedures for the huge data sets obtained by cutting-edge sampling devices; however, long-term biological monitoring activities have continued using the traditional sampling instruments. Although the continuity of traditional long-term biological monitoring activities is essential, new sampling devices based on the advanced technology will enable replacement of traditional sampling instruments after sufficient periods of comparative data collection using both traditional and advanced methods. These replacements will be achieved by new devices enabling spatiotemporal high-resolution data sets, which will exceed the resolution of the traditional sampling instruments. However, the rapid innovation of sampling methods will cause problems, because the innovation speed is rapid, and devices will not have sufficient time to become standard instruments. Under these circumstances, it is still important to secure the continuity of long-term biological monitoring in combination with the introduction of advanced technology.

This chapter introduces technological advances and data applications of fishery-independent monitoring surveys, after briefly reviewing the history of the biological monitoring and current status in Japan and in the world. These reviews include (1) long-term zooplankton monitoring, (2) long-term egg and larval surveys and spawning monitoring, and (3) sampling of larvae and juveniles (pre-recruit stages). Then, advances of technologies relating to the biological monitoring are introduced and discussed. The last part of this chapter provides recommendations for the future direction of monitoring systems and perspectives to enable the continuity of long-term biological monitoring.

7.2 History and Current Status of Biological Monitoring in Japan and in the World

7.2.1 Overview of Fish Egg, Fish Larval, and Zooplankton Surveys in Japan

Fish egg, fish larval, and zooplankton monitoring have an 80-year-old history in Japan. The Fisheries Research Institute of the Japanese Governor-General's office in Korea firstly conducted in 1931 fish egg, larval, and zooplankton surveys around the Japan Sea by RV Misago-maru. General oceanographic surveys including plankton sampling were conducted in the Japan Sea from 1932 to 1941 and on the Pacific coast of Japan from 1933 to 1941 annually. Vertical towing of several types of small mouth plankton nets (45 or 60 cm in diameter, 330 μm or 335 μm mesh size) had been adopted for sampling without a flowmeter (Nakai 1962).

The Fisheries Agency has conducted the nationwide annual surveys of small pelagic fish eggs, fish larvae, and zooplankton since 1949 to the present in cooperation with prefectural fisheries research institutes. The Fisheries Research Institute of Ministry of Agriculture and Forestry organized in 1949 the "Cooperative Research on Sardine Resource" with members of 29 prefectural fisheries research institutions. Ten prefectural fisheries research institutes along the Pacific coast and 11 institutes along the Japan Sea started fish egg, fish larval, and zooplankton monitoring under this cooperative framework (Nakai et al. 1955; Nakai 1962; Nakai and Hattori 1962). Eight national fisheries research institutes were established regionally in 1950 in Japan, and the national institutions managed the cooperative framework in each region from then. This research framework was succeeded as the "Cooperative Research on Coastal Important Fisheries Resources" with members of the 8 national fisheries research institutes and 38 prefectural fisheries research institutions from 1955 to 1961. From 1964, the objectives of fish egg, fish larval, and zooplankton monitoring changed to obtain basic information for fisheries forecasts, and each prefectural fisheries research institution continued the monitoring independently. During these changes in the survey scheme, sampling methods followed those previously used (Nakai 1962) however with the addition of flowmeter usage.

At the time of the establishment of the exclusive economic zone (EEZ) in 1977, the research framework was changed to reintegrate the assessment of fisheries resources in the Japanese EEZ. Then, national fisheries research institutes organized the framework as the "Cooperative Research on Fisheries Resources within EEZ." Four national fisheries research institutes and 38 prefectural fisheries research institutions became the members of this research project, and they have conducted monthly fish egg, larval, and zooplankton monitoring from 1978 to the present. The prefectural fisheries research institutions have responsibilities for the coastal areas of each prefecture, and the national fisheries research institutes operated the monitoring activities over broader offshore areas during the spawning season of important small pelagic species. Some prefectures with thriving offshore fisheries industries also maintained offshore monitoring lines seasonally. At the start of this cooperative research scheme, vertical towing from 150 m depth by the long-NORPAC net (45 cm in diameter, 335 μm mesh size; Zenitani 1998) was commonly used with a flowmeter. And then after 1980, it became the standard sampling procedure.

National fisheries research institutes summarized the monthly egg production and larval distribution of small pelagic fishes (sardine, anchovy, and mackerels) in $30' \times 30'$ longitudinal and latitudinal block around Japan with the information of larval abundance of horse mackerel and common squid (Watanabe 1983). Since 1981, the National Research Institute of Fisheries Science (NRIFS) has published annual reports on the monitoring along the Pacific coast after the annual meeting of cooperative research institutions. Members exchange taxonomic information on fish eggs and larvae at the meetings. Training courses on sampling techniques and fish egg identification have been occasionally held. Statistics of monthly egg production and larval distribution in the $30' \times 30'$ longitudinal and latitudinal blocks along the Pacific coast of Japan had been published as a series of data books since 1988 (Mori et al. 1988; Kikuchi and Konishi 1990; Ishida and Kikuchi 1992). After 1995, the area coverage has been expanded to the whole coastal area of Japan (Zenitani et al. 1995; Kubota et al. 1999). At present, the whole data set after species identification is stored in the closed database named "Fishery RESource COnservation system (FRESCO)," and the statistics of egg production are automatically calculated within the network system (Fig. 7.1). The total number of samples along the Pacific coast has been maintained at around 4000 annually, and the total number of samples along the Japan Sea coast has been maintained at around 1000 annually from 1978 to the present (Fig. 7.2). Fish egg and larval specimens sorted out from the egg surveys samples are stored in NRIFS, and the plankton samples are stored in Tohoku National Fisheries Research Institute (TNFRI).

7.2.2 Long-Term Zooplankton Monitoring

Biological monitoring on zooplankton as food items for fishes has been continued monthly and/or seasonally at certain stations. Simple and traditional devices have been used in the historical long-term monitoring, depending on the technological

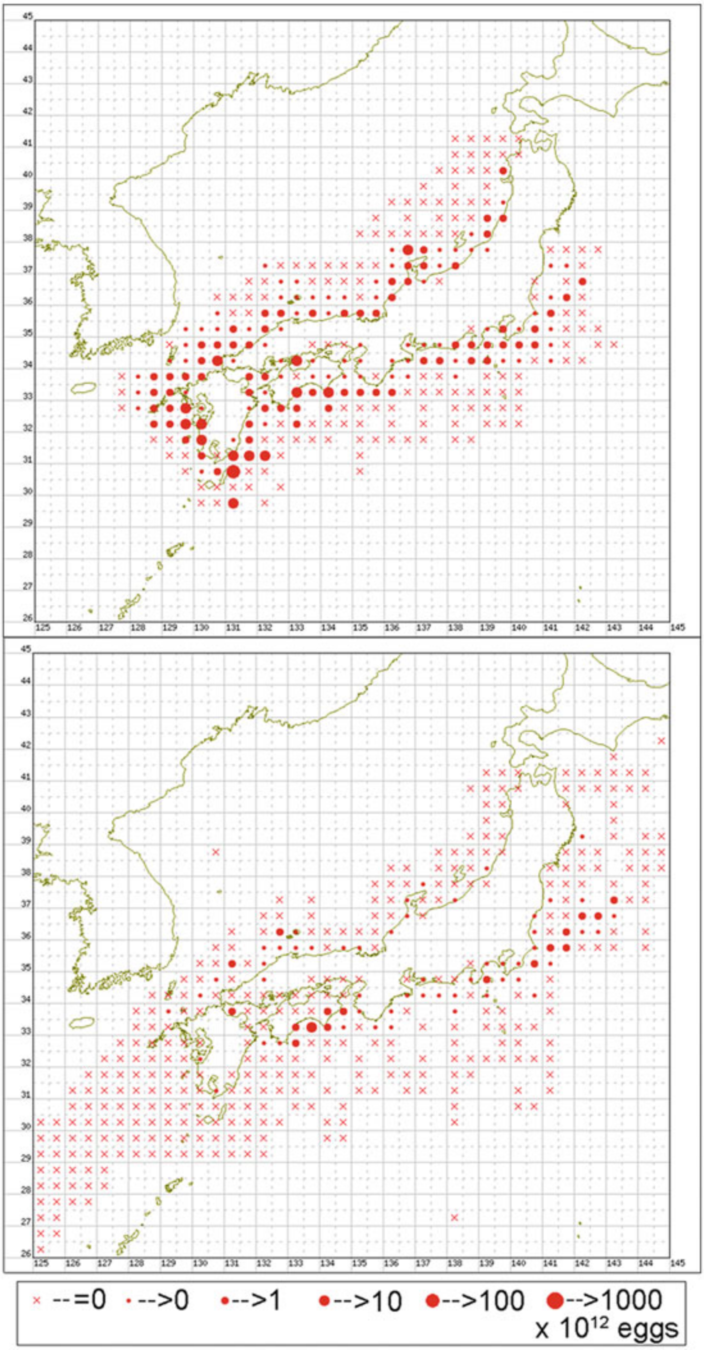

Fig. 7.1 Example of annual egg production of Japanese sardine (*Sardinops melanostictus*) in 30′ × 30′ longitudinal and latitudinal blocks in 1994 (upper) and 2010 (lower)

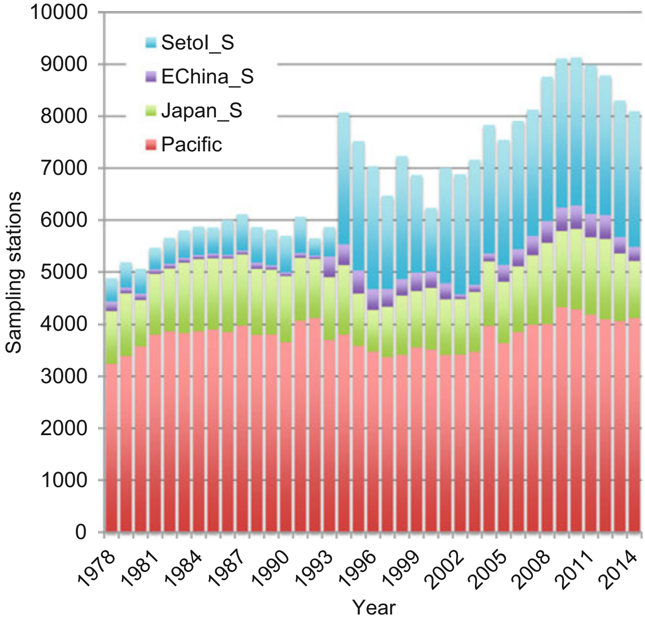

Fig. 7.2 Trend of number of sampling stations included in the fish egg database (1978–2014). Data obtained at the East China Sea (EChina_S) and Seto Inland Sea (SetoI_S) were not totally included. Japan_S, Japan Sea; Pacific, Pacific Ocean

stage of development at their starting point. Continuous Plankton Recorder (CPR) program supported by the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) is one of the well-known zooplankton monitoring programs. CPRs are mechanical self-contained instruments towed by commercial vessels without requiring scientists being onboard. Planktons at ca. 6 m depth are continuously retained between two silk rolls, filtering silk and covering silk, and preserved in a formalin tank during long cruises (up to 500 nautical miles). SAHFOS has been responsible for conducting the CPR survey since 1931. More than 170,000 samples have been obtained mainly between the east coast of America and the European coast. Survey areas of the CPR have been expanded to the North Pacific at present, from Alaska to the west coast of America and between Japan and Canada. After a CPR has been towed, the filtering silk roll in the CPR sampling mechanism is cut to represent ten nautical mile sections of the route (Batten et al. 2003). The silk on the cutting table is compared to a color chart and given a "greenness" value of 0 (no greenness), 1 (very pale green), 2 (pale green), or 3 (green), as the first indication of phytoplankton blooms (greenness index). Then, the phytoplankton within 20 fields of view across each sample on the filtering silk are identified to different taxonomic levels depending on the organism. Zooplankton specimens seen on the filtering and

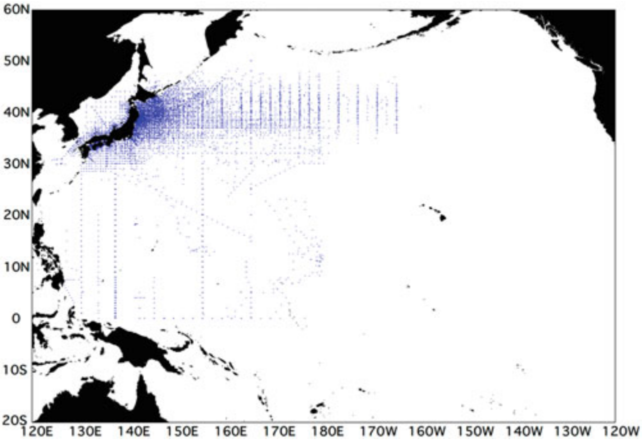

Fig. 7.3 Sampling locations included in the *Odate collection*. The total number of the specimens exceeds 60,000 from 1951 to 2014 (courtesy of Dr. Tadokoro)

covering silk along the traverse observation lines are counted and identified. All zooplankton greater than 2 mm in length are identified, often to the species level, and counted. Long-term plankton data sets provided by the CPR project have revealed remarkable changes in abundance and distributions of phytoplankton and zooplankton (e.g., Hinder et al. 2012a, b). CPRs on certain routes have been instrumented to measure sea surface temperature, salinity, sampling depth, and phytoplankton chlorophyll fluorescence since 1994 (http://www.sahfos.ac.uk/about-us/cpr-survey.aspx, June 20, 2014).

At the northern area of the Pacific coast in Japan, specimens obtained by the annual fish egg surveys have been used for analyses of zooplankton abundance as food of small pelagic species, mainly Pacific saury, *Cololabis saira.* Whole records of these samples from 1951 to 1988 were published in 1991 (Odate 1991), and these samples were called the *Odate collection* after her pioneering research based on these specimens (Odate 1994). TNFRI has continued to keep all zooplankton specimens obtained by the annual egg surveys as the national center of zooplankton samples at present (Fig. 7.3). The data set obtained from the *Odate collection* has been used in the analysis of decadal change of zooplankton community in relation to climate change (Chiba et al. 2006; Rombouts et al. 2011). This data set contains details of species abundance of copepods, and key species of copepods were used as the food index of Pacific saury larvae in Takasuka et al. (2014). Similar attempts have been conducted in different areas of Japan. It was one example that the data record of long-term zooplankton analyses from 1991 to 2012 had been published based on the specimens around Tosa Bay, southern Pacific coast of Japan (Hirota et al. 2013), and these specimens are also stored in TNFRI.

7.2.3 Long-Term Fish Egg Monitoring

In the United States, the California Cooperative Oceanic Fisheries Investigations (CalCOFI) was established in 1949 by a member of the California Department of Fish and Wildlife, NOAA Fisheries Service and Scripps Institution of Oceanography, after the sardine population collapse off California. Fish egg and zooplankton survey off southern and central California have been conducted quarterly by this organization (http://calcofi.org/, June 4, 2014). From 1981, the daily egg production method (DEPM) was adopted for assessing the spawning stock biomass of northern anchovy (*Engraulis mordax*), and the CalVET net has been operated for sampling fish eggs in this analysis (Lasker 1985). The CalVET net is a paired bongo-type small mouth area plankton net (25 cm in diameter, 150 μm mesh size) in order to make high-speed quantitative vertical tows at 1.2 m s^{-1}, for diminishing sampling error caused by ship drift and water current under the surface. Fish egg data obtained during the CalCOFI cruises are open to use via their web page (http://www.calcofi.org/data.html, June 4 2014). Barange et al. (2009) made a worldwide comparative study on the relationship between the amount of eggs and area size of spawning grounds of sardine and anchovy, based on several data sets including the Japanese fish egg survey and CalCOFI data. From 1996, continuous underway fish egg sampler (CUFES) has been used for sampling pelagic fish eggs. Its sampling layer is ca. 3 m depth from the waterline, and continuous sampling is conducted from a ship cruising at full speed even rough condition. Data obtained by CUFES are effective for describing the spatial distribution of fish eggs, especially regarding their aggregated distributions (Checkley et al. 2000).

In Japan, annual total of egg production of small pelagic fishes are used as indices of the annual spawning stock biomass for stock assessments of Japanese sardine (*Sardinops melanostictus*), chub mackerel (*Scomber japonicus*), and other species (e.g., Kawabata et al. 2015a, b). During the stock assessment process, data of annual egg production are used as a tuning index of VPA for supporting the accuracy of fishing mortality (F) in the latest year. Characteristics of spawning behavior in small pelagic species (sardine, anchovy, and round herring) were also well described by using the analyzed data sets of fish egg survey. Oozeki et al. (2007) described the spawning environment of three small pelagic species in relation to temperature and salinity preferences and compared the locations of their spawning grounds. Then the relationships between egg abundance and spawning area size were successfully compared among them (Fig. 7.4). Takasuka et al. (2008) developed the analyses of spawning grounds of small pelagic species, with special concern on the overlap of anchovy and sardine based on the same data set from 1978 to 2004. Seasonal and decadal overlap of spawning grounds between the two species suggested that the Japanese sardine population recovery was considered to be more difficult than Japanese anchovy population recovery when interspecific interactions occur (Fig. 7.5, Takasuka et al. 2008).

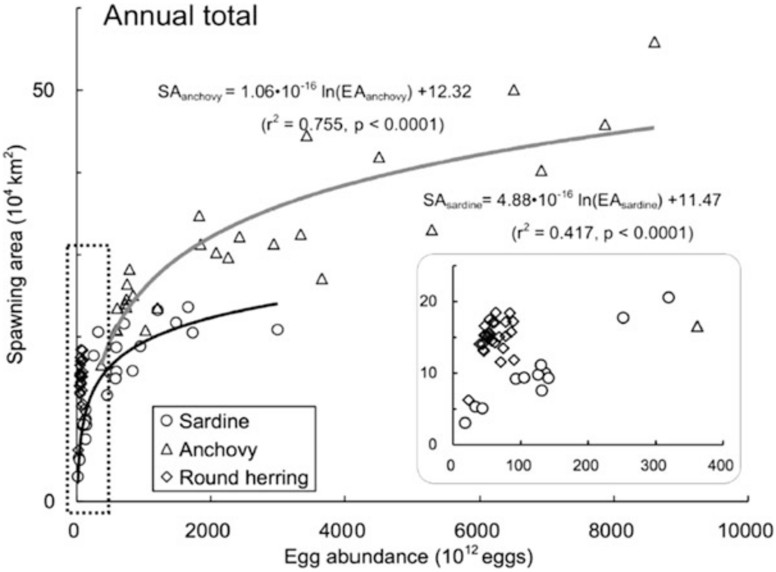

Fig. 7.4 Relationships of spawning area to egg abundance for Japanese sardine (*Sardinops melanostictus*: circle), Japanese anchovy (*Engraulis japonicus*: triangle), and Pacific round herring (*Etrumeus teres*: diamond) in the Northwestern Pacific from 1978 to 2004. Indicated data are summed from October of the previous year to September for sardine and round herring and from January to December for anchovy. A close-up of the range enclosed by dotted line is shown in the panel (from Oozeki et al. 2007)

7.2.4 Long-Term Fish Larval and Juvenile Monitoring

The CalCOFI has conducted larval and juvenile fish monitoring from the start of the program since 1949. In the earlier years, oblique towing of a 1 m mouth width ring net was adopted for sampling larval and juvenile fishes. After 1978, oblique towing of a 0.71 m diameter twin bongo net has been used for reducing net avoidance of juvenile fishes. Mesh size of the bongo net is 0.505 mm double or 0.505 mm plus 0.333 mm depending on requirements. Sampled vertical towing depth is approximately 210 m. All data identified are available from the web page (http://www.data.calcofi.org/zooplankton.html, June 4, 2014).

The Flødevigen sampling program is also a well-known long-term fish larval monitoring program, which was initiated in 1919 for studying the effectiveness of releasing cod larvae to enhance the natural cod stock. More than 250 stations between Kristiansand and the Norwegian–Swedish border have been sampled during September to October regularly with beach seines operated in the same manner throughout a period of nearly 100 years, except 1941–1944 (Fromentin et al. 1997). A 40 m long and 3.7 m deep seine net (stretched mesh size: 1.5 cm) has been used

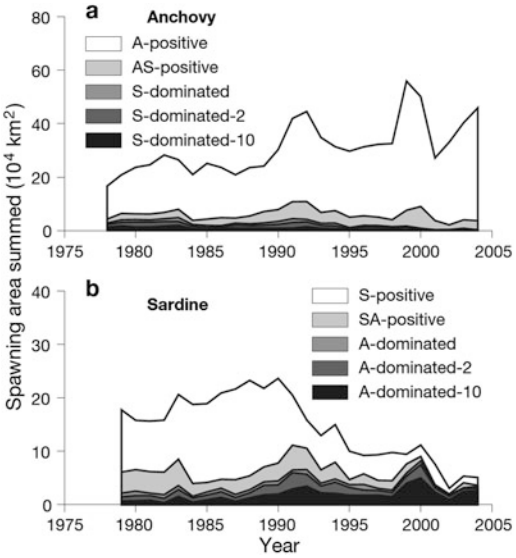

Fig. 7.5 Decadal shifts in annual total spawning areas of Japanese (**a**) anchovy (*Engraulis japonicus*) and (**b**) sardine (*Sardinops melanostictus*) showing their overlaps in the western North Pacific from 1978 to 2004. A-positive (S-positive), anchovy (sardine) eggs occurred; AS-positive (SA-positive), anchovy (sardine) eggs co-occurred with sardine (anchovy) eggs; S-dominated (A-dominated): anchovy (sardine) eggs were less abundant than sardine (anchovy) eggs; S-dominated-2 (A-dominated-2), anchovy (sardine) egg abundances were <1/2 sardine (anchovy) egg abundances; and S-dominated-10 (A-dominated-10), anchovy (sardine) egg abundances were <1/10 sardine (anchovy) egg abundances. Figures are shown as overlaid images; i.e., AS-positive area is a portion of the A-positive area (from Takasuka et al. 2008)

without modification. The sampling coverage is up to 700 m^2 per one haul. Data quality of the monitoring program has been supported by a high continuity, because only two leaders in chief, who managed the fish identifications and counts, have been assigned over the period from 1919 to 1997 (Fromentin et al. 1997). Tveite (1971) concluded that released cod did not affect the abundance of natural cod populations in relation to the initial objectives of this monitoring; however, the monitoring itself has still been continued and provides important baseline data for validation of long-term environmental changes (Fromentin et al. 2000; Lekve et al. 2002).

Yolk-sac larvae and larvae after yolk absorption of small pelagic species are sorted and counted from the specimens of the fish egg, fish larval, and zooplankton monitoring in Japan. These data are available in the FRESCO database, and the statistics of larval densities of different stages are automatically calculated within the network system (Fig. 7.6). Concerning population fluctuations of small pelagic fishes, Watanabe et al. (1995) analyzed the mechanism of the drastic decline of the sardine population after 1988 along the Pacific coast of Japan using the data set obtained from the fish egg, fish larval, and zooplankton monitoring between 1978 and 1992. The results suggested that the population decline was owing to recruitment failure from hatched yolk-sac larvae to YOY (young-of-the-year) during four

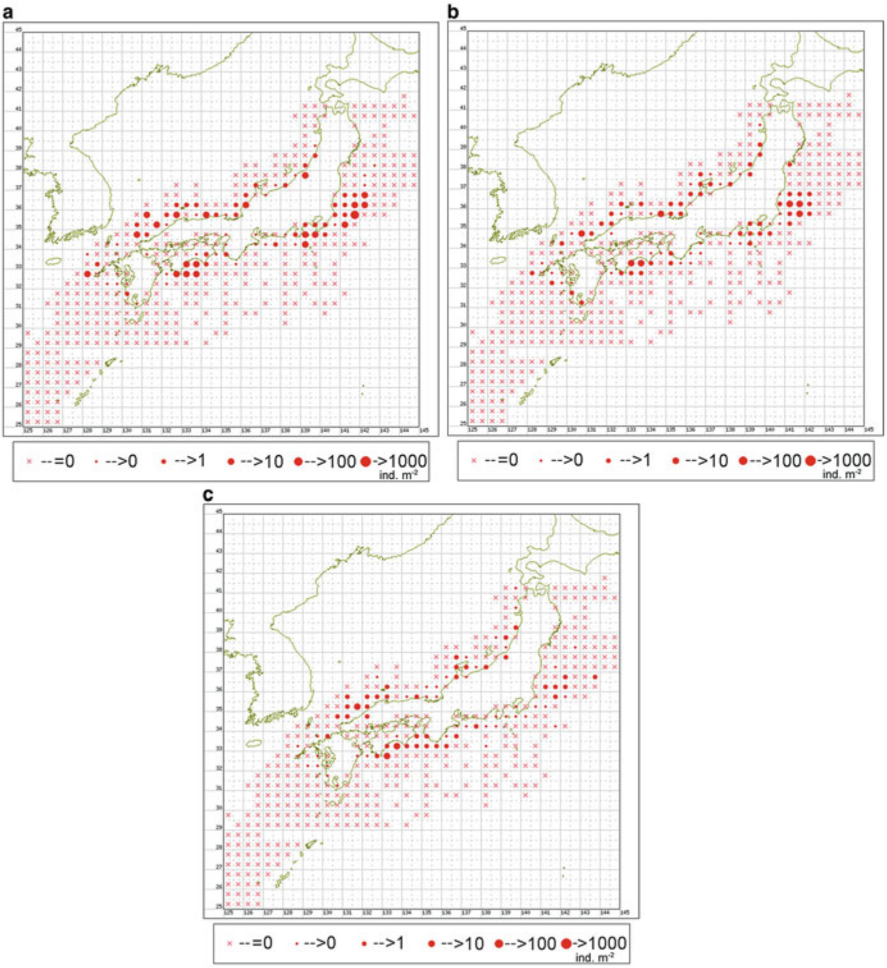

Fig. 7.6 Example of annual density of eggs (**a**), yolk-sac larvae (**b**) and larvae after yolk absorption (**c**) of Japanese sardine (*Sardinops melanostictus*) in 30′ × 30′ longitudinal and latitudinal blocks in 2012

consecutive years from 1988 to 1991. In that paper, total biomass of spawned eggs was successfully compared with the just hatched yolk-sac larvae, which were concurrently caught by vertical plankton net tows because of their lack of swimming ability, and landing data of YOY in the next winter fishing season (Fig. 7.7; Watanabe et al. 1995).

In Japan, surface ring net tows (1.3 m in mouth diameter, 0.335 mm + 1.5 mm mesh size) were also widely operated for monitoring the abundance of larval and juvenile fishes during the twentieth century concurrently with the vertical net sampling. However, studies on vertical distributions of larval fish revealed that the representativeness of larval fish abundance at the surface was low compared to the

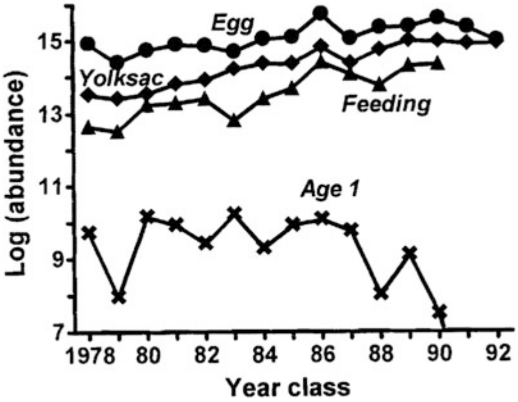

Fig. 7.7 Abundance of Japanese sardine (*Sardinops melanostictus*) in egg stage (egg), yolk-sac larval stage (yolk sac), and post first-feeding larval stage (feeding) standardized for stage duration time and available population of age one recruits (age 1) in the Doto region, Japan. The abundance of post first-feeding larvae in 1991 and 1992 was not available because the TL of feeding larvae was not measured in these years. The available population of age 1 recruits in 1991 was estimated to be 0 and that in 1992 could not be estimated because the total catch in the Doto region was too small, 11 hundred tons, in 1993 (from Watanabe et al. 1995)

whole biomass of larval fish in the water column. Only for Pacific saury larvae and juveniles, inhabiting the epipelagic stratum, neuston net samplings have been conducted along the Pacific coast off Japan in winter from 1990 to the present. Takasuka et al. (2014) analyzed environmental factors affecting appearance of Pacific saury larvae using the 10-year data obtained in the neuston net sampling. Oozeki et al. (2014) conducted particle tracking experiments in estimated current fields from 1993 to 2010, using the data set obtained in the neuston net sampling. The results of these analyses showed that the decreasing juvenile allocation rate to the Kuroshio–Oyashio transition region was coincident with the recent decreasing trend of annual landings of the Pacific saury in Japan.

7.3 Technological Advances

7.3.1 Net Sampling

Quantitative sampling methods for fish eggs, fish larvae, and zooplankton have basically been based on plankton net systems. A wide variety of net sampling systems have been developed since the late 1800s. Developmental histories and characteristics of net sampling systems were described in detail by Wiebe and Benfield (2003). Sampling methods of plankton nets for fish eggs, fish larvae, and zooplankton were described in Smith and Richardson (1977). Smith and Richardson

(1977) listed causes of sampling errors during towing of plankton nets as the following: (i) variance of sampling water volume by the fluctuation of wire angle at vertical tows, (ii) overflow at the mouth area caused by clogging due to low mouth opening ratio (ratio of filtering area to mouth area), and (iii) net avoidance by fish larvae or large zooplankton with swimming ability due to bridles or a towing cable in front of the net mouth. High-speed vertical towing with large weights can reduce the fluctuation of wire angle implemented in the CalVET net. Enlarged net area increases mouth opening ratio for reducing clogging, e.g., long-NORPAC net compared to the original NORPAC net (Zenitani 1998). Reduction of net avoidance has been tried by eliminating the bridles in front of the mouth area. Textbook examples of this idea were the bongo net (McGowan and Brown 1966), IKMT (Isaacs and Kidd 1953), and tucker trawl (Tucker 1951). Net avoidance due to the effect of the bridles and towing cable still remains as a main factor to destabilize sampling efficiency of larval and juvenile fishes, although several innovations have been implemented to minimize the avoidance. Therefore, the long-lasting plankton monitoring is mostly directed to the species or stages with low or none swimming activity, e.g., fish eggs, just hatched non-motile larval fish, and small zooplankton. Exceptionally, the bongo net adopted in CalCOFI program has been continued for larval fish monitoring (Ohman and Smith 1995).

Technological development and innovation of net sampling devices proceeded in the 1990s in order to accomplish high-speed sampling, multilayer sampling, and large size nets for sampling mesopelagic fishes, as described in the review by Wiebe and Benfield (2003). Then the interest for innovation shifted to optical or acoustic sampling devices (Fig. 7.8) because mainly of the following three reasons. Firstly, net sampling damages fragile creatures like gelatinous plankton, and researchers hardly able to observe their swimming behavior in an intact condition. Secondly, scientists hope to observe a detailed continuous vertical distribution of zooplankton from deep sea to surface. Thirdly, development of electronic devices can afford to construct the functional optical or acoustic sampling systems even in the deep sea. Automatic species identification techniques have recently advanced due to the development of computer technology and software innovations (e.g., image recognition and artificial intelligence programs). New acoustic and optical technologies are thought to have the potential to replace traditional net sampling systems (Wiebe and Benfield 2003).

However, applicability of acoustic and optical technologies may depend on the target species and their developmental stages. For example, juvenile fishes distribute too sparsely for the limited water volume surveyed by optical sampling devices and are too large in body size to be successfully automatically identified. Conversely juvenile fishes are too small to be differentiated to species level by acoustic sampling instruments as mentioned below. Sampling gear targeting juvenile fish or large zooplankton with swimming ability will be the last objectives of such recent innovations because of present technical limitations. Additionally, these juvenile fish and large zooplankton often exhibit spatiotemporal patchy distributions and daily vertical migrations. Therefore, additional progress of the quantitative sampling

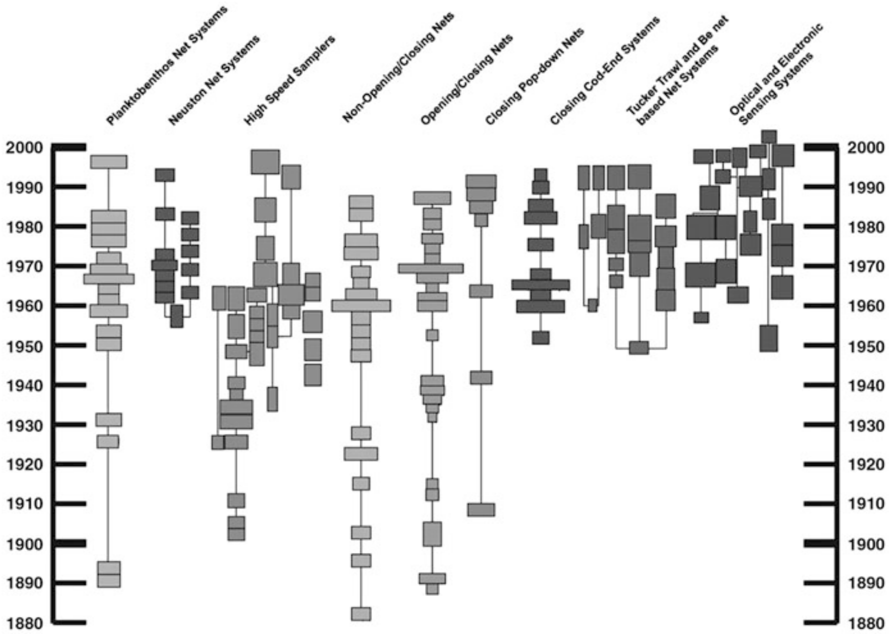

Fig. 7.8 A composite time line showing the boxes outlining the different types of plankton sampling systems. Wiebe and Benfield (2003) mentioned that the introductions of new classes of samplers often coincided with the availability of new technologies (i.e., closing codend systems, multiple net systems, and electronic/optical systems). Terminology of net systems is followed original description (from Wiebe and Benfield 2003)

devices targeting such stages is still required, even though progress in multiple net systems and/or closing codend systems has slowed after the mid-1990s (Fig. 7.8, Wiebe and Benfield 2003).

Use of high-speed tows of large mouth area frame trawls with multiple sampling devices is still a possible option to solve these problems. Since an opening/closing system for whole trawl nets is difficult to construct due to the large net sizes, midwater trawl attached with a multiple codend sampling mechanism has been developed (e.g., Pearcy 1980; Pearcy et al. 1977). However, contamination due to specimen retention in the main net mesh was pointed out as an unignorable disadvantage of the system (Wiebe et al. 1976). Autonomous codend opening/closing system attached to MOHT (COC–MOHT, Oozeki et al. 2012) is one example in order to solve the difficulty. The COC–MOHT is constructed by the quantitative frame trawl, Matsuda–Oozeki–Hu trawl (MOHT, Oozeki et al. 2004), attached with a new autonomous multiple codend opening/closing system (Fig. 7.9, Oozeki et al. 2012). The MOHT (5 m^2 mouth area) with a cambered V-shape depressor, hanging below the frame by four mutually parallel cables, was developed for sampling young pelagic fish and mesopelagic fish quantitatively. The MOHT exhibited reliable depth stability due to its depressor system and a high sampling efficiency of micronekton:

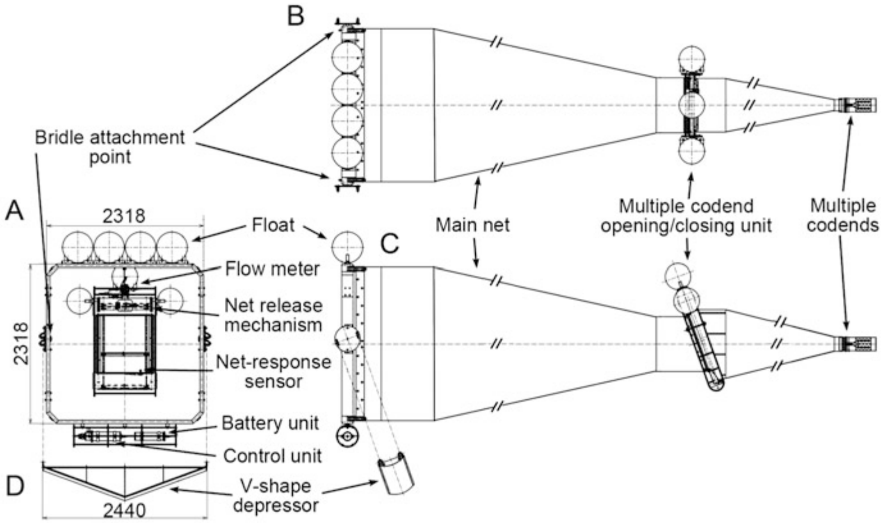

Fig. 7.9 Global design of the frame and the multiple codend opening/closing system (*A*, front view; *B*, upper view; *C*, side view; and *D*, depressor). Net length is not expressed to scale (from Oozeki et al. 2012)

it sampled ten times more than the MOCNESS (mouth area: 10 m^2) and five times more than the otter trawl (mouth area 900 m^2) equipped with a multisampler system (Yamamura and Yasuma 2010). The COC–MOHT inherited the towing ability at a fast speed and the high filtering efficiency possessed in the MOHT. Furthermore, improvement of the main net shape by adding the cylindrical part before the attachment of the multiple codend opening/closing system made contamination negligible.

7.3.2 Acoustic Method for Fish Larvae and Zooplankton Monitoring

Acoustic monitoring devices for larval fish and zooplankton are mentioned in this chapter, and a general description of high-frequency acoustic monitoring is described in Chap. 8. Target strength (TS, echo strength from an individual) is generally difficult to use for fish larvae and zooplankton monitoring due to their size range and their material properties, although the TS is widely used for assessing the body size of fishes (see Chap. 8). Information from volume backscattering (integration of the energy return from all individuals in a certain insonified water volume) have been used as an index of zooplankton biomass. In most cases of oceanographic monitoring, an acoustic Doppler current profiler (ADCP) is used for measuring ocean currents, and the ADCP enables assessment of the volume backscattering as useful information on the zooplankton biomass.

When we want to obtain detailed information, e.g., size composition or species structure of the zooplankton community, using high-frequency acoustic monitoring devices, size resolution is a functional problem for species identification during fish larval and zooplankton monitoring. Table 7.1 indicates typical relationships among sound frequency, minimum detective target size, and range of operation (from Wiebe and Benfield 2003). These values indicate that a fundamental limit exists for the usage of the high-frequency acoustic technique for identifying and counting small particles. Therefore, high-frequency acoustic systems (420, 1000 kHz) attached to the MOCNESS were used in order to correct the data of volume backscattering for assessing the distribution patchiness of zooplankton around the sampling stations (Wiebe and Greene 1994; Greene et al. 1998). Density contrast (ratio of the density of zooplankton to that of the water) is also important for analyzing the acoustic data; however, some zooplankton including gelatinous species indicate only a minimal contrast in density to that of water.

A dual-frequency identification sonar system (Fig. 7.10; DIDSON, Sound Metrics Corporation, Belcher and Lynn 2000) is a recent innovation potentially solving the functional limits for using acoustic technology for fish larval and zooplankton monitoring. DIDSON is a high-definition imaging sonar with a unique acoustic lens system that provides near-video-quality images of underwater objects and has the advantage of being able to produce an image in zero-visibility water (Belcher and Lynn 2000; Baumgartner et al. 2006). The present high-end model irradiates 128 beams at 3 MHz toward 30° horizontal field and records 4–30 frames s^{-1}.

Table 7.1 Typical description on sound frequency, minimum detectable target size, and range of operation

Frequency (kHz)	Minimum detectable target size (mm)	Range of operation (m)
120	~10	~200
420	~3	~80
720	~1.5	~30

Reproduced from Wiebe and Benfield (2003)

Fig. 7.10 Dual-frequency identification sonar system (DIDSON, Sound Metrics Corporation, http://www.soundmetrics.com/products/ARIS-Sonars/ARIS-Explorer-3000)

Resolution of the image is from 3 mm to 10 cm depending on the distance, and the nominal effective range is 5 m at 3 MHz model. DIDSON has been mainly used for studying migration and swimming behavior of adult salmonid fish around rivers and coastal areas in fisheries studies (e.g., Tiffan et al. 2004; Martignac et al. 2014). However the recent increase of resolution may enable the study of the large zooplankton community and juvenile fishes, because clear images are obtained even in turbid waters or night without light. Furthermore, useful images are captured of the large gelatinous plankton, e.g., jellyfish, whereas these species are difficult to collect by net sampling and existing acoustic or optical devices (Han and Uye 2009; Makabe et al. 2013).

7.3.3 *Optical Devices for Fish Larval and Zooplankton Monitoring*

History of optical sampling devices for zooplankton research indicates two different concepts. One is the use of optical scattering, and the other is imaging. Imaging has shown great progress in recent years in relation to the rapid innovation of video systems (Wiebe and Benfield 2003). At the beginning of the development, particle detection and counting systems were constructed as the electronic zooplankton counting device (EZCD). This system consisted of a modified Coulter counter attached with a type of high-speed plankton net and was successfully used to quantify small-scale relationships between zooplankton distributions and the thermal microstructure in North Atlantic surface waters (Boyd 1973). After several innovations for quantifying various particle-size classes, the optical plankton counter (OPC) was developed (Herman 1988). This system detected the number and size of particles via interruption of the light source. The OPC achieved great success and was adopted in several monitoring devices including the CUFES (Checkley et al. 2000) and the moving vessel profiler (MVP, Wiebe and Benfield 2003). At present the light source has been changed to a laser (LOPC) for increasing size resolution and comparative studies of OPC have been conducted (Herman and Harvey 2006).

Recent progress of image analyzing techniques strongly suggests the importance of video plankton recorder (VPR; Davis et al. 1992) as a monitoring device, although the size composition of the zooplankton community obtained by the OPC (LOPC) is still valuable information (Basedow et al. 2013). The original VPR was a towed monitoring system, which supported mounted video cameras, short-pulse duration xenon strobe synchronized to the sampling rate of the cameras, and a broadcast-quality video recorder. Several steps of improvement have been conducted following the development of electronic devices (VPR II, Davis et al. 2005). These are direct signal transfer system from the instrument to ship by an electro-optical cable, data transfer from analog signal to digital, increasing the frame rate, increasing the resolution of the CCD camera, changing from black-and-white images to color images, and so on. These improvements of the VPR system were accompanied with the development of similar systems, e.g., underwater video profiler (UVP, Gorsky et al. 1992), zooplankton visualization and imaging system (ZOOVIS, Benfield et al. 2003), and shadow image particle profiling and evaluation recorder (SIPPER, Samson et al. 2001). The continuous improvements and on-site use of VPR have acquired many users around the world and support new findings on zooplankton ecology also in Japan (e.g., Ichikawa 2008; Takahashi et al. 2013).

The limitation of the field of view is one of the points that need to be improved, although the successful use of VPR. Wiebe and Benfield (2003) introduced two projects for solving this point, which were the Towed Optical Plankton Survey Instrument (TOPSI, 2 m^2 field of view) and the Large Area Plankton Imaging System (LAPIS, 4 m^2 field of view). Despite these challenges, recent rapid developments both in the resolution of CCD cameras and image analysis software systems ensure the further progress of VPR. Video field of the original VPR was only 256 × 512 pixels with 8 bits $pixel^{-1}$ (256 gray level), and the VPR II equipped 1008 × 1018 pixels with 10 bits $pixel^{-1}$ CCD camera (Davis et al. 2005), and then the Color Auto-VPR (SeaScan) equips 1024 × 1024 pixels with color CCD camera (Takahashi et al. 2013). Recent progress in CCD cameras has been so fast that the high-definition television (HD, 1280 × 720 pixels) was replaced by the full high-definition television (FHD, 1920 × 1080 pixels). CCD camera system for 4 K ultrahigh-definition television (4 K UHD, 3840 × 2160 pixels), which is 9 times as many pixels as HD, is already popular, and the CCD camera of 8 K UHD (7680 × 4320 pixels), which is 36 times as many pixels as HD, will be marketed soon. This progress will enable the expansion of the field of view from the present Color Auto-VPR (a cube 37.9 mm on a side: 54.5 mL) to a cube 22.7 cm on a side (11.7 L), if the electrical supply and data transfer system can be adopted to support the 8 K UHD CCD camera.

The progress of image analyzing software system has also affected the data analyzing method of the images obtained by the optical monitoring devices, including the VPR. The VPR II is already equipped with an auto species identification system (Davis et al. 2005), and several different algorithms for image analyses have been proposed (e.g., Akiba and Kakui 2000; Bachiller and Fernandes 2011; Sieracki et al. 2010). Recent marked progress in image analyzing systems has been supported by the following three points: (i) rapid progress of processing speed of computers, (ii) increase of individual data quality provided from high-resolution CCD cameras, and (iii) huge quantities of original data for improving the accuracy of analyzing systems. The same is just as valid for auto identification of fish larvae and zooplankton. Increase of the information quality, which is supported by the increase of the resolution level and color information instead of gray images, provides significant additional information for auto species identification. Enlargement of the field of view due to improvement of the resolution level also the supply of a huge number of individual images of zooplankton and thus improving the accuracy of the image analyzing system (Bachiller and Fernandes 2011). These improvements have been supported by the rapid progress of computer processing speeds. Similarly the same is applicable to the case of the audio cameras. Audio images obtained by DIDSON include information of the internal structure such as CT scans, instead of color images. Auto species identification or sex identification of fishes has been started using the audio camera. The progress of auto species identification system proposed other applications of VPR system, which is the bench-top VPR for analyzing huge number of stored zooplankton specimens (Ichikawa et al. 2009). At present, bench-top VPRs with auto species identification system are used at NRIFS for analyzing decadal changes of species composition and size distributions of copepods.

Another innovational optical technology for solving two problems, i.e., limitation of field volume and improvement of information quality, might be the digital holographic imaging system. Reconstruction of full three-dimensional detailed images in air with large field volume is the most attractive characteristic of holography. This advantage enables the construction of computer-controlled in situ microscope and binarized holographic images of an object that can subsequently be identified by an auto species identification system. Holographic images of zooplankton were firstly observed by Knox (1966) by ruby laser in a laboratory. In situ zooplankton images were obtained by Katz et al. (1999) firstly. The maximum field volume of their system was a 63 mm diameter cylinder by 680 mm length (image volume, 2119 cm^3). Reconstructed holograms in the laboratory were remarkably clear and fine enough for resolving to a 10 μm size range. At the same time, Watson et al. (1998) constructed the HOLOMAR system in order to analyze high-resolution in situ holographic records of marine organisms. HOLOMAR consists of an underwater holo-camera for recording the organisms (HOLOCAM) and a facility for replaying and analyzing the hologram (HOLOSCAN). The field volume of the HOLOCAM was 50,000 cm^3 (off-axis hologram record), and several hundred holograms were successfully obtained by casts down to 100 m depth (Watson et al. 2003). Subsequently, several types of immersible in situ hologram recorders have been developed based on the development of CCD cameras for recording holograms and digital holography technology.

Immersible in situ hologram recorders contain two types of holographic geometries, in-line reference beam (ILH) and off-axis reference beam (OAH), and these two geometric systems have distinct differences and advantages. The particular benefits of ILH are its geometrical simplicity, the minimization of laser coherence and energy requirements, and the very high-resolution capabilities over a large depth of field. Instead of these advantages, ILH show essentially outlines or silhouettes of the objects. The range of object size recordable by ILH has an upper limit that is set by the requirement to record in the far field of the object (Watson et al. 1998). Therefore, the most appropriate in situ apparatus has been thought a holographic microscopy.

OAH is usually applied to primarily opaque subjects of large volume despite the more complex geometry by contrast with ILH. Diffuse front illumination allows for recording more dense aggregates of marine particles, although the sufficient power supply for enough illumination is needed in order to form a holographic image. OAH may even provide a more complete record than the ILH, by providing information on the structure of the object being recorded. Larger particle sizes than that of the ILH can be recorded by OAH, although there is a lower limit of the resolution that is set primarily by speckle and the physical constraints of the optical setup (Watson et al. 1998).

Fig. 7.11 In situ holographic microscopy system (LISST-HOLO, Sequoia Scientific Inc., http://www.sequoiasci.com/product/lisst-holo/)

ILH holographic microscopies have become popular for zooplankton monitoring (e.g., Graham and Smith 2010; Graham et al. 2012; Bochdansky et al. 2013; Yourassowsky and Dubois 2014), and commercial models are available (Fig. 7.11, LISST-HOLO, Sequoia Scientific Inc.). Low-cost easy-to-use products are also now constructed for monitoring use attached to drifting buoys (Akiba et al. 2013). Cutting-edge technologies relating to holography, e.g., full-color holography, viewing-zone-angle expansion of electronic holography, and glasses-free tabletop 3D display, are now actively studied and will be available for the observation of marine organisms in the near future.

7.3.4 Data Applications

A data integration system is an essential facility for the effective usage of fish egg, fish larval, and zooplankton monitoring data, in order to store large volumes of accumulated data and to provide outputs for analysis. In many cases of long-term biological monitoring activities which include various monitoring stations, laboratories, and institutions, the data processing systems are different. It is the first step to establish a common data policy acceptable to the scientific community for the monitoring program. Based on the data policy, data integration systems are necessary to satisfy several demands, which are swiftness for data processing, data accuracy, and accessibility for users. Although it is important for users outside of the monitoring program to access the data set freely, data priorities by original researchers belonging to the program should also be appreciated because the biological data sets are provided by highly trained technicians of species identification. Securement of the authorship belonging to the biological monitoring data set would be an option. Author tag attached to the data set would be needed at the time of contribution to the data integration system and will support the authorship of the original data. Prompt data processing including quality control and preparation of the database should be also important. At the same time, security for accessing the original data is essential for preventing any modification of the original data, although it is beyond the topic of this chapter.

In Japan, monitoring data obtained by the Fisheries Agency have been stored in FRESCO, which was designed in 1997 for examining resources, forecasting trends of landings, and developing optimal management strategies for the preservation and reasonable use of fishery resources by the Fisheries Agency. A FRESCO server has been installed in the Japan Fisheries Information Service Center (JAFIC) to collect fisheries and oceanographic information from the 10 national fishery research institutes and 54 prefectural fisheries experiment stations located throughout the country. The FRESCO server, which manages the information using a database, was fully reconstructed in 2000, and several times of hardware version up have been conducted. Data obtained by fish egg surveys are also stored in the FRESCO server just after species identification and counting, and all statistics including monthly egg production of small pelagic species are automatically updated.

A data integration platform relating monitoring activities in a more global scale had been constructed in 2006 as “Data Integration and Analysis System (DIAS)” in Japan Agency for Marine-Earth Science and Technology (JAMSTEC), with the goal of providing access to global and regional sensing data. Project team developed a pilot system for the creation of an information storage infrastructure for public benefit applications and the deepening of scientific knowledge in the areas of climate and water cycle, for application in fisheries, agriculture, and biodiversity management particularly through the linkage of information across disciplines. DIAS has been succeeded into the “Environmental information Integration Program” to extend and enhance the services (http://www.editoria.u-tokyo.ac.jp/projects/dias/?locale=en).

Physical oceanography data are essential for the biological data integration system as basic information; furthermore, constructive utilization of biological monitoring data requires reliable oceanic simulation models based on reliable observations. The Fisheries Research Agency (FRA) has constructed two model systems named Regional Ocean Modeling System (ROMS), in which the target area is the Pacific coast and adjacent seas of Japan, and Japan Sea Data Assimilation Experiment (JADE) for Japan Sea and adjacent seas of Japan. These sea condition forecast systems integrate physical oceanography data via the Global Telecommunication System (GTS) and publish the results on the web. Data integration between physical oceanography and biological monitoring data will be fruitful for assessing global changes in the oceans.

7.4 Recommendations for the Future Monitoring Systems

Typical long-term biological monitoring and innovation history of monitoring system has been reviewed. At the end of this chapter, several problems relating to the biological monitoring will be discussed.

Fish eggs, fish larvae, and zooplankton exhibit patchy distributions horizontally, and the patchiness structure becomes increasingly prominent with development for larval and juvenile fishes. Most of them also indicate concentrations at a certain depth layer and daily vertical migrations. Objectives of many sampling innovations are to enable serial samples both horizontally and vertically. Most of oceanic measuring instruments relating to physical parameters provide serial monitoring data at present and acoustic monitoring devices for adult fish supply continuous data set (Chap. 8). Sea surface temperature and sea surface height obtained by satellite remote sensing also provide continuous data set horizontally. These horizontal continuous data sets are good for analyses by geographic information system (GIS), which is a powerful tool for detecting the patchiness structures and the linkage between biological and physical environmental parameters (Nishida et al. 2007). However, effective continuous sampling instruments are not yet established for fish egg, fish larval, and zooplankton monitoring both horizontally and vertically. CPR and CUFES can provide continuous data sets horizontally; however, the representativeness over the whole water column is still disputable because of the daily vertical migration of zooplankton and of the developmental depth layer shift of fish eggs. Net sampling of fish larvae and zooplankton considering the patchy distribution, which varies depending on their development, will require too many samples to be analyzed by researchers. Continuous monitoring system equipped with wide-field volume and accurate auto species identification system will be an option to overcome this dilemma. These newly innovated sampling instruments can differentiate marine organisms to the species level and supply high-resolution spatiotemporal data.

Importance of other types of biological monitoring relating larval fish for assessing fish resources is pointed out. Long-term biological monitoring programs mentioned in this chapter provide abundance and distribution data. Several trials for monitoring juvenile fish densities, which were hoped to provide more accurate information on recruitment, have failed because of their sparse and patchy distributions during this stage. However, the biological monitoring of physical parameters such as using otolith growth rates during the juvenile stage may provide useful and reliable information on recruitment, despite the insufficient information of spatial distribution of juvenile fish. Kawabata et al. (2015b) adopted the relationship between the juvenile growth rate estimated from otolith analyses and recruit per spawning biomass (RPS), which was demonstrated by more than 10 years biological monitoring of juvenile fishes (Fig. 7.12, Kamimura et al. 2015), for estimating the recent recruitment of chub mackerel. Similarly, juvenile body length of chub mackerel at a certain date would reflect the larval growth rate (Takahashi et al. 2014). Many papers strongly suggested the relationship between larval growth and mortality during their early life history (e.g., Houde 1989). Thus the long-term monitoring of juvenile growth rate provides indices of recruitment process considering with mortality during their early life history, which is ordinary difficult to monitor.

Development of simulation models of physical oceanic processes will enable reliable estimates of underwater parameters of temperature, salinity, and current speed, based on the satellite remote sensing data. Thus, the requirement for routine

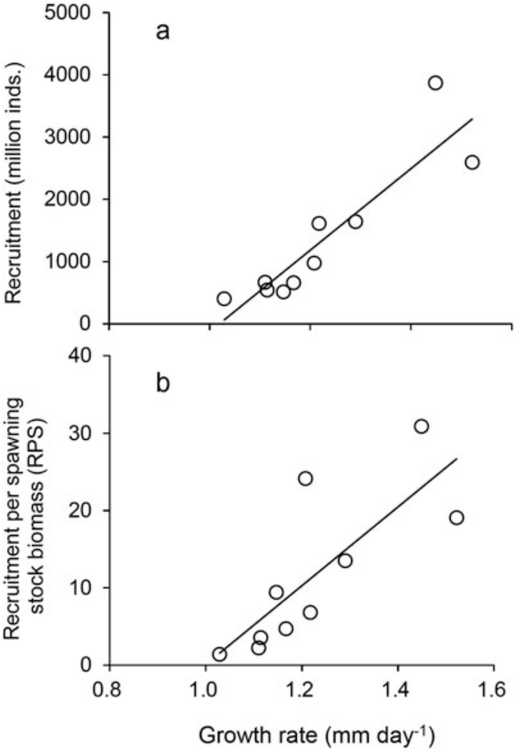

Fig. 7.12 Significant relationships between the mean daily growth rate of chub mackerel (*Scomber japonicus*) in larval and juvenile stages hatched in April and recruitment (**a**), recruitment per spawning stock biomass (**b**) from 2002 to 2011 (from Kamimura et al. 2015)

ocean monitoring cruises will decrease because of the availability of reliable estimated environmental parameters, although these types of innovation will be highly welcome. Decrease of the demand of monitoring cruises means the decrease of biological monitoring activities, which is not available via surface information obtained from satellites. In order to dissipate the discrepancy in monitoring activities, automated sampling instruments like ROV or AUV attached with a wide-field holography recorder will be important.

Finally, global and long-term biological monitoring structures are ordinarily supported by governmental funds or private donations. A kind of valuable scientific information or useful forecasts of the global change of the oceans might be expected from the funding bodies in order to improve the viability of the monitoring activities. From this point of view, appropriate data integration system mentioned above is essential for acquiring scientific usage. In addition, it is also important for the continuity of monitoring activities to reduce the cost for analyzing the biological monitoring (see Box 3 in Hays et al. 2005). Auto species identification system or remotely operated vehicle (ROV) attached with wide-field holography recorder will be also important for the reduction of the cost of biological monitoring. Furthermore, it might be more important to educate that the long-term biological monitoring is one of valuable assets for tax payment such as a health insurance system.

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Chapter 8
Acoustic Survey

Kazushi Miyashita

Abstract Hydroacoustic methods are important for marine studies because of their advantages of directness, continuity, and quickness. Acoustic data provide quantitative information from a variety of marine organisms, including not only fishery-target fish species but also nontarget zooplankton, mesopelagic fish, and the sea forest. Characterizing the acoustic environment by discriminating, classifying, and quantifying biological backscatter is promising to better understand ecological processes, such as prey-predator relationships, habitat selection, and biomass estimates, which can help with ecosystem-based fisheries management. This chapter describes how acoustic methods are beneficial for monitoring marine organisms by (1) helping identify and discriminate zooplankton and larval, juvenile, and adult fish based on backscattering strength frequency characteristics and biomass estimates, (2) describing advances in acoustic applications for ecological monitoring, and (3) developing an acoustic monitoring system for “shirasu” (Japanese anchovy post-larvae) fisheries management now in operation. Finally, we provide some perspectives on an acoustic monitoring system for ecosystem-based fisheries management.

Keywords Acoustics · Acoustic monitoring system · Biomass estimation · Ecosystem-based fisheries management · Quantitative echo sounder · SV difference method

8.1 Acoustics in Fisheries Research

Electromagnetic waves—including visible light—are attenuated greatly in water and do not reach great depths. However, acoustic waves reach deeper into water compared to electromagnetic waves. This property allows many marine organisms

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to use acoustic waves. Whales and dolphins are examples of animals that use acoustic waves as a communication and positioning tool. Killer whales vocalize to communicate with their families, and dolphins use ultrasonic pulses rather than eyesight to locate prey. Many fish use acoustic waves for communication and during reproduction. Thus, the underwater world is the "world of acoustics."

Humans have also used acoustics underwater, particularly in the oceans. For example, submarines use sonar to navigate underwater, and fishermen use sonar and fish finders known as "echo sounders" to detect fish aggregations for an efficient catch. Currently, acoustics is one of the most commonly used technologies in fisheries and marine science research. In this chapter, we introduce the acoustic survey and its application to fisheries research.

Underwater acoustic (hydroacoustic) methods play an important role in marine organism monitoring due to their technical advantages, such as time efficiency, high area coverage, and directness. Therefore, hydroacoustic methods are commonly used worldwide.

Studies on fisheries acoustics began with detecting fish and fish schools using a simple echo sounder. An echo sounder visualizes an echo image termed an "echogram," which allows the acoustics to be used to determine the presence or absence of a fish/school and determine its relative size. The present quality of visual monitors makes use of acoustics more popular than previously. For example, fish finders have become an indispensable tool for recreational and commercial fisherman. As echo sounder applications progressed, fish abundance and biomass estimates using hydroacoustic methods were actively investigated worldwide. Currently, quantitative echo sounders are commonly used to measure fish biomass. A quantitative echo sounder is a piece of scientific equipment based on acoustic theory (Fig. 8.1), in which the accuracy of a biomass estimate is sufficient to quantitatively evaluate a fish stock if calibrated correctly.

8.2 Acoustic Survey Using a Quantitative Echo Sounder

Surveys using both quantitative echo sounders and trawl nets, or the so-called acoustic and trawl survey or acoustic survey, are one of the most popular methods of estimating fish biomass in the field. In this type of survey, researchers use one or more onboard quantitative echo sounders. A combination of 38 and 120 kHz is the most common frequency set-up for an acoustic survey. Many research vessels are equipped with echo sounder systems with multifrequency channels. A low frequency, such as 38 kHz, is used mainly to estimate fish biomass, whereas a high frequency, such as 120 kHz, is used mainly for detecting zooplankton. Species (e.g., fish or zooplankton) can be identified based on the differences in acoustic frequency characteristics between marine organisms (Kang et al. 2002; Miyashita et al. 2004). Notably, there is a limit to species identification using only a quantitative echo sounder. Thus, a scientific echo sounder combined with direct trawl net sampling provides detailed size estimates, helps identify

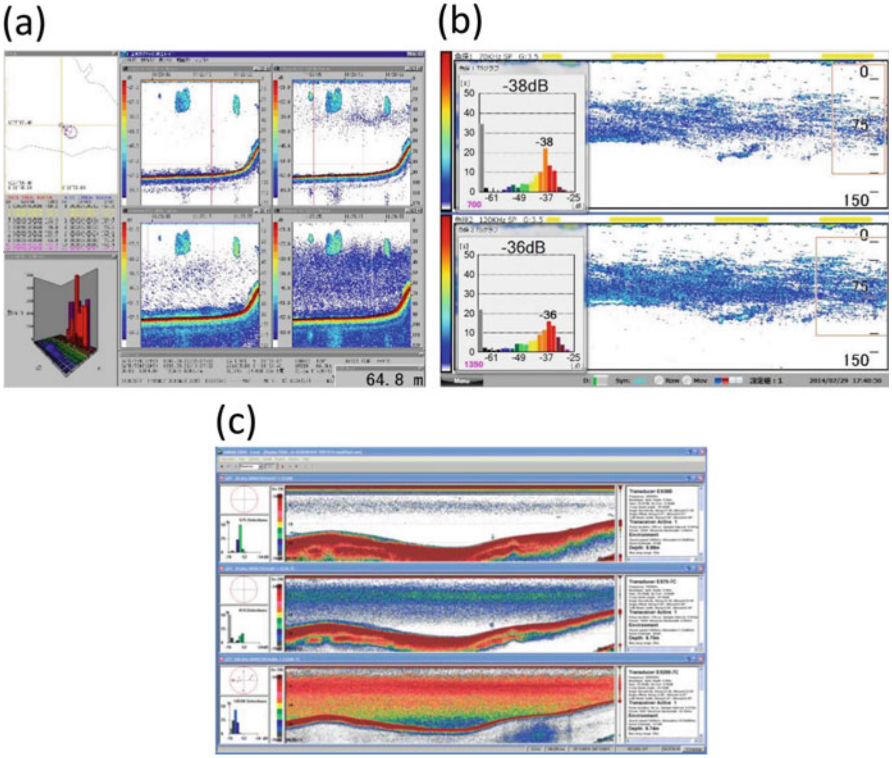


Fig. 8.1 Quantitative echo sounder echograms and operation system. (**a**) Sonic KFC3000 (reproduced from http://www.u-sonic.co.jp/product/kfc-3000.html), (**b**) Sonic KFC6000 (reproduced from http://www.u-sonic.co.jp/product/kfc-6000.html), (**c**) Simrad EK60 (reproduced from https://www.simrad.com/ek60)

species, and is essential for an acoustic survey. Sampling by trawl net is also effective for estimation of fish biomass in an acoustic dead zone, such as near the sea bottom.

8.3 Acoustic Survey Design

Three important points should be considered to conduct an accurate and efficient acoustic survey. First, the researcher must formulate a detailed survey plan. Second, the researcher should have a basic understanding of acoustic reflection characteristics. Third, the researcher must analyze the related error factors.

It is important to formulate a detailed survey plan that includes when (time and time period) and where (survey area) the survey is to be conducted and the desired information about the target organism (e.g., biomass, distribution, or life history). In addition, knowledge of the ecological characteristics around the target organisms is required. For example, if determining the biomass of an adult spawning fish is the aim of an experiment, it is necessary to know their spawning area (horizontal and vertical), season, timing, behavior, and other ecological factors. Then, transect lines with predetermined biological and environmental sampling stations can be set to cover the entire distribution area.

To understand the acoustic reflection characteristics of a target organism, it is important to convert the biological properties of the target into acoustic information. Acoustic reflection (echo) intensity of target organisms varies depending on the shape and size, swimming angle, presence or absence of a swim bladder, and differences in acoustic frequencies.

The presence or absence of a swim bladder facilitates distinguishing of target fish echo intensity. If echo intensity is compared between fish of the same size and shape with and without a swim bladder, the echo intensity of the fish with the swim bladder will be significantly greater than that of the fish without a swim bladder. For example, the echo intensity of Pacific mackerel (*Scomber japonicus*) (swim bladder) (Abe et al. 2010) is much higher than that of Atlantic mackerel (*S. scomber*) (no swim bladder) (Edwards and Armstrong 1983) for fish of the same size and of similar shape.

The swimming angle of a target organism also affects the echo intensity. In general, the echo intensity of the near dorsal aspect of a target organism is highest at all swimming angles. As swimming angle (when the dorsal aspect is 0°) decreases, the echo intensity decreases. Hence, it is essential to be aware of the average swimming angle of each target organism to properly estimate biomass. For example, the swimming angle of walleye pollock (*Gadus chalcogrammus*) differs between adult and young fish (Torisawa et al. 2006). Thus, if walleye pollock biomass is estimated in an area in which both adult and young fish are distributed, biomass must be estimated after the swimming angles have been determined.

It is also important to understand error factors, such as underwater noise, electrical noise, and interference with other acoustic equipment, to conduct an accurate acoustic survey. The presence of such noise can result in overestimation of biomass. In addition, error factors, such as underwater air bubbles, must be considered, particularly during a storm or other intense oceanographic events. If an acoustic survey is conducted during a storm, biomass might be underestimated because of attenuation due to air bubbles. The timing and location of these potential errors must be determined if an accurate acoustic survey is to be conducted.

8.4 Acoustic Species Identification and Discrimination

Species can be identified using differences in frequency characteristics between marine organisms, as mentioned in Sect. 8.2. In general, smaller organisms without a swim bladder (no gas in their body), such as zooplankton, can be identified using differences in frequency characteristics. For example, the echo intensity of *Euphausia pacifica*, a krill species, at 38 kHz is >10 dB lower than that at 120 kHz (Miyashita et al. 1996). The acoustic frequency characteristics of juvenile sand eel (*Ammodytes personatus*), which does not have a swim bladder, are similar to those of *E. pacifica* (Matsukura et al. 2013). In contrast, the echo intensity of adult sand eel at 38 kHz is a few decibels lower than that at 120 kHz (Safruddin et al. 2013), indicating that the acoustic frequency characteristics of sand eel change with life stage. The acoustic frequency characteristics of small pelagic fish also change during their life history. For example, the echo intensity of juvenile Japanese horse mackerel (*Trachurus japonicus*) at 38 kHz is a few decibels higher than that at 120 kHz (Nakamura et al. 2013). In contrast, the echo intensities of adult Japanese horse mackerel at 38 and 120 kHz are very similar. The echo intensities of sardine and anchovy change not only with life stage but also between day and night during their early life history. In addition, their acoustic frequency characteristics differ from those of Japanese horse mackerel.

Post-larvae of Japanese anchovy (*Engraulis japonicus*) and Japanese sardine (*Sardinops melanostictus*) are known as "shirasu" in Japan. The swim bladders of shirasu deflate during the day and inflate at night (Uotani 1973) (Fig. 8.2). As a consequence, the echo intensity of shirasu at 38 kHz is >10 dB lower than that at 120 kHz during the day and a few decibels higher at 38 kHz than that at 120 kHz at night, which is similar to other juvenile fish, such as juvenile horse mackerel (Miyashita 2003). Additionally, the echo intensities of young and adult sardine and anchovy at night are very similar at 38 and 120 kHz. These examples indicate that species can be identified using such biological-acoustic information.

Species have also been identified based on empirical information, such as the fish fauna of a survey area obtained from past surveys or commercial fishing. The distribution patterns and shapes of fish schools on an echogram are also collected during acoustic surveys. Distribution patterns and shapes vary depending on fish species, life stage, season, and other physical and biological factors. In general, adult and young small pelagic fish, such as anchovy and sardine, form large schools at the sea surface to mid-water layers, whereas juveniles tend to form small patchy schools near the sea surface. Adult and young demersal species, such as walleye pollock and

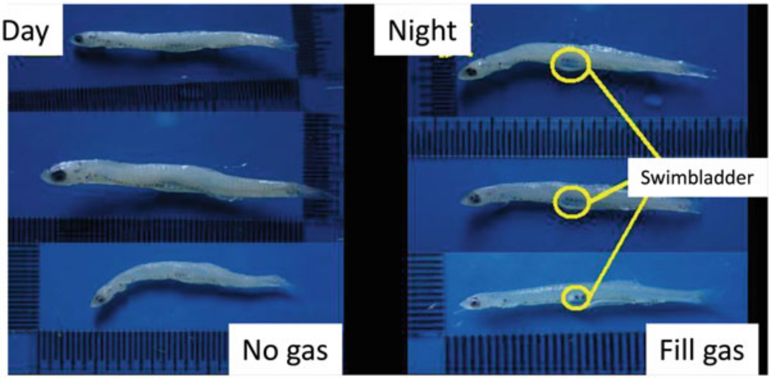


Fig. 8.2 Shirasu with a swim bladder. Left: no gas in swim bladder during day. Right: gas-filled swim bladder at night

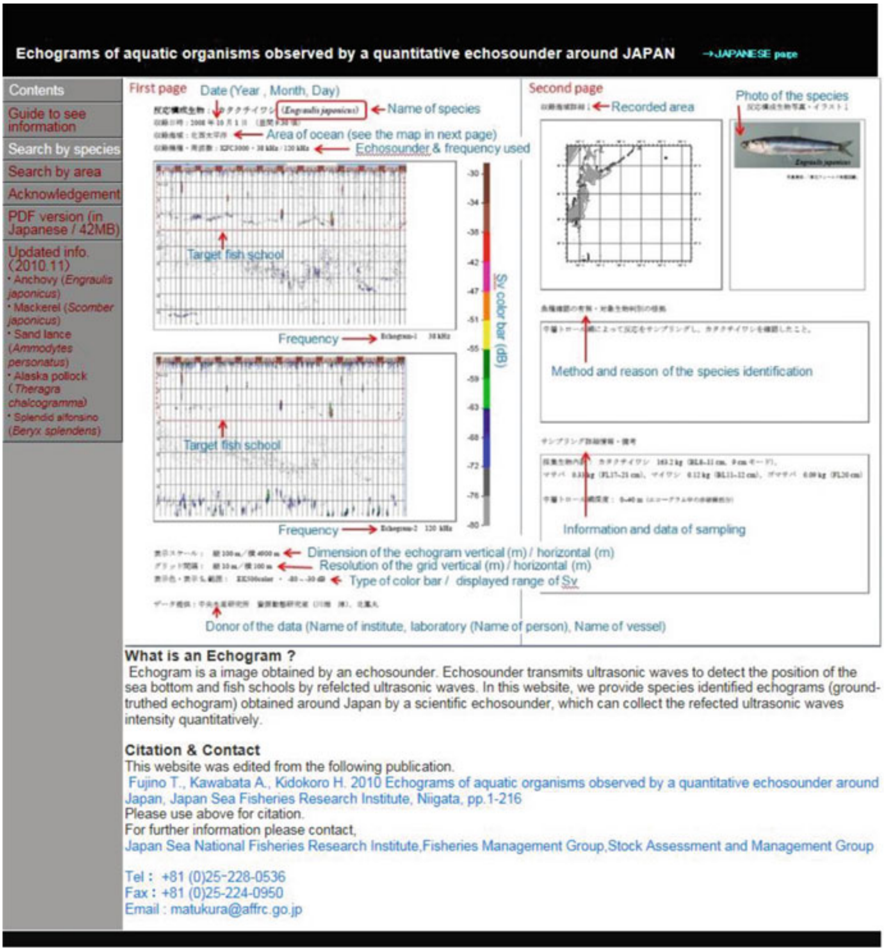
cod, form large aggregations near the sea bottom and in the mid-water layer, whereas juveniles form large aggregations near the sea surface and mid-water layer. The distributions of many marine organisms often change diurnally in the same area, season, and life stage. Mesopelagic lantern fish are the main species in the deep scattering layer (DSL). These fish are distributed in deep water during the day but tend to move to near the surface at night (Yasuma et al. 2010). Krill-like organisms also inhabit the DSL and have the same diurnal vertical distribution patterns as mesopelagic lantern fish.

Planktonic copepods are another component of the DSL. These organisms migrate vertically, following seasonal and diurnal patterns. *Neocalanus* copepods change their vertical distribution depending on season and life stage (Kobari and Ikeda 1999, 2000). Immature adult (CI–CIV) stage *Neocalanus cristatus* are distributed mainly near the surface during spring and summer, whereas mature (CV–CVI) stage *N. cristatus* are distributed mainly in the deepwater layer during fall and winter (Kobari and Ikeda 1999). *Metridia* copepods change their distribution between day and night. For example, *Metridia pacifica* are distributed mainly in deep water during the day and near the sea surface at night (Hattori 1989). The accuracy of species identification and discrimination using acoustic techniques improves depending on distribution characteristics, aggregation shape, and the background biological and ecological characteristics of the organisms detected in a survey area.

Databases that facilitate species identification and estimating biomass in an acoustic survey have been improved. The echogram catalog (Japanese portal site: http://jsnfri.fra.affrc.go.jp/shigen/echocata/; English portal site: http://jsnfri.fra.affrc.go.jp/shigen/echocata/indexEN.html) has been one of the most useful acoustic databases for fisheries researchers (particularly beginners) since 2010 (Fig. 8.3). This database collects echograms of many species obtained during acoustic surveys around Japan and in the northwestern Pacific Ocean. Echo intensity (target strength) data of some important fisheries species are summarized in the echogram catalog. Such databases will continue to improve and will be applied worldwide.

8.5 Advanced Acoustic Applications for Ecological Monitoring

Underwater acoustic technology has been developed, and a variety of acoustic equipment is utilized worldwide. Applications of this technology have extended from traditional fisheries resources surveys to other research fields. In particular, ecological research applications are popular. For example, the behavior and migration patterns of fish schools, prey-predator relationships, habitat selection, and other significant ecological studies have been conducted using acoustic equipment. In 2002, the ICES Symposium on Acoustics in Fisheries and Aquatic Ecology was held and published as a special issue of the *ICES Journal of Marine Science* (Volume



What is an Echogram ?

Echogram is a image obtained by an echosounder. Echosounder transmits ultrasonic waves to detect the position of the sea bottom and fish schools by refelcted ultrasonic waves. In this website, we provide species identified echograms (ground-truthed echogram) obtained around Japan by a scientific echosounder, which can collect the refected ultrasonic waves intensity quantitatively.

Citation & Contact

This website was edited from the following publication.
Fujino T., Kawabata A., Kidokoro H. 2010 Echograms of aquatic organisms observed by a quantitative echosounder around Japan, Japan Sea Fisheries Research Institute, Niigata, pp.1-216
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Fig. 8.3 Portal site for the echogram catalog (Reproduced from http://jsnfri.fra.affrc.go.jp/shigen/echocata/indexEN.html)

60, Issue 3, 2003). Publication of significant acoustic studies in aquatic ecology was a milestone event. In this section, some examples of these acoustic applications in ecology are introduced.

8.5.1 *Spatial Visualization of Prey–Predator Relationships: Walleye Pollock and Zooplankton*

Miyashita et al. (2004) reported that changes in the diurnal vertical distribution of walleye pollock were affected by those of prey organisms, such as zooplankton.

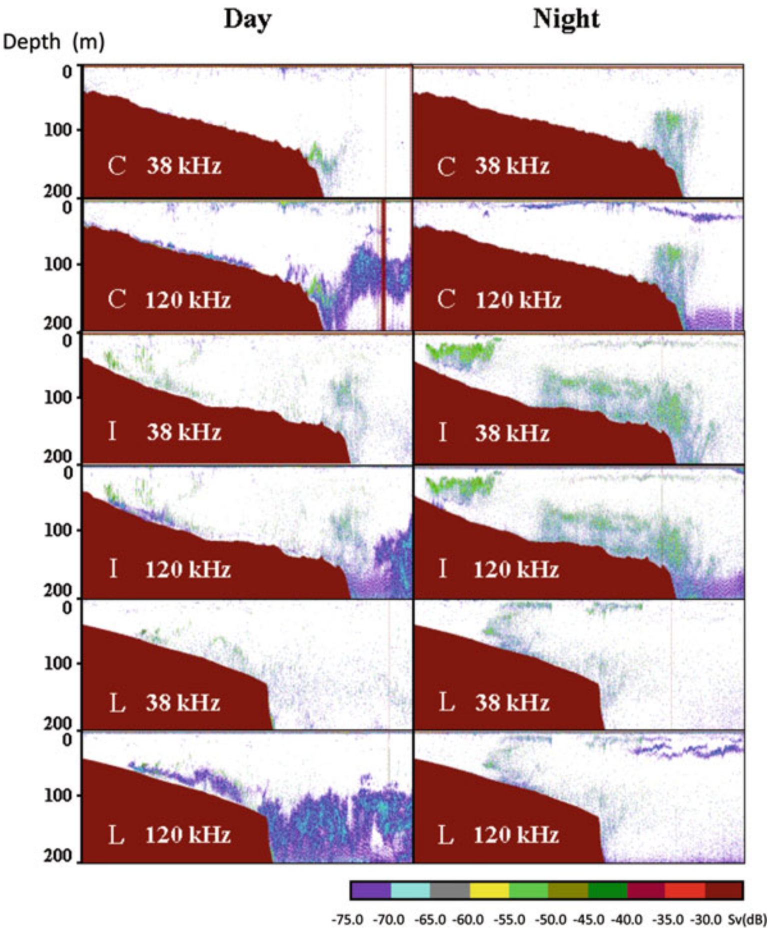

Fig. 8.4 Typical walleye pollock and zooplankton echograms off the Pacific coast of northeastern Hokkaido, Japan, in early summer during day and night. C, I, and L are lines in the eastern, central, and western parts of the survey area (Cited from Miyashita et al. 2004)

Figure 8.4 shows representative walleye pollock and zooplankton echograms taken off the Pacific coast of northeastern Hokkaido in early summer during day and night (Miyashita et al. 2004). The upper panel is the 38 kHz echogram, and the lower panel is that at 120 kHz. The echograms on the left were taken during the day, and those on the right were taken at night. Here, we observed that echoes at 120 kHz were mainly zooplankton, and those at both frequencies were mainly walleye pollock (Miyashita et al. 1997). The differences in the diel distribution patterns of walleye pollock and zooplankton are notable in these figures. Images of diel changes in early summer distribution patterns of zooplankton (prey) and walleye pollock (predator) are shown in Fig. 8.5. Layers of zooplankton were distributed over the continental shelf near the sea bottom during the day, and schools of young walleye pollock were distributed

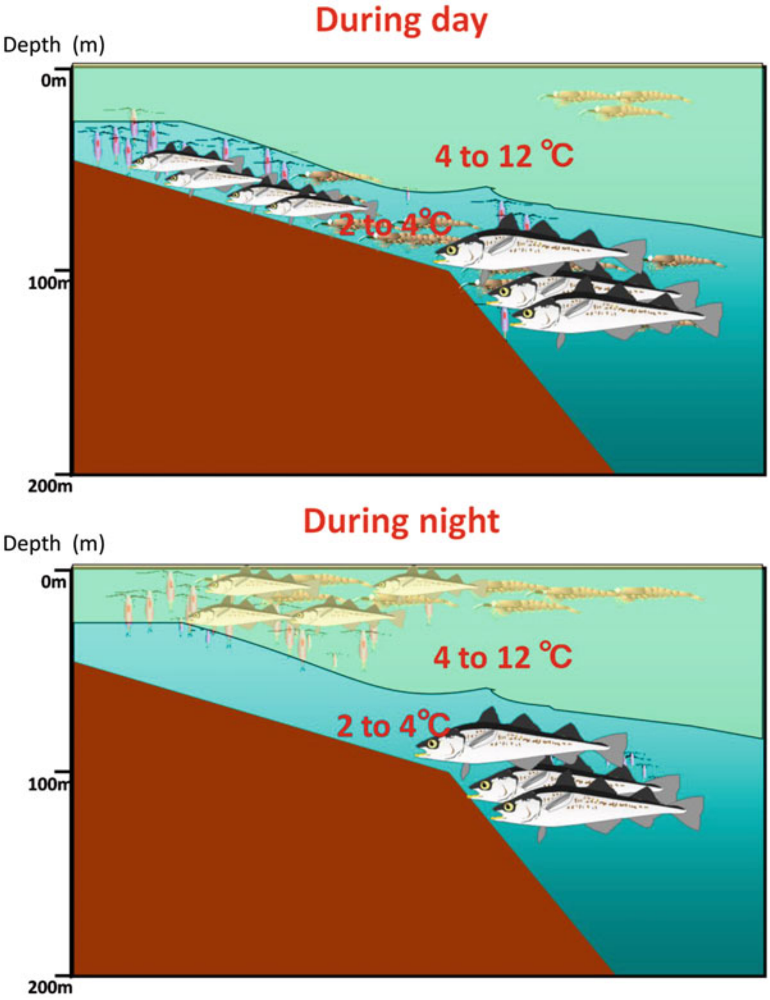

Fig. 8.5 Images of diel changes in zooplankton (prey) and walleye pollock (predator) distribution patterns in early summer off the Pacific coast of northeastern Hokkaido, Japan (Modified from Miyashita 2006)

mainly from mid-water to the sea bottom. However, near and offshore of the continental shelf, the layers of zooplankton were distributed near the sea bottom and mid-water, whereas adult aggregations of walleye pollock were near the sea bottom. The temperature range during the day, when the majority of walleye pollock and zooplankton were found, was 2–6 °C. The layers of zooplankton over the continental shelf tended to move to the sea surface at night, and the schools of young walleye pollock also tended to ascend to the upper layers at night. The layers of zooplankton outside of the continental shelf were distributed mainly near the surface, and adult aggregations of walleye pollock were distributed near the bottom to the mid-water level. The night temperature range at which young walleye pollock and zooplankton were detected was 4–12 °C. In contrast, the temperature range in which adult walleye pollock was present at night was similar to that during the day.

The observations of Miyashita et al. (2004) and Miyashita et al. (1997) show that the diel changes in vertical distribution and movement patterns of young walleye pollock and zooplankton are similar, but that those of adult walleye pollock and zooplankton are different. Miyashita et al. (2004) discussed differences in survival strategies for adult and young walleye pollock. That is, young fish feed during day and night to facilitate their growth, whereas adults feed only during the day to conserve energy for reproduction.

8.5.2 Spatial Visualization of Differences in Adult and Juvenile Distribution Patterns: Krill

Tojo et al. (2008) suggested that spatial distribution patterns of *E. pacifica*, which is called Isada krill in Japan, differ north and south of the Subarctic Front (SAF). They detected Isada krill using differences in the characteristics of the two acoustic frequencies (38 kHz and 120 kHz) and MOCNESS trawl information. Then, the spatial distribution characteristics of Isada krill were quantified using a geostatistical method, and the ecological interpretations were made by integrating acoustic echoes, biological information, and environmental data (e.g., temperature and salinity). Figure 8.6 is a conceptual model of the Isada krill distribution estimated using the abovementioned method around the SAF north of the 4 °C isotherm. The Isada krill distribution was more dispersed and extended in the north-south direction than that in the south, where aggregations

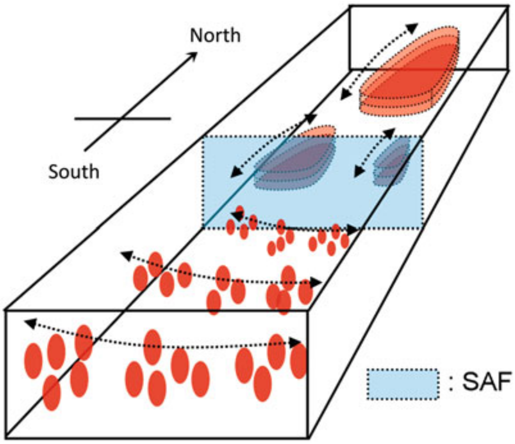

Fig. 8.6 Conceptual model of the Isada krill distribution around the Subarctic Front (SAF). Red circles, Isada krill aggregations; blue rectangle, SAF; dotted arrows, major directional distribution trends (Cited from Tojo et al. 2008).

of various densities were observed. Specimens in the north were mostly juveniles, whereas adults were found mainly in the south. Their results suggest that the Isada krill life history determines their habitat within a given oceanographic and environmental structure.

8.6 Advanced Acoustic Monitoring System: Real-Time *Shirasu* School Mapping System

Small pelagic fish, such as sardine and anchovy, are important fisheries resources worldwide. In Japan, sardine and anchovy of all life stages are caught using various methods. In particular, the so-called shirasu (post-larvae to juvenile stages) are the most economically valuable target resource at all stages, and shirasu fishing is conducted in the coastal waters of southern and eastern parts of Japan. Therefore, it is important to understand the shirasu recruitment mechanisms for resource and fisheries management. It is also necessary to quantitatively determine their abundance simply and quickly for sustainable management. Acoustics is a powerful tool, and an acoustic real-time shirasu monitoring system was introduced to support the shirasu fishery in the western part of Japan.

8.6.1 Shirasu *Fishery and Acoustics*

The most common shirasu fishing method is a trawl net during the day. Shirasu fishermen use a commercial dual-frequency echo sounder (50 and 200 kHz), which is known as a “shirasu echo sounder,” to detect shirasu schools. Figure 8.7 shows a representative echogram recorded by a shirasu echo sounder on shirasu fishing grounds during the day. The left panel shows the 50 kHz echogram, and the right panel shows that at 200 kHz. The shirasu school echoes were detected at the higher frequency (200 kHz) but not the lower frequency (50 kHz). Fishermen detect shirasu schools using differences in the acoustic frequency characteristics and their experience.

Figure 8.8 shows representative echograms recorded by a dual-frequency quantitative echo sounder on shirasu fishing grounds during the day (Miyashita 2006). The upper panel shows the 38 kHz echogram, and the lower panel shows that at 120 kHz. Here, two types of acoustic frequency characteristics were observed. That is, the 120 kHz echoes were only shirasu schools, whereas the 38 and 120 kHz echoes were young and adult anchovy, respectively. The shapes of the young/adult anchovy and shirasu schools were very similar on the 120 kHz echogram, indicating that a dual-frequency quantitative echo sounder is needed to detect a shirasu school.

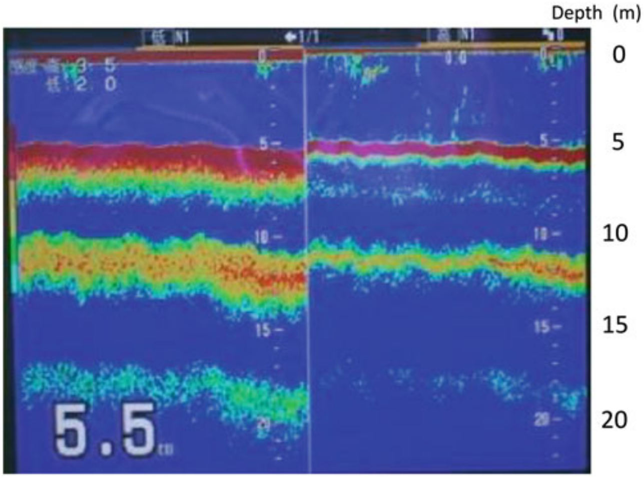

Fig. 8.7 Typical echograms recorded by a shirasu echo sounder on a shirasu fishing ground. Left, 50 kHz; right, 200 kHz

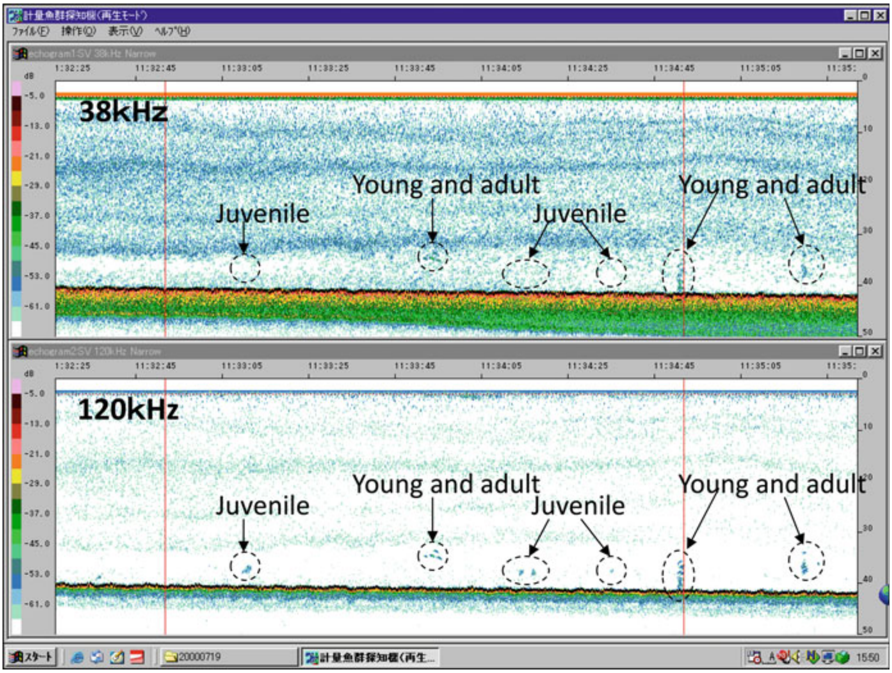

Fig. 8.8 Typical echograms recorded by a dual-frequency quantitative echo sounder on a shirasu fishing ground. Upper, 38 kHz; lower, 120 kHz (Modified from Miyashita 2011a, b)

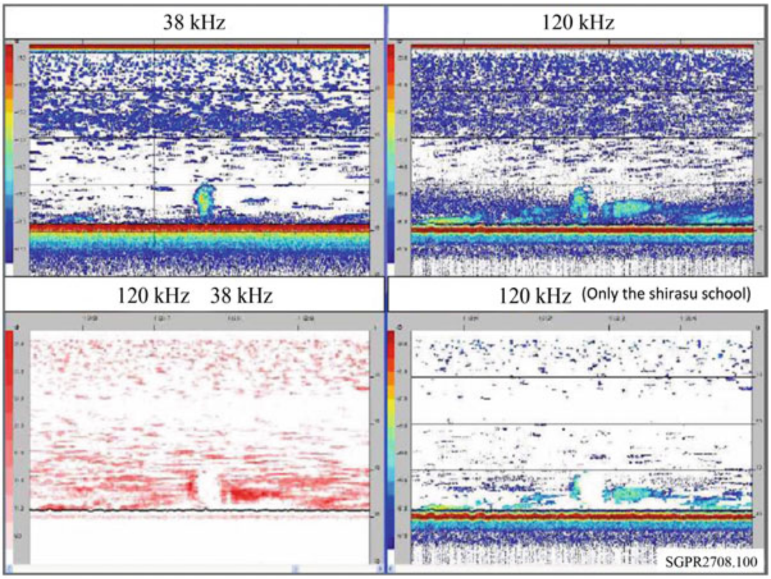

Fig. 8.9 Echograms from the automatic shirasu school discrimination system (Modified from Miyashita 2011a, b)

8.6.2 *Automatic* Shirasu *School Discrimination System*

Figure 8.9 shows echograms of an automatic shirasu school discrimination system. The left side of the upper panel shows the 38 kHz echogram, and the right shows that at 120 kHz. The left side of the lower panel shows the mean volume backscatter strength (MVBS) difference at 38 and 120 kHz (MVBS = 120–38 kHz), and the right shows the 120 kHz echogram of only the shirasu school, which was discriminated using the shirasu acoustic frequency characteristics suggested by Miyashita (2003). These computations were processed automatically.

8.6.3 *Real-Time* Shirasu *School Mapping System*

It is essential to have a shirasu school discrimination system that automatically transfers data from the vessel to land to process during a survey using this type of system. Furthermore, researchers and managers can take a practical approach to fisheries management by integrating additional information, such as environmental data (e.g., temperature, salinity, etc.) from a survey and satellite, automatically using the shirasu school information.

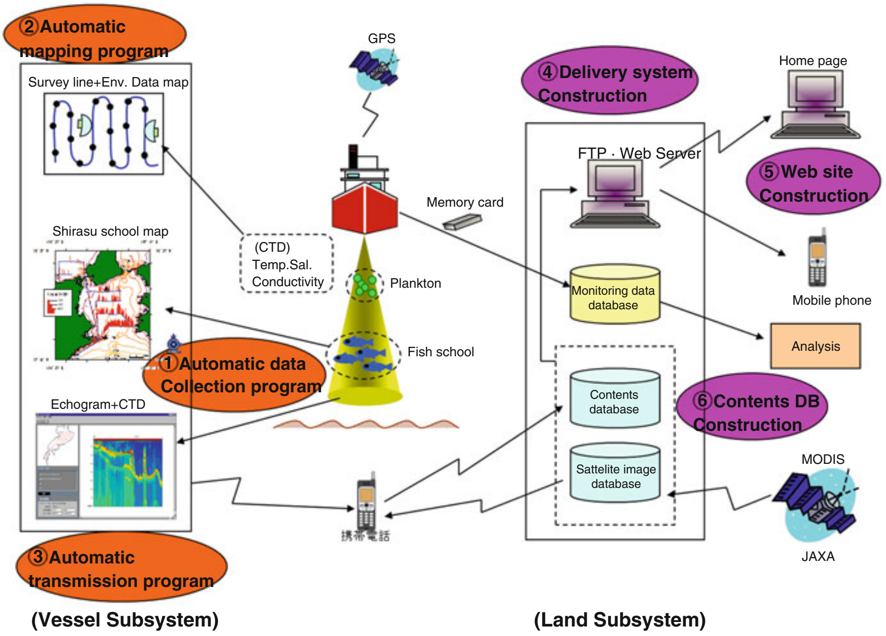

Fig. 8.10 Outline of the real-time shirasu school mapping system (Modified from Miyashita 2011a, b)

Figure 8.10 is an outline of a real-time shirasu school mapping system (Miyashita 2011a, b). This system comprises a research vessel and a land subsystem. Each subsystem is connected to a communication network. Three programs are operated by the research vessel subsystem: (1) automatic collection of shirasu school echo and sea surface temperature data, (2) automatic mapping of the collected data, and (3) automatic transmission of the maps created. The maps of the shirasu schools, echograms, vessel survey lines, and sea surface temperatures are processed. Additionally, there are three programs for transferring the shirasu school maps to the on-land subsystem: (4) content database (processed maps and satellite images), (5) map transport, and (6) an Internet-based interface.

Figure 8.11 shows a view of the portal site from the Internet-based interface for the real-time shirasu school mapping system operated from 2009 to 2013 in the coastal waters of western Japan (areas around Kii Channel and Bungo Channel, http://fishmap.ddo.jp/shirasu/). This portal site was developed using web-based GIS, and the interface can be operated easily by anyone clicking on the area polygons. A mobile site was also developed and is accessed by a hyperlink from the portal site (http://fishmap.ddo.jp/shirasu/mobile/). Shirasu fishermen can monitor the web site on a fishing vessel during the fishing.

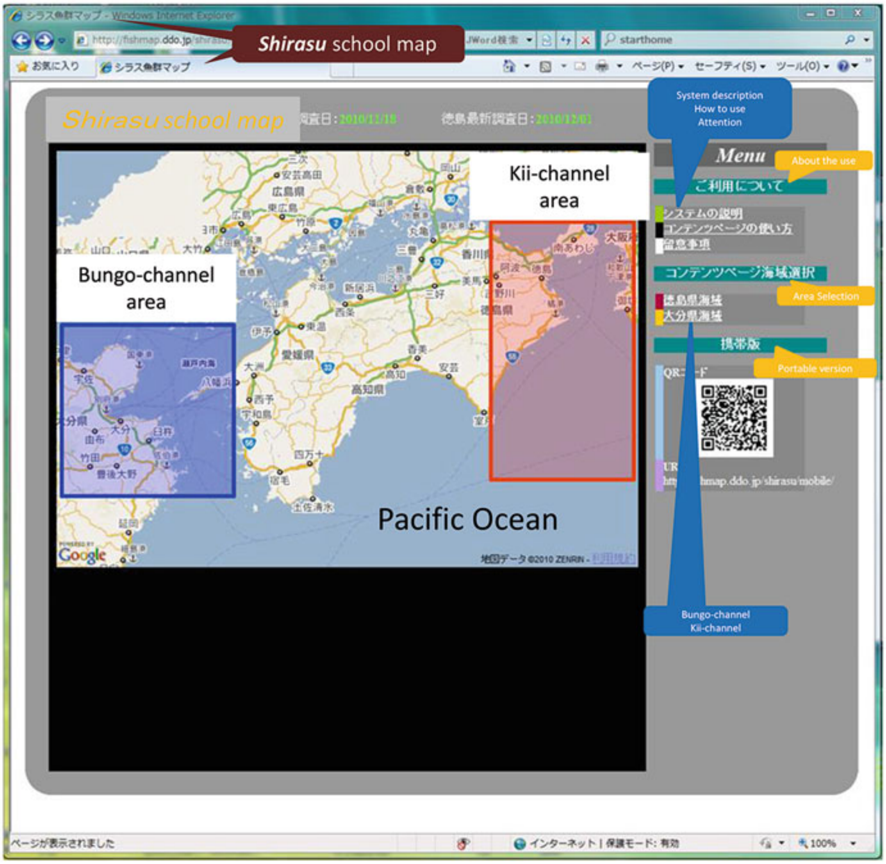

Fig. 8.11 Portal site for the real-time shirasu school mapping system, displayed in Japanese (Modified from Miyashita 2011a, b) http://fishmap.ddo.jp/shirasu/

Figure 8.12 is an example of a shirasu school map obtained from Bungo Channel, Japan. In the upper panel, the estimated individual shirasu densities and the measured sea surface temperatures are displayed using a color classification system on the vessel survey line. Individual shirasu density was estimated using target strength based on Itoh et al. (2011). Furthermore, satellite images, such as those for sea surface temperature or ocean color, can be overlaid with individual shirasu density. Original echograms (38 and 120 kHz) and the shirasu school echogram estimated using the automatic shirasu school discrimination system were also monitored, as shown in the lower panel of Fig. 8.12.

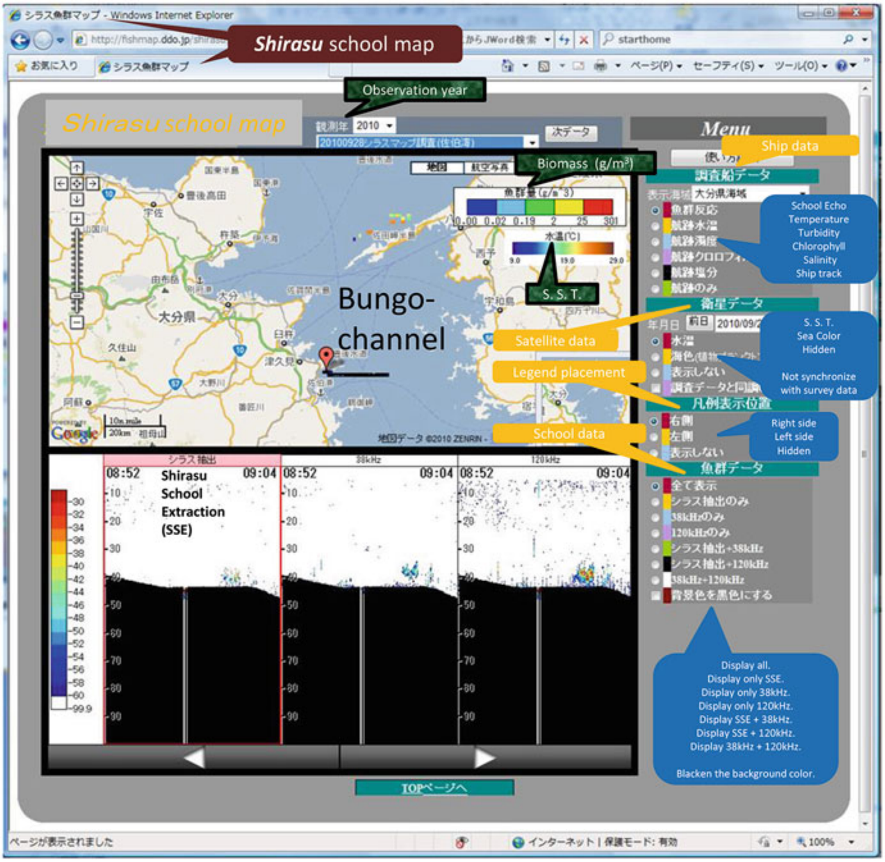

Fig. 8.12 Example of a shirasu school map obtained in the Bungo Channel, displayed in Japanese (Modified from Miyashita 2011a, b)

8.6.4 *Applying the Real-Time* Shirasu *School Mapping System*

The real-time shirasu school mapping system is one of the first practical applications of an interactive acoustic integrated system in the world. Fish schools were automatically discriminated based on valid theoretical information using a quantitative echo sounder system, and the processed data were shared through the Internet in real time.

This system is being improved through field applications and the comments of fishermen. However, the system relies on the operations of a research vessel in each area. Thus, it is difficult to spatially and temporally estimate many shirasu school distributions. To resolve this time problem, low-cost and compact quantitative echo sounders are expected to be introduced to commercial fishing vessels in the near future. Use of the system by fishermen will facilitate efficient management of fishing. Then, data monitoring using the system will assist researchers and managers in evaluating fisheries resources and taking better decisions.

8.7 Perspectives on an Acoustic Monitoring System for Ecosystem-Based Fisheries Management

Acoustic methods are essential to visualize aquatic organisms. There is no doubt that acoustic applications are the only means of quantifying live underwater resources in situ, particularly dynamic organisms such as small pelagic fish.

However, a few limitations must be overcome for further applications, such as stock assessments of aquatic living resources. For example, the data obtained from an acoustic survey are snapshots in the water column. Imagine that an acoustic survey is conducted continuously for 3 days. The estimated overall biomass from the survey may not be representative of the total biomass. The distributions of marine organisms change rapidly. Therefore, the biomass estimated in a survey is not equal to the actual standing stock. I suggest two means of overcoming this “snapshot” problem. The first would be to establish a continuous acoustic monitoring system, and the second would be to visualize and conceptualize ecological processes around target marine organisms in their ecosystem. Continuous acoustic monitoring surveys for target marine organisms during all seasons, and integration and conceptualization of ecosystem processes, would enable highly accurate estimation of biomass and the variability thereof following correct interpretation of distribution changes. Moreover, an acoustic monitoring system will enhance conceptualization of the ecological processes in marine ecosystems. The information provided will assist quantitative diagnosis of the health status of a marine ecosystem.

A new research field known as “marine acoustic ecology” has developed, as mentioned above (Miyashita 2006). The aims of marine acoustic ecology are to visualize marine organisms in situ and quantify ecological characteristics using acoustics science and technology. In this chapter, various applications of acoustics in ecological research were introduced as marine acoustic ecology. As the field of marine acoustic ecology advances due to a new and quantitative understanding of marine ecosystems, new methods of managing fisheries will be established. Management of fisheries resources using “marine acoustic ecology” (Miyashita 2006) will be recognized as an important part of the novel and (intensively) applied research field of marine ecosystem metrology.

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Chapter 9
Fisheries Stock Assessment

Kazuhiko Hiramatsu

Abstract Fisheries stock assessment methods are categorized into two types: survey-based methods, such as acoustic surveys and swept area and line transect methods, and model-based methods, such as virtual population analysis (VPA), surplus production models, DeLury method, and age-structured production models. The advantages and disadvantages of each are briefly reviewed, followed by a more extensive review and discussion of VPA and several extensions of it. Tuned VPA and statistical catch-at-age analysis have been used globally for many different stocks. An example of tuned VPA and its reliability and validity is presented based on experience in Japanese fisheries stock assessment. Stock assessment methods have been developing in two directions—simple and complex models. The former relates to the recent development of management strategy evaluation. An example of the latter approach is integrated analysis. Complex models are used for data-rich stock assessments and simple assessment models for management purposes and data-poor stock assessments.

Keywords Integrated analysis · Production model · Statistical catch-at-age analysis · Stock assessment · Tuned VPA · VPA

9.1 Introduction

How many fish are there in the sea, and how much can we sustainably catch? To answer these questions we conduct fisheries stock assessments. Because of the variability of fisheries stocks and uncertainties in data and biological parameters, specific considerations should be given to the fisheries stock assessments.

There are two fundamental fisheries stock assessment methods: survey-based methods, such as acoustic surveys and swept area and line transect methods, and model-based approaches, such as virtual population analysis (VPA), surplus

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Fisheries Science Series, https://doi.org/10.1007/978-4-431-56621-2_9

Table 9.1 Methods of stock assessment in Japanese waters

Assessment method	Number of stocks
VPA	28 (10)
DeLury method	1 (0)
Swept area method	8 (4)
Abundance index from survey	5 (3)
CPUE[a]	35 (2)
Catch	8 (1)

The number in parentheses indicates the number of stocks regulated with TAC

[a] Abundance index based on commercial catch and effort data

production models, the DeLury method, and age-structured production models (ASPM). The mark-recapture method is somewhat intermediate between these two. Catch per unit effort (CPUE) or total catch is also used as a relative index of abundance, when estimates of absolute stock size are difficult.

The Fisheries Agency and Fisheries Research Agency of Japan conduct stock assessments for 52 species (84 stocks) in Japanese waters (Fisheries Agency and Fisheries Research Agency of Japan 2014) using assessment methods detailed in Table 9.1. Half of the total allowable catch (TAC)-regulated stocks are assessed with VPA and seven stocks with research surveys. Several stocks are assessed on the basis of CPUE or simple catch information, while many non-TAC stock assessments rely on CPUE and catch data.

In this chapter, both survey-based and model-based assessment methods are briefly reviewed, and some discussion of the advantages and disadvantages of each method is provided. Then the VPA assessment method (frequently used and adopted worldwide) is extensively reviewed and discussed based on Japanese fisheries stock assessment experience for estimating allowable biological catch (ABC) to determine TAC. Finally, future perspectives on stock assessment methods are discussed.

9.2 Overview of Stock Assessment Methods

To begin with, the characteristics of survey-based assessment methods and mark-recapture methods are discussed, followed by a review of several model-based assessment methods. Despite potential biases, model-based methods are widely used in stock assessments.

9.2.1 Characteristics of Survey-Based Assessment Methods

Typical survey-based assessment methods are acoustic surveys, the swept area method, and the line transect method. In each method, surveys are conducted on randomly (or systematically) chosen courses. An estimate of total stock size is obtained by multiplying the average density estimated from the surveys by the total area of the stock distributed. Survey-based assessment usually is based on sampling design, and the precision of estimated stock size can be quantified relatively easily by using sampling theory. However, these methods are costly, especially for widely distributed species. In contrast, fishery data can be obtained from a wide area at relatively low cost. It should be noted that the fishery is not a scientific survey but a commercial activity, and hence care should be exercised when analyzing fishery data. Further details on survey-based assessment methods can be found in Chaps. 7 and 8 in this book and other fisheries texts, such as Jennings et al. (2001).

9.2.2 Mark-Recapture Methods

For exploited stocks, fish are usually tagged aboard a research vessel, with tagged fish being recaptured by a fisher. In the simplest case, abundance N can be estimated by

$$N = \frac{nC}{m}, \tag{9.1}$$

where n is the number of tagged fish, C is catch in number, and m is the number of tagged fish in the catch. The underlying assumptions for this method are that tags are not lost and are reported correctly on recapture; that there is no recruitment, mortality, immigration, or emigration; that all tagged and untagged fish have an equal probability of being recaptured; and so forth. Because assumptions would often be violated, many extensional models where some assumptions are released have been developed and applied.

9.2.3 Surplus Production Models

Surplus production models have an advantage over other model-based methods in data-poor situations. Basic data in this model are catch and effort (or abundance index). The simplest form is

$$\frac{dB_t}{dt} = rB_t\left(1 - \frac{B_t}{K}\right) - qB_tX_t, \tag{9.2}$$

where B_t is the biomass at time t, r is the intrinsic rate of population increase, K is the carrying capacity, q is the catchability coefficient, and X_t is the fishing effort at time t.

If parameters like r and K are given, several management reference points can be calculated as follows:

$$MSY = \frac{rK}{4}, \tag{9.3}$$

$$F_{MSY} = \frac{r}{2}, \tag{9.4}$$

$$B_{MSY} = \frac{K}{2}, \tag{9.5}$$

where MSY is maximum sustainable yield, F_{MSY} is the fishing mortality coefficient corresponding to MSY, and B_{MSY} is biomass at MSY. There are several ways to estimate parameters in Eq. (9.2) from catch and effort data. It is useful to understand the procedures and assumptions of statistical estimation using the surplus production model.

Equilibrium Method

If we assume that the stock is in equilibrium, then Eq. (9.2) is

$$\frac{dB_t}{dt} = rB_t\left(1 - \frac{B_t}{K}\right) - qB_tX_t = 0, \tag{9.6}$$

and

$$B_t = K - \frac{qK}{r}X_t. \tag{9.7}$$

Assuming

$$qB_t = CPUE_t = \frac{Y_t}{X_t}, \tag{9.8}$$

where Y_t is catch in weight at time t, Eq. (9.7) is

$$CPUE_t = qK - \frac{q^2K}{r}X_t, \tag{9.9}$$

From the linear regression of $CPUE_t$ on X_t, we can obtain qK and q^2K/r. MSY can be calculated as

$$MSY = \frac{rK}{4} = \frac{(qK)^2/(q^2K/r)}{4}. \tag{9.10}$$

The advantage of this method is its simplicity in calculation; its disadvantages are its unrealistic equilibrium assumption and impossibility of estimating absolute abundance.

Multiple Regression Method

Equation (9.2) can be discretized as follows:

$$B_{t+1} = B_t + rB_t\left(1 - \frac{B_t}{K}\right) - qB_tX_t. \tag{9.11}$$

Using Eq. (9.8),

$$CPUE_{t+1} = qY_t + (1 + r)CPUE_t - \frac{r}{qK}CPUE_t^2. \tag{9.12}$$

From the multiple regressions of $CPUE_{t+1}$ on Y_t, $CPUE_t$, and $CPUE_t{}^2$, we can obtain q, r, and K. We can also estimate abundance as $B_t = qCPUE_t$. This method assumes that Eq. (9.8) exactly holds but Eq. (9.11) has an error. Error in the population dynamics model is called process error. For precise parameter estimation, a strong contrast between Y and $CPUE$ is desirable. An alternative formula for Eq. (9.12)

$$\frac{CPUE_{t+1}}{CPUE_t} = (1 + r) - \frac{r}{qK}CPUE_t - qX_t, \tag{9.13}$$

also can be used for the regression analysis (Hilborn and Walters 1992).

Time Series Fitting

In contrast to the previous model, we assume that Eq. (9.11) exactly holds and observed CPUE in Eq. (9.8) has an observation error η:

$$CPUE_t = \frac{Y_t}{X_t} = qB_t + \eta. \tag{9.14}$$

In this case, unknown parameters like B_0, q, r, and K can be estimated by minimizing the sum of square SS

$$SS = \sum\nolimits_t \left(\frac{Y_t}{X_t} - qB_t\right)^2, \tag{9.15}$$

where B_t is calculated from Eq. (9.11). This is a nonlinear regression problem, and hence an optimization method is needed to estimate model parameters.

In some cases, parameters are highly correlated, and unrealistic parameter estimates may be obtained. Since both observation and process errors exist in the actual situation, a method for estimating a model with both errors has been developing. Surplus production models have not recently been used in stock assessment by the Fisheries Agency and Fisheries Research Agency of Japan, possibly because of this difficulty in estimation. Further details on surplus production models can be found in most fisheries texts, such as Hilborn and Walters (1992) and Haddon (2011).

9.2.4 DeLury Method

The DeLury method, also known as the "depletion method," uses basic catch and effort data. Fundamental assumptions of this method are that the stock is closed and the natural mortality is negligible. Using decreasing trend in CPUE, stock size can be estimated assuming that the cause of decline in stock size is catch only. The following two types of model are used:

$$C_i = qX_iN_i = qX_i\left(N_0 - \sum\nolimits_i C_i\right), \tag{9.16}$$

$$CPUE_i = qN_i = qN_0 \exp\left(-q\sum\nolimits_i X_i\right) \tag{9.17}$$

The initial stock size N_0 and q are unknown parameters that are estimated using linear regression or maximum likelihood methods. Because of the strict assumptions, the application of DeLury method is limited. The Japanese sandeel (*Ammodytes personatus*) stock in Ise and Mikawa Bay is assessed with this method (Yamamoto and Shibuno 2014).

9.2.5 VPA

VPA has been developed and used since the late 1960s. Basic data of VPA are catch at age. The relation between $N_{a,y}$, the number of fish at age a in year y, and $N_{a+1,y+1}$ can be written as

$$\begin{aligned} N_{a,y} &= N_{a+1,y+1}\exp\left(M + F_{a,y}\right), \\ C_{a,y} &= \frac{F_{a,y}}{F_{a,y} + M} N_{a+1,y+1}\left(\exp\left(M + F_{a,y}\right) - 1\right), \end{aligned} \tag{9.18}$$

or, assuming catches are made in the middle of the year, Eq.(9.18), described:

$$N_{a,y} = N_{a+1,y+1}\exp(M) + C_{a,y}\exp(M/2), \tag{9.19}$$

where M is the natural mortality coefficient, $F_{a,y}$ is the fishing mortality coefficient at age a in year y, and $C_{a,y}$ is the catch in number at age a in year y. M is assumed to be known. If we know $N_{a+1,y+1}$, then we can calculate $N_{a,y}$, $N_{a-1,y-1}$, . . ., $N_{0,y\text{-}a}$ using Eq. (9.18) or (9.19) by recursive procedure. Usually, instead of N, the Fs in the most recent year or at the oldest age are assumed and referred to as terminal F.

An advantage of this method is that N at age and F at age can be calculated. Using these estimates, the relationship between stock and recruitment and age-dependent selectivity can be obtained and used for fishery management. Detailed descriptions of VPA are presented in Sect. 9.3.

9.2.6 Age-Structured Production Model (ASPM)

Basic ASPM data are total catch and abundance index. Because the population dynamics model in ASPM is age structured, selectivity at age is needed for the assessment. Furthermore, a stock and recruitment model g and M are also needed for the calculation. Population sizes are given by

$$N_{a+1,y+1} = N_{a,y}\exp\left(-M - s_a f_y\right), \tag{9.20}$$

$$N_{0,y+1} = g\left(SSB_{y+1}\right), \tag{9.21}$$

where SSB_y is the spawning stock biomass in year y, s_a is the selectivity, and f_y is the fishing mortality coefficient at age of selectivity 1. f_y is calculated from

$$Y_y = \sum\nolimits_a w_a \frac{s_a f_y}{M + s_a f_y} N_{a,y}\left\{1 - \exp\left(-M - s_a f_y\right)\right\}. \tag{9.22}$$

Unknown parameters such as s_a and parameters in the stock-recruitment relationship are estimated by minimizing the following objective function:

$$SSQ = \sum\nolimits_y \left(I_y - qB_y\right)^2 \tag{9.23}$$

where I_y is the abundance index in year y, q is coefficient, and B_y is model estimates of abundance corresponding to I_y. When age structure is not negligible in the population dynamics, but estimation of age composition of catch is difficult, ASPM may be used as an intermediate assessment method between age-structured VPA and age-aggregated production model.

Basic data, population model, and basic output of the aforementioned models are summarized in Table 9.2. A family tree of model-based assessment methods is presented in Fig. 9.1.

Table 9.2 Basic data, population model, and basic output of each assessment method

Method	Basic data	Population model	Basic output
Production model	Catch, effort	Age combined	MSY, biomass
VPA	Catch at age	Age structured	Number at age
Tuned VPA	Catch at age, abundance index	Age structured	Number at age
DeLury	Catch, effort	Age combined	Initial biomass
ASPM	Catch, abundance index	Age structured	Number at age

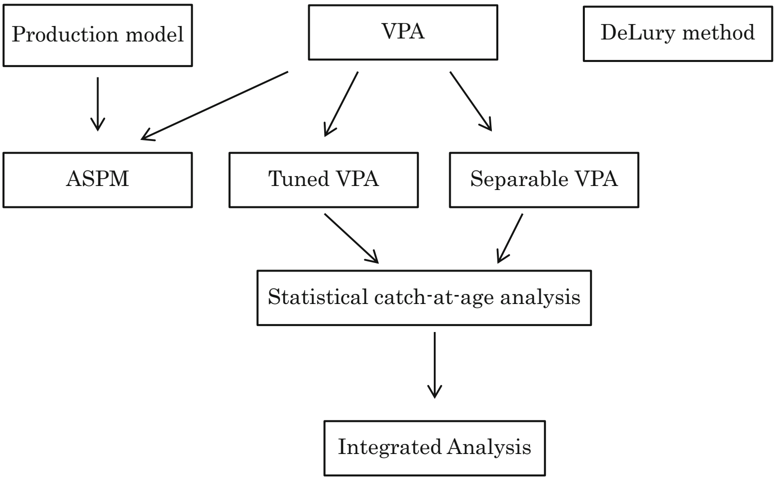

Fig. 9.1 Family tree of model-based assessment methods

Table 9.3 An example of catch-at-age table used for VPA

	Year										
Age	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010
0	1070	784	21	150	324	217	167	795	408	117	206
1	255	1458	467	413	365	81	576	456	159	621	406
2	377	560	137	128	65	18	42	219	32	29	206
3	322	195	49	74	12	30	22	21	14	11	14
4	235	103	26	31	8	39	12	8	2	6	10
5	89	71	17	12	4	19	3	3	1	2	8

9.3 Details of VPA

In this section, VPA and extensions of it are reviewed. Unfortunately, the terminology of VPA and related methods is confusing, so caution must be exercised when reading other papers.

9.3.1 Basic VPA

Let's assume that we have catch-at-age data from years 2000 to 2010 and ages 0 to 5 (Table 9.3) and that natural mortality M is known. Assuming terminal Fs, i.e. Fs on age 5 or Fs on year 2010, number at age can be calculated using Eq. (9.18) or Eq. (9.19). Terminal Fs are assumed arbitrary or based on the assumptions. Typical assumptions are that terminal Fs are set at the same value as F of the previous year, or average of previous years at the same age, or at the younger age in the same year. For example, in the case of Table 9.3, $F_{5,y} = F_{4,y}$ and $F_{a,2010} = F_{a,2009}$ are assumed. The former assumption means that selectivity at older age are the same, and the latter means that fishing mortality is constant from 2009 to 2010. Using these assumptions, a unique number at age can be determined. However, these assumptions do not always hold, for example, because of variations in fishing effort. Moreover, the intrinsic assumption of VPA that does not hold in practice is that the catch-at-age data are precise. To overcome these difficulties, a variety of extensions of VPA have been developed.

9.3.2 Extensions of VPA

Tuned VPA

The assumption that terminal F equals F of previous years is not always applied. Stock size in the most recent year is important for stock management; violation of this assumption can lead to false management. One extension of VPA is to estimate terminal Fs so as to minimize the difference between abundance indices qB, which are predicted by (or calculated from) VPA and observed indices I:

$$SSQ = \sum\nolimits_y \left(I_y - qB_y\right)^2 \tag{9.24}$$

This type of VPA is called “tuned VPA” or “ADAPT VPA.” Terminal Fs are estimated using an optimization method. Integrating an abundance index into a VPA is relatively straightforward if there is a single abundance index but becomes more complicated if there are several indices due to index weighting. Standardized CPUE is a typical abundance index used for tuned VPA. Maunder and Punt (2004) reviewed recent developments in standardizing CPUE.

Separable VPA

Although catch-at-age data have observation errors, VPA assumes that no error is included in catch at age. The other extension of VPA is related to consideration of error in catch-at-age data. The fishing mortality coefficient at age a in year y, $F_{a,y}$, is assumed to be the product of year-dependent f_y and age-dependent s_a:

$$F_{a,y} = s_a f_y \tag{9.25}$$

This assumption is called separability, and VPA using separability assumption is called separable VPA. Historically, separable VPA had been developed before the introduction of tuned VPA. Unknown parameters in separable VPA are s_a, f_y, $N_{0,y}$, and $N_{a,y0}$, all of which are estimated from minimization of the following objective function:

$$SSQ = \sum_y \left(C_{a,y} - \widehat{C}_{a,y} \right)^2, \tag{9.26}$$

where $C_{a,y}$ is catch-at-age data and $\widehat{C}_{a,y}$ is VPA predicted catch calculated from

$$\widehat{C}_{a,y} = \frac{s_a f_y}{M + s_a f_y} N_{a,y} \left\{ 1 - \exp\left(-M - s_a f_y \right) \right\}, \tag{9.27}$$

$$N_{a+1,y+1} = N_{a,y} \exp\left(-M - s_a f_y \right). \tag{9.28}$$

Parameters are estimated using an optimization method. A criticism of this method is that there are too many unknown parameters.

Statistical Catch-at-Age Analysis

Tuning is also introduced to the separable VPA. In this case, objective function is given by

$$SSQ = \sum_y \left(C_{a,y} - \widehat{C}_{a,y} \right)^2 + w \sum_y \left(I_y - q\widehat{B}_y \right)^2, \tag{9.29}$$

where w is a weighting parameter and usually defined externally. This method is also referred to as integrated catch-at-age analysis. Many extensions of this approach are possible: for example, fishing mortality coefficient estimated from the mark-recapture method or fishing effort data can be introduced in the objective function, and selectivity s_a can be extended to year-dependent selectivity, $s_{a,y}$. It should be noted that the latter case is considerably more computationally demanding. Although statistical catch-at-age analysis has not been used in stock assessment by the Fisheries Agency and Fisheries Research Agency of Japan, it has been widely used elsewhere.

Length-Based VPA

For some species such as crustaceans, age determination is difficult. Length-based VPA uses catch in number at length instead of catch in number at age. The number of fish at length can be calculated in a manner similar to the VPA using the growth model (Quinn and Deriso 1999).

9.3.3 An Example of Tuned VPA

Many TAC stocks in Japan are assessed using tuned VPA methods. Taking the walleye pollock (*Gadus chalcogrammus*) assessment from the northern Sea of Japan stock of as an example, tuned VPA was conducted as follows (Chimura et al. 2014).

Catch in number at age and spawning stock size estimates from acoustic survey are the basic data. Age-dependent natural mortality coefficient (0.3/year for age 2 and 0.25/year for ages older than 2), weight at age, and fecundity at age are assumed to be known. The youngest fish in the analysis is aged 2, and ages 10 and over are treated as a plus group. The number of fish from ages 2 to 8 in year y is given by

$$N_{a,y} = N_{a+1,y+1}\exp(M_a) + C_{a,y}\exp(M_a/2) \tag{9.30}$$

and at ages 9 and 10+ by

$$N_{a,y} = \frac{C_{a,y}}{C_{9,y} + C_{10+,y}} N_{10+,y+1}\exp(M_a) + C_{a,y}\exp(M_a/2). \tag{9.31}$$

The number of fish at ages 5 to 10+ in the most recent year (2012) is given by

$$N_{a,2012} = \frac{C_{a,2012}\exp(M_a/2)}{1 - \exp(-F_{a,2012})}. \tag{9.32}$$

The number of fish at ages from 2 to 4 in 2012 is calculated from assumed recruitment by the forward calculation. F at ages from 5 to 9 in 2012 is given by

$$F_{a,2012} = \frac{1}{5}\sum\nolimits_{y=2007}^{2011} \frac{F_{a,y}}{F_{10+,y}} F_{10+,2012} (5 \le a \le 8), \tag{9.33}$$

$$F_{9,2012} = F_{10+,2012} \tag{9.34}$$

$F_{10+,2012}$ is an unknown parameter and estimated from minimizing the objective function

$$SSQ = \sum\nolimits_y \left(\ln\left(I_y\right) - \ln\left(qSSB_y\right)\right)^2, \tag{9.35}$$

where I_y is the spawning stock size estimates from acoustic survey, q is a proportionality coefficient, and SSB_y is the VPA predicted spawning stock size. Although q is also an unknown parameter, it can be obtained analytically.

There are many ways to estimate the most recent Fs (Fisheries Agency and Fisheries Research Agency of Japan 2014), such as independently estimating the F at each age using age-disaggregated CPUE as tuning indices (Tsushima stock of chub mackerel) and estimating F overall by tuning using selectivity derived from untuned VPA (Pacific stock of walleye pollock). Ichinokawa and Okamura (2014) developed integrated software that covers all VPA methods used for TAC-regulated stocks in Japan. Important Japanese fisheries stocks including walleye pollock and chub mackerel are assessed every year. The assessment results (in Japanese) are published on the website (http://abchan.fra.go.jp/). The status of these stocks are reviewed by Ichinokawa et al. (2017).

9.3.4 Reliability and Validity of VPA

It is not straightforward to evaluate the reliability and validity of VPA estimates. Several empirical methods and statistical methods such as bootstrap, Bayes, and the profile likelihood method are considered and applied in actual assessments.

Empirical Methods
In VPA, estimates in the early years are considered to be more precise than estimates in recent years. The comparison of previous with the latest estimates is a simple evaluation of VPA results, with the discrepancy between them identifying estimate bias or error. Figure 9.2a shows stock size estimates for Pacific stock of walleye pollock from 2007 to 2013 (Funamoto et al. 2008; Mori and Funamoto 2009; Mori et al. 2010, 2011, 2012, 2013, 2014). Year by year, biomass estimates were revised upward. Figure 9.2b shows recruitments from 2004 to 2006 estimated in the 2006 to 2013 assessments (Funamoto et al. 2007, 2008; Mori and Funamoto 2009; Mori et al. 2010, 2011, 2012, 2013, 2014). In the 2006 assessment, recruitment in 2005 was less than in 2004. After that, estimates of recruitment in 2005 increase in a linear manner, and the 2005 year class is a dominant year class in the recent assessment. This is the cause of bias in biomass estimates.

As methods used in assessment may have changed from one year to another, a retrospective analysis is conducted to evaluate reliability of the present method. Such an analysis involves omitting data from the most recent year. For example, in the case of Table 9.3, we first conduct assessment to 2009 ignoring 2010 data, then conduct to 2008 ignoring 2009 and 2010 data, and so forth. A figure similar to Fig. 9.2 can be generated from the retrospective analysis. An upward or downward trend in estimates (a retrospective pattern) indicates the potential assessment bias. A systematically biased estimate of stock size can lead to inappropriate management advice for several consecutive years. Causes of retrospective patterns and a method for adjusting estimates have been investigated (Deroba 2014; Hurtado-Ferro et al. 2015).

Sensitivity analysis is often used to investigate the effect of uncertainty in parameter values, data sets, and model structure. For example, although the natural mortality coefficient is an important parameter for VPA, its uncertainty is usually high. Hence, VPA with different natural mortality coefficients is conducted in stock assessments in Japan.

Statistical Methods
The bootstrap method is computer-intensive and uses resampling of data to generate sampling distribution of an estimate. Standard errors and confidence intervals can be calculated from resampling distribution. A typical example of bootstrap for tuned VPA follows. (1) Obtain point estimates. (2) Residuals between observed and predicted indices are calculated from Eq. (9.24). (3) Resample the residuals with replacement, and add to the predicted values to create a new data set. (4) Tuned VPA

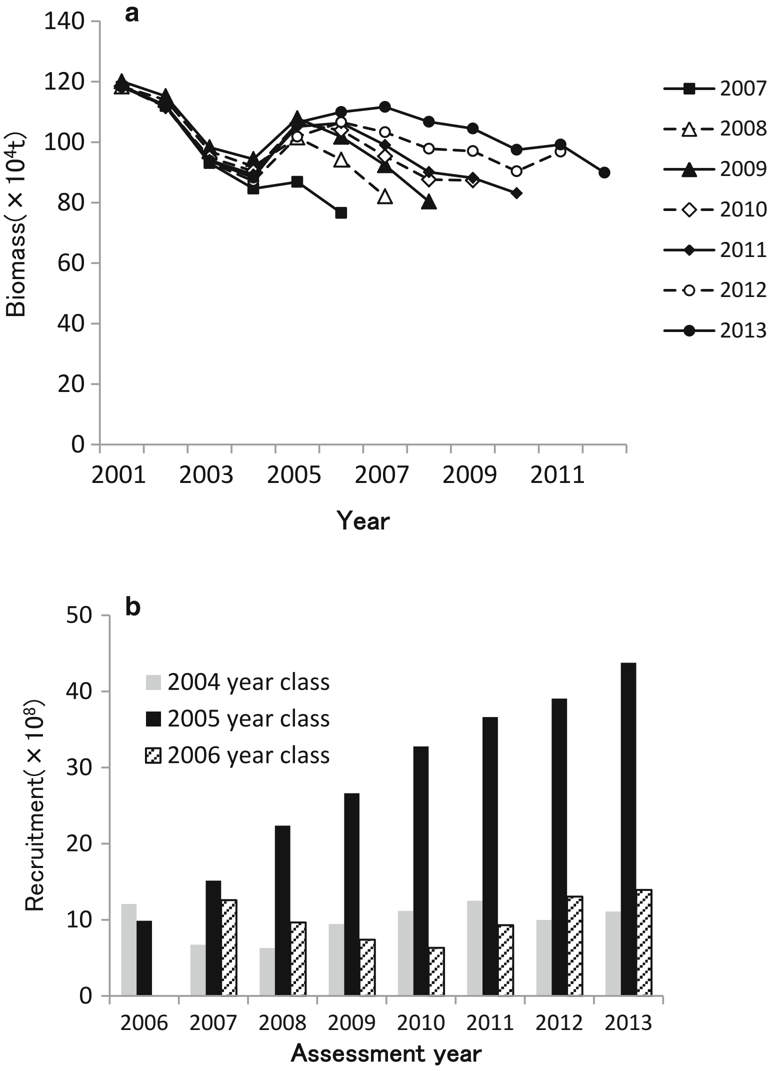

Fig. 9.2 (**a**) Pacific walleye pollock (*Gadus chalcogrammus*) stock size estimates based on assessments from 2007 to 2013. (**b**) Recruitments of Pacific walleye pollock stock for 2004 to 2006 cohorts estimated yearly from 2006 to 2013

is conducted using new abundance indices, and point estimates are obtained. (5) Repeat above process hundreds or thousands times, and obtain resampling distribution of estimates, in this case, stock size estimates. The bootstrap method has been used in various stock assessment methods to construct confidence intervals.

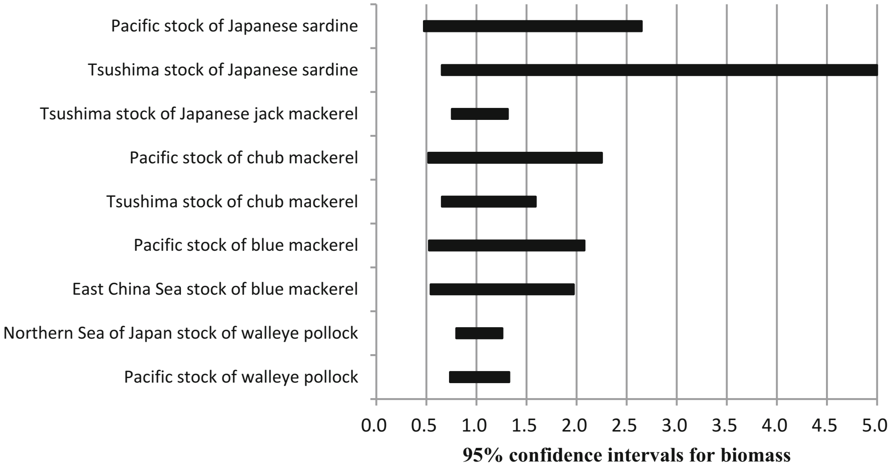

Fig. 9.3 Comparison of 95% confidence interval for biomass in 2007. Point estimates are set at 1 (Reproduced from Nakayama and Hiramatsu 2010)

The profile likelihood method can also be used to generate confidence intervals. To apply this method, the objective function should be expressed in the likelihood function. For example, the likelihood function for Eq. (9.35) is

$$L\left(F_{10+,2012}, q, \sigma^2\right) = \prod\nolimits_y \left\{ \frac{1}{2\pi\sigma^2} \exp\left(-\frac{\left(\ln\left(I_y\right) - \ln\left(qSSB_y\right)\right)^2}{2\sigma^2} \right) \right\}, \tag{9.36}$$

where L is the likelihood function and σ^2 is the variance of $\ln I_y$. The 95% confidence interval of $F_{10+,2012}$ can be calculated from

$$-2\left(\ln L\left(F_{10+,2012}, \hat{q}, \hat{\sigma}^2\right) - \ln L\left(\hat{F}_{10+,2012}, \hat{q}, \hat{\sigma}^2\right)\right) \leq \chi^2(1, 0.05), \tag{9.37}$$

where the hat (^) denotes the maximum likelihood estimates and $\chi^2(1,0.05)$ is the upper 5th percentile of a chi-square distribution with one degree of freedom. Hiramatsu (2009) and Nakayama and Hiramatsu (2010) applied this method to the VPA used for assessment of TAC-regulated species in Japan and evaluated the reliability of stock size estimates. Figure 9.3 indicates approximate 95% confidence intervals for each biomass in 2007. For comparison, point estimates are set at 1. Confidence intervals for some stocks are large and indicate poor precision. The VPA software developed by Ichinokawa and Okamura (2014) contains both the bootstrap method and the profile likelihood method and can compare confidence intervals.

Bayesian statistics have been applied to various stock assessment methods in recent years. The advantage of these statistics is that they take into account the uncertainties in parameters directly and can use the information of other species or expert judgment as a prior distribution.

9.3.5 Application to the Management

From VPA, we can obtain number at age and F at age. We can also obtain historical trends in biomass, the stock and recruitment relationship, selectivity, and so forth. Furthermore, several biological reference points such as F_{MSY}, B_{MSY}, and F_{med} can be derived from the stock and recruitment relationship and the selectivity.

F_{med} is the F value which satisfies the following equation:

$$\frac{1}{RPS_{med}} = \sum\nolimits_{a=0}^{T} m_a w_a \exp\left(-\sum\nolimits_{t=0}^{a-1} (s_t F + M_t)\right), \tag{9.38}$$

where T is the life span, w_a is the weight at age, m_a is the maturity at age, and RPS_{med} is the median of recruitment per spawning stock derived from the stock assessment. Similarly, F_{MSY} is given by the F value which maximizes the yield Y:

$$Y = \sum\nolimits_{a=0}^{T} R_e w_a \exp\left(-\sum\nolimits_{t=0}^{a-1} (s_t F + M_t)\right) \frac{s_a F}{s_a F + M} \{1 - \exp(-(s_a F + M_a))\}, \tag{9.39}$$

where R_e is the equilibrium recruitment under the assumed stock and recruitment relation.

9.4 Perspective

A variety of stock assessment methods have been developed and recently used in stock assessment and management. ICES (2012) classified assessment methods into eight categories: catch-only models, time series models (abundance index), biomass dynamic models (production models), delay-difference models, age-structured production models, VPA-based approaches, statistical catch-at-age models, and integrated analysis models (see below). However, the advantages and disadvantages of each have not been fully evaluated. A systematic simulation for evaluating the stock assessment methods was conducted under various conditions (Deroba et al. 2015). Thirty different assessment models, including VPA, statistical catch-at-age analysis, and surplus production model, were applied to data from representative fish stocks. Results are still preliminary but indicate that similar types of models tend to perform similarly.

Stock assessment methods seem to have developed in two opposing directions—simple and complex. The former relates to the recent development of management strategy evaluation (MSE; see Chap. 11, in this book). MSE reveals that simple assessment models can be more effective than complex models from a stock management point of view (Geromont and Butterworth 2015).

An example of the latter approach is integrated analysis (IA), which is a statistical method that combines several sources of information into a single analysis (Maunder and Punt 2013). As there are often inadequate data to reliably estimate stock sizes, it is necessary to combine several sources of data. Data can be combined by constructing a joint objective function or a joint likelihood function. The actual situation is more complicated than typical assessment model assumptions, i.e., selectivity may vary in time and the abundance index may not be linearly related to the biomass. Accommodating these assumptions makes the model more complicated. Maunder and Punt (2013) reviewed the history and recent development of IA and discussed its pros and cons. They pointed out several advantages to using the raw data with IA instead of the summarized data in traditional analysis. IA is computationally intensive and usually conducted using a software package like Stock Synthesis (Methot and Wetzel 2013), MULTIFAN-CL (Fournier et al. 1998), or A-SCALA (Maunder and Watters 2003), which enable a fisheries scientist unfamiliar with coding to conduct IA. However, the reality is that experience and skill are required to implement the assessment with IA in practical applications.

Development of MSE also affects the stock assessment methods. Using an operating model used for generating the true population dynamics and sampled data in the MSE, the performance of stock assessment models can be evaluated. Simple assessment methods are suitable for management procedures, partly because complex models such as IA are unfit for time-consuming simulation, but mainly because the simple model is robust to uncertainties. The simple model can be applied in data-poor situations and is relatively easy to understand by stakeholders.

These opposing trends—simple and complex—may not be a contradiction. They may in fact complement each other. On one hand, complex models are used for data-rich stock assessments, and on the other, simple assessment models are used for the management purpose and for data-poor stock assessments.

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Part III
Management Models

Chapter 10
Part III Description

Takashi Yamakawa

Abstract Part III discusses management models. Chapter 11 reviews the management strategy evaluation (MSE) framework, in which the performance of harvest control rules (HCRs) or management procedures (MPs) are continually evaluated using operating models (OMs). Then, the authors introduce the fish stock management system and an example of the HCR development process in Japan. Chapter 12 reviews the ecosystem models developed and employed so far in fisheries science worldwide. The authors also propose a new ecosystem assessment model for use in data-limited situations and conduct a simple simulation test to investigate the performance of the new model, applying it to North Pacific multispecies data.

In order to realize sustainable fisheries, all information related to the dynamics (Part I) and the estimated states of target stocks derived from data collected by repeated monitoring (Part II) should be integrated and directed toward planning effective fisheries management actions. When, where, and how should the fishing effort be devoted to stocks? How should the amounts of catches from the stocks be controlled and allocated spatiotemporally? What harvest strategy should be planned to fulfill the management objective by avoiding risk in a broad range of uncertainties inherent in the natural system?

Management science in fisheries has recently made great progress as a systematic approach to implementing a system for such decisions by integrating all related information with the aid of computer capacities and applications to conduct intensive simulations. The management strategy evaluation (MSE) framework represents a systematic approach, and the number of examples reported in the literature is growing. Chapter 11 reviews the MSE framework, in which the performance of harvest control rules (HCRs) or management procedures (MPs) are continually evaluated through intensive computer simulation testing using operating models (OMs) on virtual stock dynamics and information from repeated monitoring of the

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status of target stocks. In this framework, sequential information update is an essential process in feedback control and for adaptive management of stocks under various uncertainties. Next, following the review of the MSE approach, the authors introduce the fish stock management system and an example of the HCR development process in Japan in Chap. 11, which seldom appear in the English literature until now. However, it would be impossible to review all of the current developments in this fast-evolving research field within the limited space of this book. The text in this book will recommend specialized books and journals that exclusively focus on this theme for readers who are more concerned about this subject (e.g., Rice and Connolly 2007; Bence et al. 2008; Holland 2010; Punt et al. 2014; Edwards and Dankel 2016; Punt et al. 2016).

In recent years, the concerns in fisheries management have been evolving from conventional single-species management to an ecosystem approach to fisheries (EAF) or ecosystem-based fisheries management (EBFM), which pursues sustainable fisheries while conserving ecosystem integrity. The EAF and EBFM account for the community structure, interactions among species, and environmental influences in the ecosystem and try to receive valuable ecosystem services from the natural system continually. Chapter 12 reviews the ecosystem models developed and employed so far in fisheries science worldwide: Ecopath with Ecosim, Atlantis, MSVPA, GADGET, and so on. These models are generally "data-hungry" and require intensive data collection and/or many assumptions related to the complicated interactions among species. In practical fisheries management, however, data to evaluate ecosystem status are generally limited. Thus, the field needs simple models to assess ecosystems that only require accessible data and minimal and realistic assumptions for rapid and robust global ecosystem evaluation. In Chap. 12, the authors propose a new ecosystem assessment model for use in even data-limited situations and conduct a simple simulation test to investigate the performance of the new model, applying it to North Pacific multispecies data.

In the present book, we could not mention or discuss case studies of actual ecosystem management currently underway. This is partly because these activities are very diverse, and they are now in the process of development and seeking for innovative and effective solutions. Balanced, less-selective harvesting in body size and species while conserving community structure and functions (Kolding et al. 2016), using network systems of marine protected areas (MPAs) (e.g., Almany et al. 2009), and coastal spatial zoning including tenure system based on territorial use rights (e.g., Yagi et al. 2010), among others, will be promising research areas. Since there are quite a few publications related to EAF and EBFM (e.g., Garcia et al. 2003; Plagányi 2007; Bianchi and Skjoldal 2008; Link 2010; Glazier 2011; Belgrano and Fowler 2011; Christensen and Maclean 2011), readers are also recommended to refer to them in addition to this book.

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Chapter 11
Harvest Control Rules

Seiji Ohshimo and Takashi Yamakawa

Abstract Harvest control rules (HCRs) and management procedures (MPs) are used after stock assessment to determine the desirable amount of catch to achieve specified management objectives. These rules play a core role in linking the scientific stock assessment and practical fisheries management activities. Robust HCRs with respect to uncertainties are required for sustainable resource management, especially in light of the uncertainties inherent with fluctuating environmental conditions and climate systems. HCRs have to be evaluated to ensure that they maintain optimal biological production, stock size, and economic efficiency, but these objectives are not always compatible. Recently, a management strategy evaluation (MSE) framework for fisheries resource management has been developed that creates operating models (OMs) to simulate virtual population dynamics and evaluates the performance of the HCRs based on different strategies. We discuss feedback HCRs, which are one of the most effective strategies to manage fluctuating fisheries stocks. Feedback HCRs are empirical approaches to adjusting fishing intensity by sequentially updating information through the continuous monitoring of the state of the target stocks in response to present management activities. We also show a case study to test the performance of feedback HCRs with the aim of applying them to manage Japanese fish stocks and recommend allowable biological catches (ABCs).

Keywords Adaptive management · Climate change · Feedback control · Harvest control rule · Management objective · Management procedure · Management strategy evaluation · Operating model

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11.1 Background

The demand for fish as a food resource has steadily increased. According to an FAO report (FAO 2014), the proportion of marine fish stocks fished within biologically sustainable levels declined from 90% of assessed stocks in 1974 to 71.2% in 2011, when 28.8% of stocks were estimated as fished at a biologically unsustainable level and, therefore, overfished. Natural resource management practices are littered with examples of overexploitation and ineffectual management, leading to the loss of both biodiversity and human welfare (Hauser et al. 2002; Milner-Gulland 2011; Watson and Pauly 2001). Thus, the management of marine fisheries needs to undergo dramatic change in the new millennium in response to the well-documented evidence of global overfishing and the general depletion of commercial fish stocks (Caddy and Seijo 2005).

Fluctuations in ecosystems and fisheries resources have been well documented (e.g., Francis and Hare 1994; Chavez et al. 2003). The ability of management strategies to achieve fisheries management goals is impacted by environmental variation and, therefore, also by global climate change (Punt et al. 2014). Global climate change and ocean warming pose new challenges to populations that rely on the oceans by modifying the distribution and productivity of marine and freshwater species, affecting biological processes and altering food webs (Barange et al. 2014). These issues serve to highlight the immediate need to develop adaptation plans to minimize the effect of warming (Cheung et al. 2013). Thus, coping with the fluctuations in fisheries resources stemming from climate change and enabling adaptive and sustainable utilization of these resources is an urgent issue.

Scientific and rational management practices for fisheries resources are necessary, and we must prepare effective tools to flexibly cope with fluctuations in fisheries resources. Any new paradigm should assert the basic unpredictability of fisheries at the system level and require a broader range of performance indicators to be incorporated into the decision-making framework. The paradigm must reflect the non-equilibrium nature of marine systems and give greater importance to resource continuity in the face of regime shifts (Caddy and Seijo 2005). Feedback control is considered as an effective tool for such adaptive management (e.g., Tanaka 1980; Hilborn and Walters 1992; Geromont et al. 1999), and developing effective harvest control rules (HCRs) incorporating feedback control could be a key factor in coping with the fluctuations and uncertainties associated with utilizing fisheries resources. Thus, many fisheries scientists and management organizations worldwide have worked on the development of HCRs (e.g., Deroba and Bence 2008; Froese et al. 2011; Restrepo and Powers 1999).

This chapter reviews the management strategy evaluation (MSE) framework to evaluate the performance of HCRs and management procedures (MPs), which utilize operating models (OMs) to simulate virtual stock dynamics. We first overview the management objectives related to fisheries resources and the associated harvest strategies used to attain the objectives and then discuss some technical aspects of HCRs under uncertainties. Next, we briefly review the current stock management system in Japan and show a case study to test the performance of feedback HCRs (Hiramatsu 2004; Ohshimo and Naya 2014; Ichinokawa et al. 2015) to manage Japanese fish stocks. Finally, we discuss the use of HCRs in the context of coping with climate change.

11.2 Management Objectives and Harvest Strategies

The objectives of modern fisheries management should be to ensure sustainable harvests, viable fishing communities, and healthy ecosystems to sustain a mix of production, economic, and ecological values (Walters and Martell 2004). Management objectives of fisheries resources are different among the stakeholders. For example, the biological objectives commonly found in legislation and international agreements are maximization of biological production (MSY, maximum sustainable yield), the economic objectives usually consider economic efficiency (MEY, maximum economic yield), the social objectives are often to ensure employment and spread income among many participants, and the political objectives primarily concern the avoidance of conflict (Hilborn 2007). These objectives are sometimes compatible and sometimes in conflict (Cochrane 2000). Thus, the central mission of modern fisheries science should be to clearly delineate the trade-offs among conflicting objectives, and the central mission of modern fisheries management should be to develop effective ways to decide where and when to successfully operate given the trade-offs (Mangel 2000).

A harvest strategy sets out the management actions necessary to achieve predefined biological and economic objectives in a given fishery. Harvest strategies must contain (1) a process for monitoring and conducting assessment of the biological and economic conditions of the fishery and (2) rules that control the intensity of fishing activity according to the biological and economic conditions of the fishery. These rules are generally referred to as HCRs or MPs (Australian Government, Department of Agriculture, Fishery and Forestry 2007). Hilborn and Walters (1992) reported that a harvest strategy is a plan that states how the catch taken from the stock will be adjusted from year to year depending upon the size of stock, the economic or social conditions of the fishery, conditions of other stocks, and perhaps the state of uncertainty regarding the biological knowledge of the stock.

Normally, harvest strategies implicitly involve major decisions about trade-offs between average yield and year-to-year variability and between robustness of stock size and maximization of catch size (Hilborn and Walters 1992). Those trade-offs are related to the HCRs, but there is no single rule that covers all of these objectives. In addition, the presence of uncertainty, such as regime shifts and climate change, makes it difficult to balance trade-offs.

The most common and simplest harvest strategy is to set the target catch in each year as a linear function of population size; these types of strategies are known as stock-size-dependent strategies (Hilborn and Walters 1992). The constant escapement strategy (CES) leaves a constant biomass uncaught (escaped) every year as the next spawning stock, irrespective of the current stock size. Theoretically, this strategy maximizes the long-term average catch under ideal and accurate stock assessments, although the variation in the catch size can be large (Hall et al. 1988). The constant harvest rate strategy (CHR) catches a constant fraction of the stock every year. The long-term average catch in CHR will be somewhat lower than that in CES under ideal conditions, but the variation will be smaller than that of CES (Hall et al. 1988). CHR is considered to be more robust in performance than CES when the accuracy of the stock assessment is low. The constant catch strategy (CCS) catches a fixed amount every year, irrespective of the current stock size. Theoretically, this strategy minimizes the variation of the catch, but it has a great risk of incurring stock collapse if the stock decreases to a very low level. Coastal stocks such as abalone are sometimes managed using CCS (Matsumiya 1996). Each of these basic harvest strategies is based on a single parameter that is adjusted—the escapement level in CES, the harvest rate in CHR, and the catch amount in CCS. Because each of them has advantages and disadvantages, it is more effective to use them in combination with each other in consideration of the trade-offs between management objectives and the current status and features of the target stocks.

11.3 Harvest Control Rules and Management Strategy Evaluation with Uncertainty

Predicting the results of any management action is very uncertain because the dynamics of ecosystems are complex and poorly understood (Sainsbury et al. 2000). Techniques applicable to quantitative fisheries management are currently rapidly evolving, with an increasing reliance on rapidly changing computers, programming languages, and computational algorithms (Schnute et al. 2007). The MSE framework in fisheries management (Fig. 11.1) has also been developing, revolutionizing the management of harvested stocks by evaluating management scenarios in a virtual world and assessing their robustness to uncertainty (Bunnefeld et al. 2011).

MSE involves developing OMs to represent the underlying virtual reality of the resource dynamics and evaluating HCRs or biological reference points (BRPs) based on data simulated by using the OMs with reference to some performance measures. As stated above, as there are trade-offs between management objectives (e.g., maximizing average yield, minimizing year-to-year variability of yields, and keeping higher stock size), the performance measure shall be changed according to the objectives of stock management.

The HCRs, which are the key components for decision-making in fisheries management, are used to calculate recommended catch levels given estimates of present stock biomass or levels of fishing mortality. MSE is undertaken to examine the robustness of performances of HCRs to errors and uncertainties, and it shares many features with adaptive management. Skagen et al. (2013) proposed a

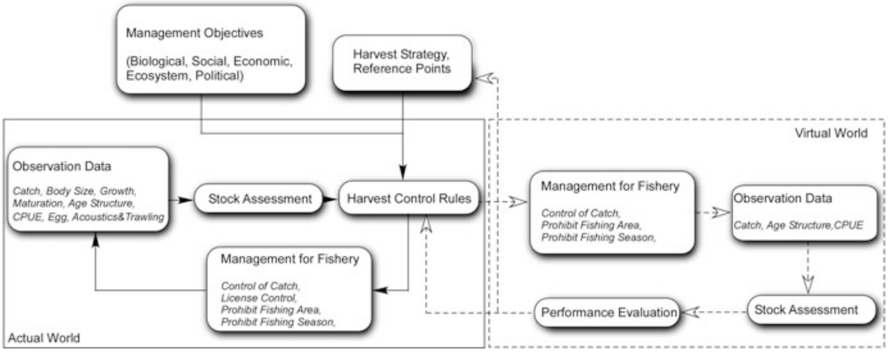

Fig. 11.1 Schematic diagram of stock assessment and management practices using the management strategy evaluation (MSE) framework. Solid squares and lines represent the actual world and actual processes, respectively. Dashed squares and lines represent the virtual world and virtual processes, respectively. Harvest control rules play a role in connecting the actual and virtual worlds

simulation framework for evaluating fisheries management schemes that use environmental information as part of the basis for decision-making. The HCRs are used to adjust the fishing intensity adaptively by sequentially updating information through continual monitoring of the state of the target stocks in response to present management activities. The process is based on the premise that stock variability and other uncertainties are inherently inevitable.

Recently, feedback control management systems with MSE simulations were reviewed (Edwards and Dankel 2016), and many examples of HCRs with MSE approach have been reported (e.g., Butterworth 2007; Butterworth and Punt 1999; Hillary et al. 2016). In South Africa, HCRs were developed and have been used to regulate the demersal fishery (Punt 1993) and the pelagic fishery for sardines and anchovies (Butterworth and Bergh 1993; Cochrane et al. 1998). Zheng et al. (1997) reported HCRs for red king crab (*Paralithodes camtschaticus*) in Bristol Bay using a length-based simulation model. In Japan, Watanabe et al. (2012) evaluated the fishing impacts on the Pacific chub mackerel (*Scomber japonicus*) using an age-structured OM. Horbowy (2011) compared HCRs for Baltic cod stock using a similar OM. Punt and Smith (1999) evaluated MPs for gemfish (*Rexea solandri*) in southeastern Australia and compared the performance of MPs based on estimates from virtual population analysis (VPA) and from the Schaefer production model using age-structured OMs. Southern bluefin tuna (*Thunnus maccoyii*) have been managed since 2011 based on an agreed MP developed using an OM (Kurota et al. 2010; CCSBT 2011; Hillary et al. 2016). Zhang et al. (2013) compared four HCRs for bigeye tuna (*Thunnus obesus*) and yellowfin tuna (*Thunnus albacares*) in the Indian Ocean using age-structured OMs. In general, these HCRs are mainly based on CHR when the stock size is sustainable, but the fishing coefficient (F) or catch amount should be reduced if the stock level becomes lower than a certain threshold, such as B_{pa} or B_{limit}.

11.4 Summary of Fish Stock Management and HCRs in Japan

11.4.1 TAC System in Japan

In July 1996, Japan ratified the United Nations Convention of the Law of the Sea. In accordance with the convention, the Government of Japan enacted the Act on Preservation and Control of Living Marine Resources. In 1997, the first output control measure to be formally adopted in Japan—the total allowable catch (TAC) system—was introduced (Makino 2011). The traditional approach of formal fisheries management in Japan takes the form of input control and technical control. The government controls the total amount and quality of fishing pressure by granting rights and licenses that specify gear types, fishing season, vessel size, target species, and other related factors.

The TAC system directly manages the catch of specified species with an upper limit of total catch. At present, seven TACs are applied to eight species: Pacific saury (*Cololabis saira*), walleye pollock (*Gadus chalcogrammus*), jack mackerel (*Trachurus japonicus*), sardine (*Sardinops melanostictus*), chub mackerel and spotted mackerel (*Scomber australasicus*), common squid (*Todarodes pacificus*), and snow crab (*Chionoecetes opilio*). The stock status of 44 species (75 stocks) was assessed in 2013, and the ABC (allowable biological catch) for each species was reported (Table 11.1) including non-target species of TAC management.

Japan is surrounded by the Pacific Ocean, East China Sea, Japan Sea, and Okhotsk Sea (Fig. 11.2), and fisheries productivity in the waters around Japan is high. There are numerous species in this area and many types of fisheries fleets. Each population of TAC species is divided into stocks (Fig. 11.2). For example, there are two stocks of sardine, jack mackerel and spotted mackerel (Pacific Ocean stock and Tsushima Warm Current stock), four stocks of walleye pollock (Pacific Ocean, North Japan Sea, Okhotsk, and Nemuro Strait stocks), a single stock of saury (northwest Pacific Ocean stock), two stocks of common squid (autumn and winter spawning stocks), and four stocks of snow crab (Pacific Ocean, Japan Sea, Okhotsk, and west Hokkaido stocks). Stock assessment is performed every year, and the results are disclosed to the public on the website of Fisheries Agency (http://abchan.fra.go.jp/index1.html).

Regarding the management procedure in Japan, two general management objectives are considered in stock assessments: (1) to prevent growth overfishing, an appropriate range of age and/or body size of fish caught is considered, and (2) to prevent recruitment overfishing, the amount of spawning stock must remain above an appropriate threshold level to maintain or restore the stock size. The United Nations Convention on the Law of the Sea states that “such measures shall also be designed to maintain or restore populations of harvested species at levels which can produce the maximum sustainable yield.” MSY is ideally interpreted as the maximum sustainable yield from a stock under present biological and environmental conditions. However, in practical terms in Japan, MSY is recognized as the yield

Table 11.1 List of species for recommendation by ABC

Common name	Scientific name	Stock	Used HCR	Method
Japanese sardine	*Sardinops melanostictus*	PO	Type I	Tuned-VPA
Japanese sardine	*Sardinops melanostictus*	TWC	Type I	Tuned-VPA
Jack mackerel	*Trachurus japonicus*	PO	Type I	Tuned-VPA
Jack mackerel	*Trachurus japonicus*	TWC	Type I	Tuned-VPA
Chum mackerel	*Scomber japonicus*	PO	Type I	Tuned-VPA
Chum mackerel	*Scomber japonicus*	TWC	Type I	Tuned-VPA
Spotted mackerel	*Scomber australasicus*	PO	Type I	Tuned-VPA
Spotted mackerel	*Scomber australasicus*	ECS	Type I	Tuned-VPA
Pacific saury	*Cololabis saira*	NWPO	Type I	Vessel survey
Walleye pollock	*Gadus chalcogrammus*	NJS	Type I	Tuned-VPA
Walleye pollock	*Gadus chalcogrammus*	Nemuro	–	–
Walleye pollock	*Gadus chalcogrammus*	OHS	–	–
Walleye pollock	*Gadus chalcogrammus*	PO	Type I	Tuned-VPA
Snow crab	*Chionoecetes opilio*	OHS	Type II	
Snow crab	*Chionoecetes opilio*	NPO	Type I	Vessel survey
Snow crab	*Chionoecetes opilio*	JS	Type I	Vessel survey
Snow crab	*Chionoecetes opilio*	WHKD	–	–
Japanese common squid	*Todarodes pacificus*	Winter	Type I	Vessel survey
Japanese common squid	*Todarodes pacificus*	Fall	Type I	Vessel survey
Round herring	*Etrumeus teres*	PO	Type II	
Round herring	*Etrumeus teres*	TWC	Type I	VPA
Japanese anchovy	*Engraulis japonicus*	PO	Type I	VPA
Japanese anchovy	*Engraulis japonicus*	SIS	Type I	VPA
Japanese anchovy	*Engraulis japonicus*	TWC	Type I	VPA
Deep sea smelt	*Glossanodon semifasciatus*	JS	Type II	
Deep sea smelt	*Glossanodon semifasciatus*	PO	Type II	
Longfin codling	*Laemonema longipes*	PO	Type II	
Pacific Cod	*Gadus macrocephalus*	HKD	Type II	
Pacific Cod	*Gadus macrocephalus*	NPO	Type I	Vessel survey
Pacific Cod	*Gadus macrocephalus*	JS	Type II	
Yellow goosefish	*Lophius litulon*	NJS	Type II	
Broadbanded thornyhead	*Sebastolobus macrochir*	OHS	Type II	
Broadbanded thornyhead	*Sebastolobus macrochir*	EHKD/ SHKD	Type II	

(continued)

Table 11.1 (continued)

Common name	Scientific name	Stock	Used HCR	Method
Broadbanded thornyhead	*Sebastolobus macrochir*	NPO	Type I	Vessel survey
Arabesque greenling	*Pleurogrammus azonus*	Nemuro	Type II	
Arabesque greenling	*Pleurogrammus azonus*	NHKD	Type II	
Arabesque greenling	*Pleurogrammus azonus*	SHKD	Type II	
Tilefish	*Branchiostegus* spp.	ECS	Type II	
Amberjack	*Seriola quinqueradiata*		Type II	
Scads nei	*Decapterus* spp.	ECS	Type II	
Red seabream	*Pagrus major*	ESIS	Type I	VPA
Red seabream	*Pagrus major*	WSIS	Type I	VPA
Red seabream	*Pagrus major*	WJS/ECS	Type I	VPA
Yellow seabream	*Dentex hypselosomus*	WJS/ECS	Type I+II	VPA
Sailfin sandfish	*Arctoscopus japonicus*	WJS	Type II	
Sailfin sandfish	*Arctoscopus japonicus*	WJS	Type II	
Largehead hairtail	*Trichiurus japonicus*	JS/ECS	Type II	
Spanish mackerel	*Scomberomorus niphonius*	ECS	Type II	
Spanish mackerel	*Scomberomorus niphonius*	SIS	Type I	VPA
Olive flounder	*Paralichthys olivaceus*	NPO	Type I	VPA
Olive flounder	*Paralichthys olivaceus*	SIS	Type I	VPA
Olive flounder	*Paralichthys olivaceus*	NJS/CJS	Type I	VPA
Olive flounder	*Paralichthys olivaceus*	WJS/ECS	Type I	VPA
Roughscale sole	*Clidoderma asperrimum*	NPO	Type II	
Round-nose flounder	*Eopsetta grigorjewi*	JS	Type I	tuned-VPA
Pointhead flounder	*Hippoglossoides pinetorum*	JS	Type I	tuned-VPA
Pointhead flounder	*Hippoglossoides pinetorum*	NHKD	Type II	
Flathead flounder	*Hippoglossoides dubius*	JS	Type II	
Willowy flounder	*Tanakius kitaharai*	NPO	Type I	VPA
Yellow striped flounder	*Pleuronectes herzensteini*	NPO	Type II	
Yellow striped flounder	*Pleuronectes herzensteini*	JS	Type II	
Black scraper	*Thamnaconus modestus*	JS/ECS	Type II	
Japanese pufferfish	*Takifugu rubripes*	JS/ECS/SIS	Type I	VPA
Japanese pufferfish	*Takifugu rubripes*	Ise/Mikawa	Type I	VPA
Alaskan pink shrimp	*Pandalus eous*	JS	Type II	
Red snow crab	*Chionoecetes japonicus*	JS	Type II	
Swordtip squid	*Loligo edulis*	JS/ECS	Type II	
Spear squid	*Loligo bleekeri*	PO	Type II	

PO, TWC, ECS, NWPO, NJS, Nemuro, OHS, NPO, JS, WHKD, SIS, HKD, EHKD, SHKD, ESIS, WSIS, WJS, and Ise/Mikawa represent Pacific Ocean, Tsushima Warm Current, East China Sea, Northwestern Pacific Ocean, North Japan Sea, Nemuro straight, Okhotsk, North Pacific Ocean, Japan Sea, West Hokkaido, Seto Inland Sea, Hokkaido, East Hokkaido, South Hokkaido, East Seto Inland Sea, West Seto Inland Sea, West Japan Sea, and Ise/Mikawa Bay, respectively

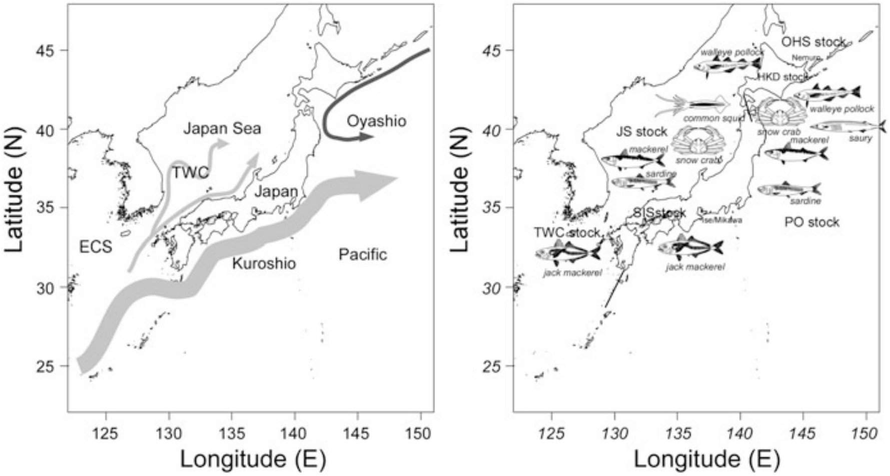

Fig. 11.2 (**a**) Oceanographic conditions around Japan and (**b**) distribution of fish stocks. JS, PO, TWC, SIS, HKD, and OHS represent the Sea of Japan, Pacific Ocean, Tsushima Warm Current, Seto Inland Sea, Hokkaido, and Okhotsk, respectively

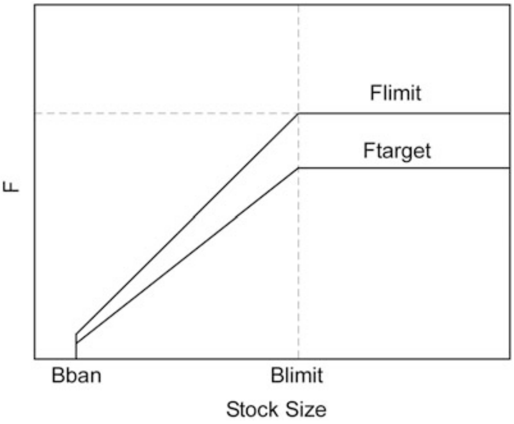

Fig. 11.3 Conceptual diagram of a Type I HCR in Japan. The fishing coefficient F should be reduced if the stock size goes below B_{limit}. B_{ban} is the stock level below which catches should be prohibited. F_{target} represents the precautionary F for a given F_{limit}

gained over a certain period of time by management schemes with appropriate HCRs.

When calculating the ABC, scientists in Japan principally consider two types of HCRs: one is based on controlling the fishing coefficient (F), defined as instantaneous rate of the population harvested by fishing, as a biological reference point derived from certain population dynamics models (Type I rule: Fig. 11.3), and the other is based on controlling the catch amount directly using information such as current trends of stock abundance indices as a type of feedback control rule (Type II rule). In addition to these, for specific stocks with in-season stock monitoring systems (e.g., the sand lance, *Ammodytes personatus*), a special CES is used to calculate ABC.

11.4.2 HCR Based on Controlling the Fishing Coefficient F (Type I Rule)

For a Type I rule (Fig. 11.3), fishing coefficient F should be determined to efficiently utilize the stock while also minimizing the risk of reducing the stock to an undesirable level. If the biomass of a stock is less than the threshold (B_{limit}), measures for stock recovery should be proposed. B_{limit} is determined as a biomass level (the spawning stock biomass) below which poor recruitments are anticipated and/or an empirically undesirable level of biomass. If the biomass is equal to or higher than B_{limit}, F_{limit} (the upper limit of an appropriate F) should be determined such that the management objectives can be achieved using a biological reference point deduced from the spawner-recruit relationship, F_{msy}, F_{med}, and F_{sus} (where $F_{\mathrm{sus}} = F$ replacement), an appropriate F in a given year (or years), and an empirical reference point ($F_{\%\mathrm{SPR}}$, F_{max}, $F_{0.1}$, and others). If the biomass becomes less than B_{limit}, F_{limit} should be reduced to a level at which stock recovery is expected. If the biomass is extremely low (less than B_{ban}), a fishing moratorium or other measures with a similar effect should be imposed.

Stock assessment includes a degree of uncertainty. Most notably, stock recruitment fluctuations can be remarkably large. To prevent management failures associated with these uncertainties, a precautionary approach should also be examined (F_{target} in Fig. 11.3). In this case, F is reduced from F_{limit} to F_{target} so that the possibility of the biomass decreasing to less than B_{limit} is sufficiently low or that of recovering to or above B_{limit} is sufficiently high. The upper limit of ABC ($\mathrm{ABC}_{\mathrm{limit}}$) is calculated using F_{limit}, and the target value of ABC ($\mathrm{ABC}_{\mathrm{target}}$) is calculated using F_{target}. When using stock indices (the Type II rule), a similar precautionary approach should be considered. For stocks that have spawner-recruit relationships that are subject to large changes over a long period, corresponding to long-term environmental fluctuations, the reference points (F_{limit} and others) and ABC should be determined based on the current stock status and biological characteristics.

11.4.3 Feedback HCR (Type II Rule)

As mentioned above, scientists also consider the Type II rule to control the catch amount using information such as trends of stock abundance indices. The following harvest control formula was used for available abundance indices until 2011:

$$ABC_y = \gamma \times C_{y-2}, \tag{11.1}$$

where ABC_y is the allowable biological catch in year y, γ is a coefficient reflecting the trend in stock abundance indices, and C_y is the catch in year y. Normally, the ABC for year y is determined in year $y - 1$ using information available through year $y - 2$.

Although this HCR has been applied to several Japanese stocks since 1997, it has not yet been extensively or quantitatively evaluated. Hiramatsu (2004) recommended revising the rule (i.e., Eq. 11.1) based on an OM and proposed an alternative harvest control formula:

$$ABC_y = \delta \times C_{y-2} \times \left(1 + k\frac{b}{\bar{I}}\right), \tag{11.2}$$

where δ is a safety factor depending on the stock status level, C_y is the catch in year y, k is a feedback factor to adjust the rate of change of ABC, b reflects the current trend in the stock abundance index I, and $\bar{I}$ is the mean of the stock abundance index I. Although Hiramatsu (2004) showed that Eq. 11.2 is superior to Eq. 11.1, the appropriate values for the safety and feedback factors were not explicitly shown. Therefore, the appropriate values of δ and k shall be evaluated by MSE in practical use.

11.5 A Case Study of Management Strategy Evaluation for Feedback HCR

Next, we will show a case study to evaluate the performance of HCR by exemplifying the case of the feedback HCR in Japan (Type II rule in Eq. 11.2) by extending the result of Ohshimo and Naya (2014).

11.5.1 Operating Model (OM)

The OM based on the production model as shown by Hiramatsu (2004) is given by

$$B_{y+1} = \left\{B_y + rB_y\left(1 - \frac{B_y}{K}\right)\right\}\hat{\varepsilon} - qX_yB_y, \tag{11.3}$$

where B_y is the biomass in year y, r is the intrinsic rate of natural increase, k is the carrying capacity, q is the catchability coefficient, and X_y is the fishing effort in year y. The term $\hat{\varepsilon}$ is a log-normal process error, which is defined as

$$\widehat{\varepsilon} = \exp\left(\sigma_R \varepsilon_y - \frac{1}{2}\sigma_R^2\right), \tag{11.4}$$

where ε_y is described by a normally distributed random value with mean = 0 and standard deviation = 1 and σ_R is the scale of variance for the process error. In this study, we modified Eqs. 11.3, 11.4, and 11.5 (Hilborn and Mangel 1997) to avoid stock extinction when the process error is large:

$$B_{y+1} = \left\{B_y + rB_y\left(1 - \frac{B_y}{k}\right) - qX_yB_y\right\}\widehat{\varepsilon}. \tag{11.5}$$

The actual catch was assumed to be equal to the ABC during the management period. The stock abundance index at year y (I_y) is given by introducing a log-normal observation error:

$$I_y = \frac{B_y + B_{y+1}}{2}\exp\left(\sigma_I \eta_y - \frac{1}{2}\sigma_I^2\right), \tag{11.6}$$

where η_y is described by a normally distributed random value with mean = 0 and standard deviation = 1 and σ_I is the scale of variance for the observation error.

The carrying capacity K was assumed to be 10,000, the intrinsic rate of natural increase r was set at either 0.3 or 0.5 (see Sect. 11.5.2), and the total duration of the simulation was 50 years, consisting of a pre-management and a subsequent management period (20 and 30 years, respectively). During the pre-management period, nine stock trajectory scenarios (e.g., shifting from a high to low stock level, shifting from a mid- to low stock level, and so forth) were assumed (Hiramatsu 2004; Ohshimo and Naya 2014). The ABC in year y was calculated using the catch in year $y - 2$ and the trend in the stock abundance index (Eq. 11.6) from years $y - 4$ to $y - 2$ during the management period. The stochastic simulation was repeated 1000 times for each of the nine scenarios.

11.5.2 Biological Parameters for OMs

In general, the longevity of pelagic fish is shorter than that of demersal fish (Hiyama et al. 2002; Narimatsu et al. 2010; Ohshimo et al. 2011; Shiraishi et al. 2008). In addition, tropical fish have rapid growth rates, small final size, and a short lifespan. Fish in the deep sea or at high latitudes often grow slowly to a large size and can live longer (Bone et al. 1995). The growth rate is negatively linked to longevity (Lee et al. 2013). The intrinsic rate of natural increase (r) is considered to be the key parameter for estimating population dynamics:

$$\frac{1}{N}\frac{dN}{dt} = r, \tag{11.7}$$

where N is the population size and dN/dt is the rate of population growth. Winemiller and Rose (1992) reported a methodology for estimating the intrinsic rate of natural increase for fishes as follows:

$$r \cong \frac{\ln\left(\sum_x l_x m_x\right)}{T} \tag{11.8}$$

$$T = \frac{\sum_x x l_x m_x}{\sum_x l_x m_x}, \tag{11.9}$$

where l_x, m_x, and T represent age-specific survivorship, fecundity at age x, and mean generation time (i.e., mean age for spawning), respectively. Mito and Yatsu (unpublished) analyzed the intrinsic rate of natural increase for several species in the waters around Japan. The derived relationship between longevity and the intrinsic rate of natural increase is shown in Fig. 11.4. The intrinsic rate of natural increase decreased with increasing longevity, and the maximum and the minimum values were 0.79 for anchovy (Pacific Ocean stock) and 0.17 for walleye pollock (North Japan Sea stock), respectively. We incorporated these intrinsic rates of natural increase into the production-model OM in Eq. 11.5.

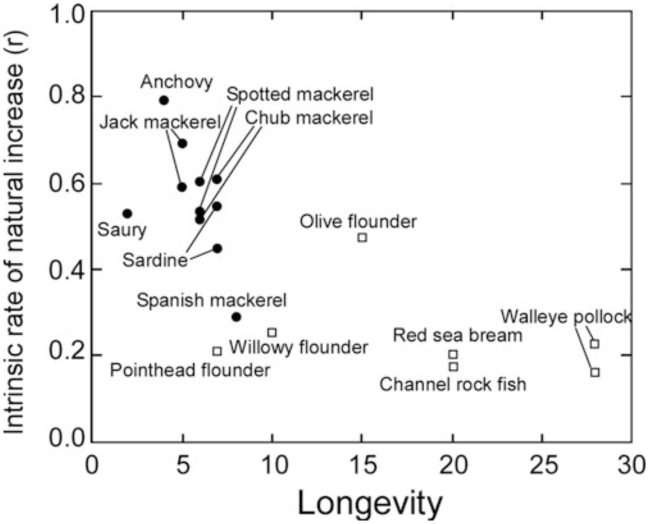

Fig. 11.4 The relationship between longevity in years and the intrinsic rate of natural increase for various fish species in waters around Japan. Closed circles and open squares represents small pelagic fish and demersal fish, respectively

11.5.3 Performance Measure

To evaluate the performance of HCRs with different parameter values, three performance statistics were formulated: (A) rate of stock collapse ($B < 0.2B_{\mathrm{msy}}$) during the management period (years 21–50), (B) ratio between the mean catch and MSY (C_{MSY}) during the management period, and (C) AAV (average absolute variation; Punt and Smith 1999) in catch. AAV was calculated as follows:

$$\mathrm{AAV} = \frac{\sum \left| C_y - C_{y-1} \right|}{\sum C_y}. \tag{11.10}$$

11.5.4 Performance Evaluation of the Revised Feedback HCR

Ohshimo and Naya (2014) examined the effect of different combinations of values among the safety (δ) and the feedback (k) factors in Eq. 11.2. In addition, more combinations of the safety factors were evaluated in the present study. Hereafter, the naming nomenclature of HCR combinations is based on the order of values of the safety factor in the high, middle and low stock levels and the value of feedback factor. For example, "HCR 1.0-0.8-0.6-0.5" indicates an HCR whose safety factor values in the high, middle, and low stock levels are 1.0, 0.8, and 0.6, respectively, and the feedback factor value is 0.5.

We reanalyzed the effects of different combinations of values of the safety factor (1.0, 1.1, and 1.2 for the high stock level; 0.8, 0.9, and 1.0 for the middle stock level; and 0.6, 0.8, 0.9, and 1.0 for the low stock level) and the feedback factor (0.5, 1.0, and 2.0) when the process error is larger ($\sigma_R = 0.2$ or 0.4) than that of our previous study ($\sigma_R = 0.05$, Ohshimo and Naya 2014), because the process error of the previous study was too low. The scale value of the observation error σ_I is set at 0.2 and 0.4 in the present study (Hiramatsu 2004).

The probability of stock collapse was high in the combinations when the value of the safety factor at the low stock level was high and the value of the feedback factor was low (Fig. 11.5a, b). Ohshimo and Naya (2014) reported that there were some trade-offs between performance indices according to the value of the feedback factor; that is, higher values of the feedback factor led to lower probabilities of a stock collapse but also to a lower mean catch/C_{MSY} (Fig. 11.5c, d) and higher catch AAV (Fig. 11.5e, f). A higher probability of stock collapse, lower mean catch/C_{MSY}, and higher median catch AAV were observed when the process and observation errors were large ($\sigma_R = 0.4$, $\sigma_I = 0.4$) as compared with the case when they were small ($\sigma_R = 0.2$, $\sigma_I = 0.2$) (Figs. 11.6 and 11.7). We concluded that the optimum value of the feedback factor is 1.0 based on the robustness for the stock collapse and the catch stability.

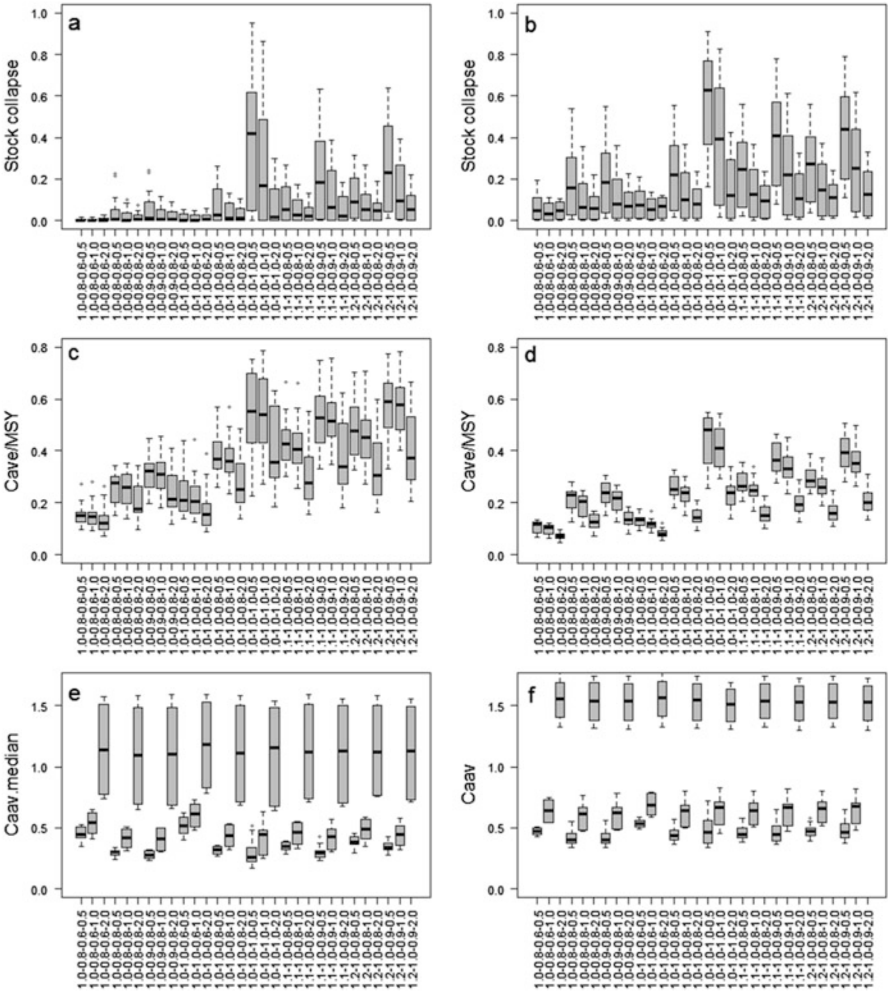

Fig. 11.5 Values of the performance indices for HCRs with different combinations of parameter values: rate of stock collapse (**a**: $r = 0.3$, **b**: $r = 0.5$, where r is the intrinsic rate of natural increase), average catch/MSY (**c**: $r = 0.3$, **d**: $r = 0.5$), and catch AAV (**e**: $r = 0.3$, **f**: $r = 0.5$). Process and observation errors ($\sigma_R = 0.2$ or 0.4 and $\sigma_I = 0.2$ or 0.4) were pooled. Box plots show median values (solid horizontal lines), 50th percentile values (box outline), 90th percentile values (whiskers), and outlier values (open circles)

Defining the optimum value of the safety factor remains difficult, because there are trade-offs between the performances for different objectives. For example, low values of safety factors, such as HCR 1.0-0.8-0.6-1.0, led to a low probability of a stock collapse but also to low catch amount, whereas high values of safety factors, such as HCR 1.2-1-0.8-1.0 or HCR 1.0-1.0-1.0-1.0, led to high probabilities of a stock collapse but also a high catch amount. Thus, there was a considerable trade-off

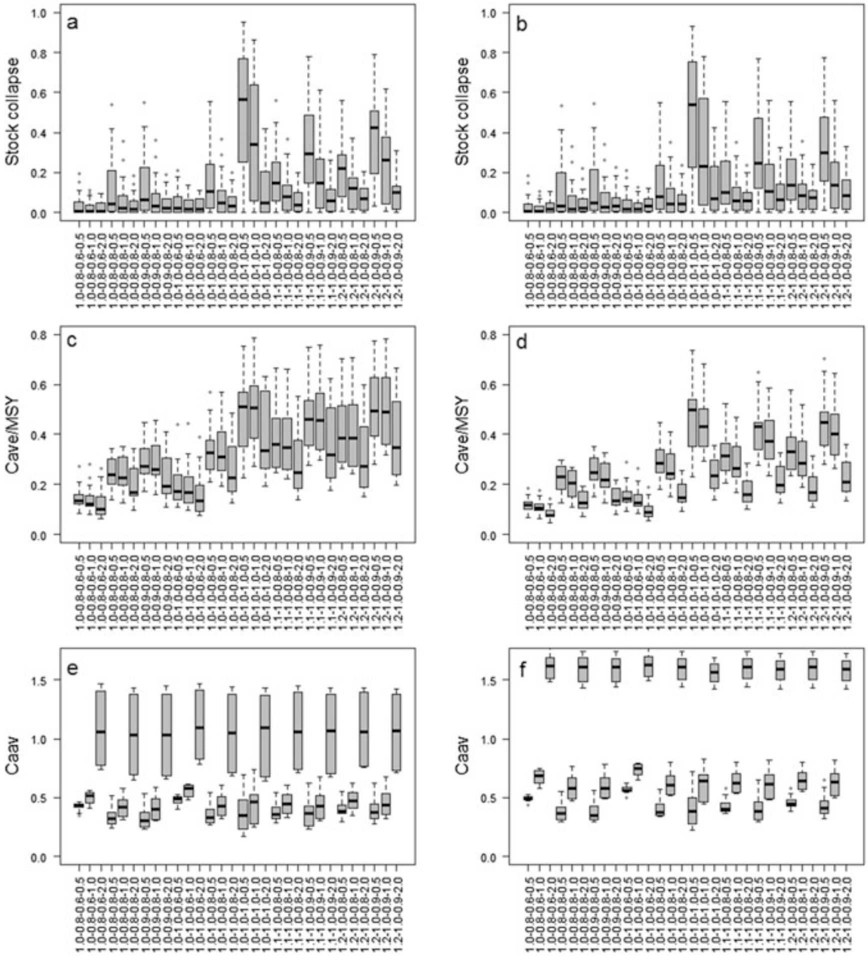

Fig. 11.6 Values of the performance indices for HCRs with different combinations of parameter values: rate of stock collapse (**a**: $\sigma_R = 0.2$, **b**: $\sigma_R = 0.4$, where σ_R is the scale of the process error), average catch/MSY (**c**: $\sigma_R = 0.2$, **d**: $\sigma_R = 0.4$), and catch AAV (**e**: $\sigma_R = 0.2$, **f**: $\sigma_R = 0.4$). Intrinsic rate of natural increase r was set at 0.3. Observation errors ($\sigma_I = 0.2$ or 0.4) were pooled. Box plots show median values (solid horizontal lines), 50th percentile values (box outline), 90th percentile values (whiskers), and outlier values (open circles)

between the probability of stock collapse and catch amount: the official recommended HCR at present in Japan is HCR 1.0-1.0-0.8-1.0 (Ichinokawa et al. 2015).

We applied three different HCRs to actual data gathered for Japanese sardines from the late 1980s and early 1990s (Fig. 11.8). The stock size of the Japanese sardines declined drastically in the 1990s after successive recruitment failures from 1988 to 1991 (Watanabe et al. 1995). In those years, no ABC for Japanese sardines

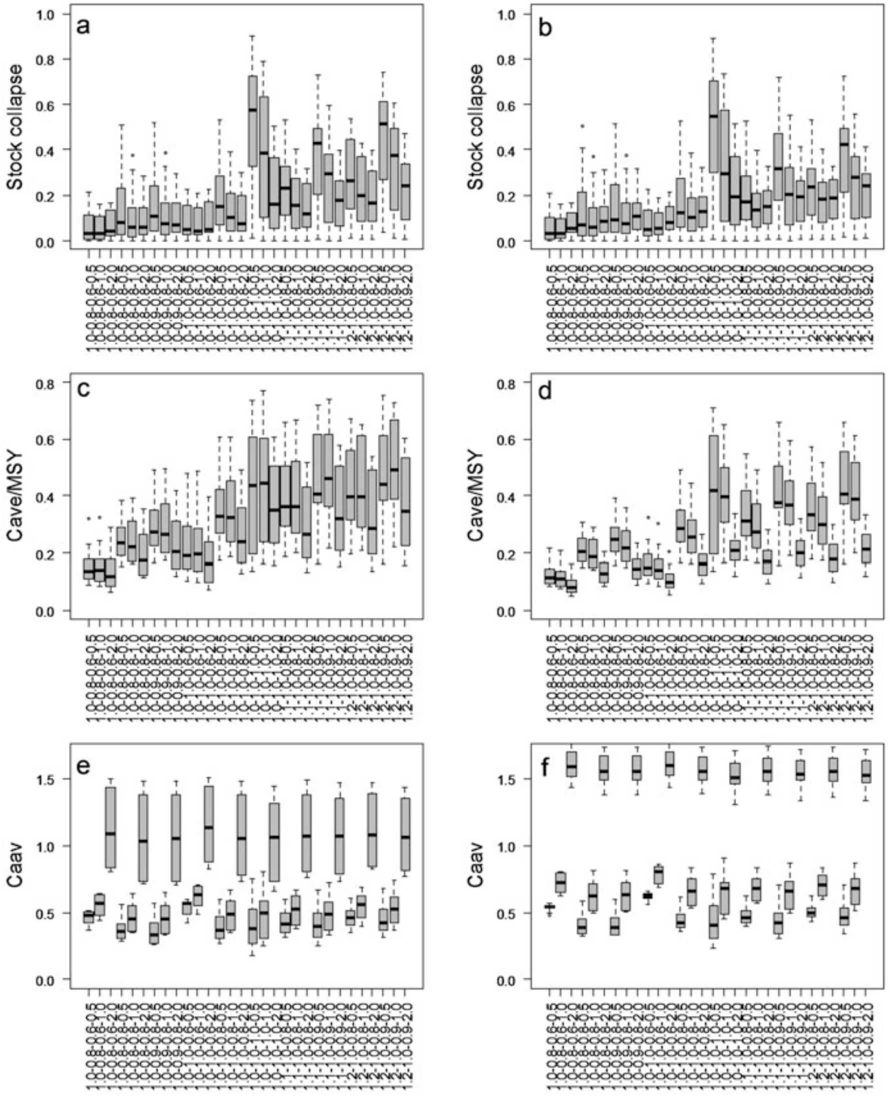

Fig. 11.7 Values of the performance indices for HCRs with different combinations of parameter values: rate of stock collapse (**a**: $\sigma_I = 0.2$, **b**: $\sigma_I = 0.4$, where σ_I is the scale of the observation error), average catch/MSY (**c**: $\sigma_I = 0.2$, **d**: $\sigma_I = 0.4$), and catch AAV (**e**: $\sigma_I = 0.2$, **f**: $\sigma_I = 0.4$). Intrinsic rate of natural increase r was set at 0.5. Process errors ($\sigma_R = 0.2$ or 0.4) were pooled. Box plot shows median values (solid horizontal lines), 50th percentile values (box outline), 90th percentile values (whiskers), and outlier values (open circles)

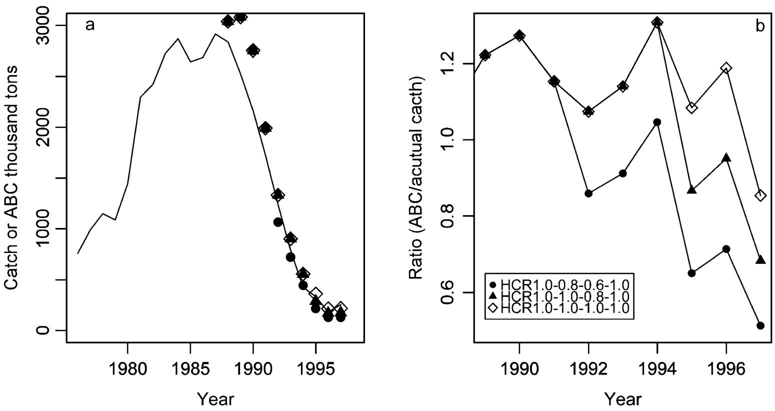

Fig. 11.8 (**a**) Comparison between the actual catch (solid line) and three simulated ABCs calculated by present feedback HCRs for Japanese sardines from the late 1980s to the 1990s and (**b**) ratios of the actual catch and the three calculated ABCs

was proposed because the TAC/ABC system had not yet been put in place. Here, we derived three different hypothetical series of ABCs for Japanese sardines using HCR 1.0-0.8-0.6-1.0, HCR 1.0-1.0-0.8-1.0, and HCR 1.0-1.0-1.0-1.0. All of the three calculated ABCs follow the trends of the actual catch after 1988, but the ABCs derived using HCR 1.0-0.8-0.6-1.0 and HCR 1.0-1.0-0.8-1.0 were lower than the actual catch from 1992 to 1995 (Fig. 11.8). Therefore, these feedback HCRs could have been effective in alleviating the decline of the Japanese sardine stock after 1992. However, developing OMs that include the effects of regime shift and conducting close examinations through MSEs are necessary to develop optimal HCRs to effectively cope with regime shift.

11.6 HCRs Under Climate Change

A central and classic question in ecology is what causes populations to fluctuate. Understanding the interaction between natural drivers of fluctuating populations and human exploitation is an issue of paramount importance for conservation and natural resource management (Shelton and Mangel 2011). Three main hypotheses have been proposed to explain fluctuations: (1) species interactions, such as predator–prey interactions, (2) strongly nonlinear single-species dynamics, and (3) environmental variation (Shelton and Mangel 2011). In particular, for small pelagic fishes around Japan, such as sardine and chub mackerel, recruitment fluctuates because of environmental changes (Hiyama et al. 2002; Yatsu et al. 2005; Ohshimo et al. 2009). Kawasaki (1983) proposed the concept of a "regime shift," which is a synchronized fluctuation between the abundance of small pelagic fish and climate.

Regime shifts are a prominent feature of the physical environment of some ecosystems and have the potential to influence stock productivity (Szuwalski and Punt 2013). Hollowed et al. (2013) reviewed current literature on the projected effects of climate change on marine fish and shellfish, their fisheries, and fishery-dependent communities throughout the northern hemisphere. Climate change will have impacts through a complex suite of linked processes. Fish stocks fluctuate both in abundance and productivity, and there are many examples demonstrating that productivity increased or decreased as a result of changes in abundance caused by fishing as well as where productivity shifted for reasons entirely unrelated to abundance (e.g., Vert-pre et al. 2013). Fisheries responses to climate change occur on a time scale relevant to the provision of short-term management advice. The application of harvest strategies utilizing biological reference points that do not account for the effects of the changing environment may lead to unsustainable catch recommendations (Wayte 2013).

Fisheries management agencies need to recognize that irregular changes in productivity are common and that harvest regulation and management targets may need to be adjusted whenever productivity changes (Vert-pre et al. 2013). When recruitment is irregular, the probability of stock extinction increases (Suda and Akamine 1998). However, few management strategies or HCRs consider the possibility of changes in stock productivity. Identifying changes in productivity that are definitely driven by an environmental regime rather than fishing pressure is the largest single difficulty in implementing these rules (Szuwalski and Punt 2013). There are, however, studies of HCRs based on the MSE approach that include population dynamics incorporating regime shifts (e.g., Haltuch et al. 2009; Hurtado-Ferro et al. 2010). Feedback HCRs should be also evaluated based on this type of MSE.

Punt et al. (2013) stated that two approaches have been developed to apply MSE to evaluate the impact of environmental variation on the performance of management strategies. The “mechanistic approach” estimates the relationship between the environment and elements of the population dynamics of the fished species and makes predictions for population trends by using the outputs from global climate models. In contrast, the “empirical approach” examines possible broad scenarios without explicitly identifying mechanisms. As it stands now, both approaches are necessary. If the mechanisms of recruitment have been well studied (e.g., for sardines), the mechanistic approach can be used, but the population dynamics mechanisms of most fisheries resources are not well known. As a result, a simple or “empirical” feedback HCR should be used.

In addition, other management strategies, such as the use of marine-protected areas and restrictions on catch seasons, are also available. Takenaka and Matsuda (1997) examined the optimal harvesting policy to maximize the long-term yield of chub mackerel and concluded that (1) the maximum sustainable yield is unlikely to be obtained with pulse fishing, and (2) in any case, the fish should be protected until the end of the first spawning season. Combining catch quota control with a large closed area is the most effective system for reducing the risk of stock collapse and maintaining both short- and long-term economic performance (Stefansson and

Rosenberg 2005). Watanabe et al. (2011) reported the case of a three-year moratorium of catching sandfish (*Arctoscopus japonicus*) in the Sea of Japan, and the stock has been drastically increasing after the end of the moratorium. We conclude that it is necessary to improve HCRs, from simple feedback HCRs as discussed above into more comprehensive HCRs combined with other effective measures to manage highly fluctuating and vulnerable species of fish.

11.7 Future Prospects

Fisheries research and management have been gradually evolving to broaden their focus from the management of a single target species toward a more holistic view of fisheries' impacts on the ecosystem and the socioeconomic issues of user reliance on fishing (Milner-Gulland et al. 2010). The MSE framework is increasingly being used in this wider context to address the trade-offs that are necessary when the entire ecosystem and multiple stakeholders are considered (Smith et al. 2007; Levin et al. 2009; Fulton et al. 2014). Recent MSE applications include the use of OMs that account for plausible climate drivers, species interactions, and behavior of fishermen and fleets (Kell et al. 2005). The MSE approach has the potential for use in linked socio-ecological systems far beyond the realm of fisheries (Milner-Gulland et al. 2010).

Ecosystem-based fisheries management (EBFM) has emerged during the past 10 years as an alternative approach to single-species fisheries management (Pikitch et al. 2004). The tools include extension of the MSE approach to evaluate broader EBFM schemes, development of new approaches to ecological risk assessment for evaluating the ecological impacts of fishing, and development of a harvest strategy framework and policy that forms the basis for a broader EBFM strategy (Smith et al. 2007). A shift in objectives from single-species to multi-species or ecosystem management is normally assumed, and scientists already have some footholds such as the Ecopath with Ecosim system (Christensen and Walters 2004). However, it is difficult to develop the structural modeling for multi-species management because of the need for more detailed information such as species interactions, predator–prey relationships, and physiological differences under the condition of climate change. For these reasons, interdisciplinary interactions among scientists are needed to develop a mechanistic management approach.

Socioeconomic objectives are also important in fisheries management. Hoshino et al. (2012) reported on bio-economic adaptive management schemes that respond to changes in economic conditions, stock abundance, and catchability, using fisheries targeting short-lived common squid and saury as case studies. They suggested that such adaptive schemes have the potential to support the successful implementation of profit-maximizing (MEY-based) harvest policies. We believe that the

HCRs using the MSE approach and taking biological, economic, and social objectives into consideration will become available in the future.

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Chapter 12
Ecosystem Model in Data-Poor Situations

Hiroshi Okamura, Momoko Ichinokawa, and Osamu Komori

Abstract Ecosystem assessment is one of the most interesting topics in ecology and fisheries science; modeling is an essential and indispensable part of ecosystem assessment. We briefly review existing ecosystem models that are employed around the world and present a new ecosystem model that can be applied in data-poor situations, e.g., when diet-composition data are unavailable. The new model is based on a multivariate state-space model with an allometric relationship between the biological parameters and body mass. The model generally does not require unrealistic assumptions, such as equilibrium prior to fishing and mass balance during a certain period. The simulation study demonstrated that the model outperformed a single-species assessment in terms of the inference of biological reference points. As an illustration, we applied the model to environmental index data and three species in the western North Pacific, which are known to show conspicuous species replacement (chub mackerel, sardine, and anchovy). The model can be extensively applied to various multispecies data in data-poor situations.

Keywords Allometric relationship · Body size · Ecosystem modeling · Gompertz–Fox model · Random effects · State-space modeling · Species replacement

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12.1 Introduction

Ecosystem assessment and management is one of the most interesting and important topics in ecology and fisheries science (Walters and Martell 2004). Fisheries management is an abundant repository of the failure to sustain natural resources. One reason for this failure is the assessment of a single species without considering multispecies interactions in the ecosystem (Pauly et al. 2002). For example, culling one species may cause an unexpected influence on a second species (Walters and Kitchell 2001). In addition, we should consider fish as not only food but also a component in our ecosystem that provides various services to the ecosystem (Worm et al. 2006). Fish and fisheries are closely related to the surrounding environment. Long-term environmental changes simultaneously affect many species and fisheries (Barange et al. 2014).

One solution to these problems is the development and use of an ecosystem or multispecies model. Many ecosystem models have been developed and employed with applications to real data (Plagányi 2007). However, ecosystem models are generally data-driven and require many assumptions. Global data for evaluating ecosystem status are generally limited. A simple model for ecosystem assessment that only requires accessible data and minimal and realistic assumptions enables a rapid evaluation of global ecosystems and the use of swift measures for ecosystem conservation and restoration.

We review ecosystem models that have been employed in fisheries science around the world. The review is not exhaustive and comprehensive but is based on our interests and connection to subsequent sections of this chapter. We propose a new ecosystem assessment model that can be applied to data-poor situations, e.g., when diet-composition data are unavailable. We conduct a simple simulation test to investigate the performance of our new model and apply it to North Pacific multispecies data. We discuss the merits and demerits of our model and the future direction of ecosystem modeling for data-poor situations.

12.2 Brief Review of Ecosystem Models

Ecosystem models serve an important role in understanding complicated species interactions and environmental effects, functioning of an ecosystem, and future services obtained from the ecosystem in fisheries science. Fisheries ecosystem models are categorized based on several aspects (Plagányi 2007): end-to-end models (from primary producers and detritus to top predators) vs. minimum realistic models (part of ecosystems that focus on a hypothesis) or biomass-based models vs. nutrients-based models. The models tend to be based on nutrients when they focus on lower trophic levels, whereas the models tend to be based on biomass when they focus on upper trophic levels. Some models are considered to be end-to-end models, some models are minimum realistic models, and some hold both

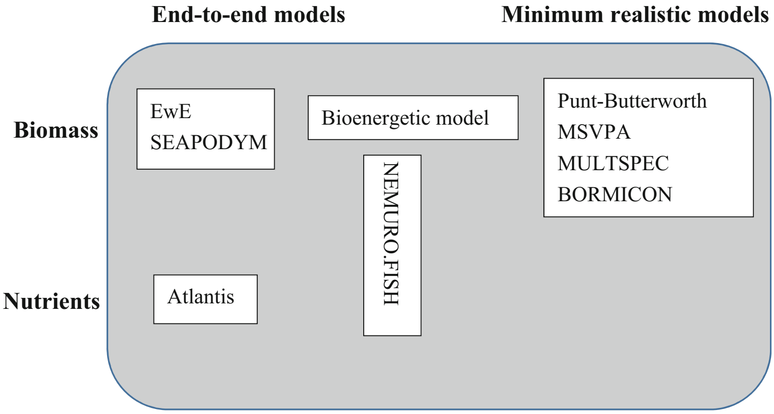

Fig. 12.1 Schematic summary of existing ecosystem models that were examined in this article

characteristics. Thus, strict categorization is somewhat difficult. For this reason, we focus on some typical end-to-end models, minimum realistic models, and other models, including bioenergetics models. This selection of ecosystem models is based on our interests and their relation to a new ecosystem model, which will be subsequently discussed. The characteristics of the models that are examined in this section are summarized in Fig. 12.1. Plagányi (2007) provides a comprehensive review of contemporary fisheries ecosystem models.

12.2.1 End-to-End Models

These models deal with all trophic levels from primary producers and detritus to top predators, such as tuna and cetaceans in the ecosystem. The population dynamics model for each species is generally simple, and many assumptions are required to simultaneously address the dynamics of many components.

Ecopath with Ecosim (EwE)
EwE is the most commonly employed ecosystem modeling tool in fisheries science; it has broad and powerful functions for ecosystem assessment. Ecopath is based on "mass balance" equations:

$$B_i(P/B)_iEE_i = \sum_j (Q/B)_jDC_{ij}B_j + Y_i + \cdots$$

where B_i and B_j are the biomass of prey (i) and the biomass of predator (j), respectively; $(P/B)_i$ is the production/biomass ratio for i; EE_i is the fraction of the production of i that is consumed within or caught from the ecosystem; Y_i is the fishing mortality (landings and discards) of i; $(Q/B)_j$ is the total food consumption per unit biomass of j; and DC_{ij} is the fractional contribution of i to the diet of j. A change in biomass over the time period and/or net emigration can be added to the right-hand side of this equation (Pauly et al. 2000; Plagányi 2007).

The parameters (unknown variables) are obtained by solving these simultaneous linear equations. $(P/B)_i$ is approximated by the total mortality Z_i, and $(Q/B)_j$ is inferred from the ration estimates that are obtained from the laboratory experiment. Although EE_i is difficult to directly measure, it is expected to be close to one for groups with high fishing pressures. Therefore, given the diet composition DC_{ij}, B_i or EE_i is estimated with ad hoc trial and error adjustments to achieve mass balance (because EE_i should be between zero and one, other input variables must be adjusted when $EE_i > 1$).

Ecopath provides a "snapshot" description of an ecosystem. It is the building block of its extensions: Ecosim, which is a time-dependent dynamic simulation model, and Ecospace, which is a spatial and temporal model. In Ecopath, we can evaluate the ecosystem status using ascendency (a measure of average mutual information in the ecosystem), mixed trophic impacts (qualitative evaluation of the impact of direct and indirect interactions), or the omnivory index (Christensen and Pauly 1992). However, its static nature hinders dynamic future prediction.

Ecosim enables dynamic time-dependent prediction using mass-balanced Ecopath estimates as the starting point. It is described as coupled differential equations (Pauly et al. 2000). The most important characteristic is to divide the biomass of each prey into a vulnerable and a nonvulnerable component. The transfer rate between vulnerable components and nonvulnerable components determines whether the system is top-down-controlled (Lotka–Volterra) or bottom-up-controlled (donor-driven). It can be estimated using the time-series fitting of abundance indices and fishing rates (Pauly et al. 2000; Walters and Martell 2004).

Ecospace is a spatial extension of Ecopath and Ecosim. It allocates a biomass into a grid map and conducts future dynamic simulation while accounting for spatial movements among grid cells (Pauly et al. 2000).

EwE has been employed to inspect and verify various global ecosystem hypotheses (Branch et al. 2010; Garcia et al. 2012). Okamura et al. (2002) constructed the 30-species Ecopath model for the western North Pacific region to examine the impact of whale predation on forage fish species and conducted Ecosim simulations using some hypothetical transfer rates between vulnerable components and nonvulnerable components.

Atlantis

Atlantis is based on the flow of nutrients, not biomass (Fulton et al. 2011). It includes all trophic levels at which the dynamics of lower trophic levels are typically modeled by biomass pool models and high trophic level species are modeled by age-structured models (Plagányi 2007). Atlantis is divided into some submodels: biophysical, industry and socioeconomic, monitoring and assessment, and management (Fulton et al. 2011). The most important characteristic is that Atlantis is intended for use in a management strategy evaluation (MSE) framework (Chap. 11; Punt and Donovan 2007). Atlantis has been employed for several ecosystems—primarily in Australia and the USA—and has produced numerous important findings about ecosystem function and possible forms of effective ecosystem-based management. The characteristics and flexibility of many submodels indicate that Atlantis can only be employed in data-rich situations. Although this seems true to some extent, the framework remains arguably useful for asking "what if" questions in a data-poor situation (Plagányi 2007). The flexibility also hinders the role of Atlantis as a statistical model; for example, model fitting to real data or data assimilation seems intractable.

Others

The Spatial Ecosystem And POpulation DYnamics Model (SEAPODYM) is a coupled physical–biological interaction model on the ocean basin scale, which was developed for tropical tuna in the Pacific Ocean (Plagányi 2007). The model accounts for the spatial movement of tuna based on a diffusion–advection model and habitat quality and incorporates a description of intermediate trophic levels in three vertical layers, as well as handles multiple predators.

12.2.2 Minimum Realistic Models

Minimum realistic models address the part of the ecosystem components that typically includes a few species with the objective of testing a specific hypothesis. As a component in the ecosystem model, each species tends to have a complex population dynamics model, such as an age-structured model. Therefore, modeling each component species generally demands strong data.

Punt and Butterworth Model

Punt and Butterworth (1995) developed a minimum realistic model to examine whether the hake fisheries in South Africa were positively affected by culling fur seals, which prey on hakes. Hakes consisted of two species with different habitats. Their population dynamics were separately modeled using detailed age-structured models. The natural mortality for hakes was divided into interspecies predation/cannibalism, seal predation, predation by other fish, and other sources of mortality. The predation rate was modeled by a Holling's type II function (Koen-Alonso 2007). The simulation model for the base-case scenario showed that seal culls had minimal or even detrimental effects on the hake fisheries.

MSVPA

MSVPA (multispecies virtual population analysis) is a multispecies version of the virtual population analysis frequently employed in single-species assessments (Magnússon 1995; Lassen and Medley 2000) and requires catch-at-age data and fish stomach content data. Predation is addressed as part of natural mortality via "suitability." This model generally requires a considerable amount of stomach content data for reliable parameter estimation. Application of this model in the North Sea required tens of thousands of stomachs (Plagányi 2007).

MULTSPEC/BORMICON/GADGET
MULTSPEC is a computer program for future prediction; it employs length-, age-, and area-structured multispecies population dynamics models for species, including cod, capelin, herring, polar cod, harp seals, and minke whales in the Barents Sea (Bogstad et al. 1997). BORMICON is another multispecies model for Arcto-boreal ecosystems. These models are currently integrated into the Globally Applicable Area-Disaggregated General Ecosystem Toolbox (GADGET). An important characteristic of GADGET is that refined and advanced statistical methodologies, such as the maximum likelihood approach, are employed for parameter estimation.

Others
Extended single-species assessment models (ESAMs) and multispecies statistical catch-at-age models are other types of minimum realistic models (Plagányi 2007). The Mori and Butterworth (2006) multispecies model that was developed in the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR) to address the interactions between krill and its predators, such as whales, is another variant of minimum realistic models.

12.2.3 Other Ecosystem Models

Yodzis (1998) developed an end-to-end ecosystem model that is based on bioenergetic or allometric relationships. Many biological parameters have an allometric relationship with body size, i.e., a linear relationship of log(biological parameter) against log(body size) (Charnov 1993). The model used a 29-species food web to investigate the effect of a fur seal cull on fisheries in the Benguela ecosystem. Parameter estimates were obtained using the assumption of equilibrium dynamics. The model determined that a cull of seals was more likely to be detrimental to total yields from all exploited species than it was likely to be beneficial (Yodzis 1998).

Koen-Alonso and Yodzis (2005) developed an improved multispecies trophodynamic model of the marine community, which included squid, anchovy, hake, and sea lions for northern and central Patagonia, using an allometric approach. The model does not require the assumption that each species was at equilibrium when the fishery started, which is a classic and common requirement of many single-species models (Koen-Alonso and Yodzis 2005). The uncertainty of parameter estimates was addressed using a sampling–importance resampling (SIR) algorithm. The model supported Holling’s type III functional response based on the Akaike information criterion.

NEMURO is a model of marine ecosystems that is based on lower trophic levels (nutrients, phytoplankton, and zooplankton (NPZ)). It has been extended to incorporate higher trophic levels (fish); this extension is named NEMURO.FISH (Kishi et al. 2011).

For recent developments of tactical ecosystem models with intermediate complexities, see Plagányi et al. (2014).

12.3 An Ecosystem Model for Data-Poor Situations

A key component in ecosystem models such as EwE and the bioenergetic model is the functional response, which is the change in the predation rate as a function of prey density (Holling 1959; Koen-Alonso and Yodzis 2005; Koen-Alonso 2007). It is commonly estimated using the diet-composition data from the stomach contents of predator species and abundance information. However, the diet-composition data usually have large uncertainties that are likely to produce biased results for ecosystem assessments.

Another problem in ecosystem modeling is the number of parameters to be estimated. The number of parameters usually rapidly increases as the number of species in the ecosystem model increases, which produces unstable and unreliable estimations from the model. One method for reducing the number of estimated parameters and stabilizing the results is the random-effects model or hierarchical model structure (Clark and Gelfand 2006).

The third problem in ecosystem modeling is that the model must simultaneously address many species that have different data quality, biological characteristics, and life histories. Some species have sufficiently long time-series data, whereas other species have only limited time-series data with some missing and incomplete values. Ecosystem models need to integrate data of different quality.

Ecosystem models comprise a data-driven approach that usually requires the integration of a considerable amount of data from various surveys and experiments. Fisheries provide us with a tremendous amount of data about fish, fisheries, and their environments (Ricard et al. 2012). If the data were easily accessible and obtainable, we could make an assessment of global and data-poor ecosystems without much difficulty.

An ecosystem model that is not based on prey–predator interactions that are estimated from diet composition would be useful as a null model and as an alternative ecosystem model that is robust to the uncertainties of diet-composition data.

Our objective in this section is to develop a fundamental structure for ecosystem models that can resolve the previously mentioned problems. Our model does not require diet-composition data to model prey–predator interactions and fundamentally only requires data that are usually obtained from fisheries and global databases. It addresses many parameters using random effects or a hierarchical structure and enables missing data and differences in data quality.

12.3.1 The Gompertz–Fox Model

We apply the Gompertz–Fox model as a basic population model to describe the dynamics of each species in the ecosystem model. A recent study using meta-analysis demonstrated that the Gompertz–Fox model provides a better description of population dynamics than the traditional Schaefer production model (Thorson et al. 2012). An attractive feature of the Gompertz–Fox model is that it becomes a linear model that employs logarithmic transformation (Spencer and Ianelli 2005). The Gompertz–Fox model is described using a differential equation:

$$\frac{\mathrm{d}P}{\mathrm{d}t} = rP[\log(K) - \log(P)] - FP$$

where P is the biomass, r is the intrinsic natural increasing rate, K is the carrying capacity, and F is the fishing rate. The fishing rate and biomass that produce the maximum sustainable yield (F_{MSY} and B_{MSY}) are r and K/e (e is Napier's constant, 2.71828. . .), respectively.

Discretizing the model using $X_t = \log(P_t)$ from $X_{t+1} - X_t = r(B_t - X_t)$ gives

$$X_{t+1} = rB_t + (1 - r)X_t$$

where $B_t = \log[K\exp(-F_t/r)]$ (Spencer and Ianelli 2005).

12.3.2 *The Basic Model Structure*

The model assumes the form of state-space models or hierarchical models to properly address large uncertainties and missing data (Carlin et al. 2005), that is, the model is composed of three parts: data (observation), process, and parameters. Each level is modeled in a stochastic manner, and the joint distribution,

$$\begin{aligned}\Pr(\text{data, process, parameters}) = \; & \Pr(\text{data}|\text{process, parameters}) \\ & \times \Pr(\text{process}|\text{parameters}) \times \Pr(\text{parameters}),\end{aligned}$$

is employed for inferences.

To model multispecies, we introduce the subscript that denotes different species s ($s = 1, \ldots, S$). The population dynamics model (the process model) for species s is

$$X_{s,t+1} = r_s B_{s,t} + (1 - r_s)X_{s,t} + \varepsilon_{s,t}$$

where $(\varepsilon_{1,t}, \cdots, \varepsilon_{S,t})^T \sim N(0, Q)$ and Q is the $S \times S$ variance–covariance matrix

$$Q = \begin{pmatrix} \sigma_{11} & \cdots & \sigma_{1S} \\ \vdots & \ddots & \vdots \\ \sigma_{S1} & \cdots & \sigma_{SS} \end{pmatrix}$$

and $B_{s,t} = \log[K_s\exp(-F_{s,t}/r_s)]$. The species interaction in this model is entered into the variance–covariance matrix Q.

The observation model is composed of two models. The first model is the abundance index:

$$I_t = X_t + d_t + \nu_t$$

where $X_t = (X_{1,t}, \ldots, X_{S,t})^T$ is the vector of $\log(P_{s,t})$; $I_t = (I_{1,t}, \ldots, I_{S,t})^T$ is the logarithm of the abundance index of species s and time t; and $d_t = (d_{1,t}, \ldots, d_{S,t})^T$ is the $S \times 1$ vector whose components are $d_{s,t} = \log(q_s)$ ($s = 1, \ldots, S$), where q_s is the proportionality between abundance and abundance index, and

$$\nu_t = (\nu_{1,t}, \cdots, \nu_{S,t})^T \sim N(0, H)$$

where H is the diagonal matrix and $\mathrm{diag}(H) = (\tau_1, \ldots, \tau_S)$. The second observation model is the catch statistics:

$$Y_t = X_t + e_t + \omega_t$$

where $Y_t = (Y_{1,t}, \ldots, Y_{S,t})^T$ is the vector whose component is the logarithm of catch $C_{s,t}$ for species s and time t. Here, $e_\mathrm{t} = (e_{1,t}, \ldots, e_{S,t})^T$ is the $S \times 1$ vector whose component is $\log(F_{s,t})$, where $F_{s,t}$ is the fishing rate, and

$$\omega_t = (\omega_{1,t}, \cdots, \omega_{S,t})^T \sim N(0, G)$$

where G is the diagonal matrix and $\mathrm{diag}(G) = (\xi_1, \ldots, \xi_S)$ (Spencer and Ianelli 2005).

The parameters to be estimated are r_s, K_s, q_s, and $F_{s,t}$ and the components of Q, H, and G. The number of $F_{s,t}$ increases as the length of the time series and the number of species increase. We assume that the logarithm of $F_{s,t}$ follows a normal distribution:

$$\log(F_{s,t}) \sim N\left(\log\left(\bar{F}_s\right), \eta_s^2\right)$$

This modeling using random effects decreases the number of parameters about F from $T \times S$ to $2 \times S$.

The increasing rates r_s and the carrying capacities K_s have a relationship with body size W_s (Charnov 1993):

$$\log(r_s) \sim N\left(\log\left(\bar{r}_s\right), \sigma_{r,s}^2\right)$$

where $\log\left(\bar{r}_s\right) = A_r + B_r \log(W_s)$ and

$$\log(K_s) \sim N\left(\log\left(\bar{K}_s\right), \sigma_{K,s}^2\right)$$

where $\log\left(\bar{K}_s\right) = A_K + B_K \log(W_s)$. This modeling reduces the number of parameters about r and K from $2 \times S$ to $2 \times 3 = 6$. The assumption of an allometric relationship permits us to stably estimate the parameters, for example, enabling $X_{s,1} \neq \log(K_s)$.

The posterior probability that is used to estimate the parameters is proportional to

$$\prod_t \Pr(I_t|X_t)\Pr(Y_t|X_t)\Pr(X_t|X_{t-1}, r, K, \log(F_t))\Pr(X_1)\Pr(r)\Pr(K)\Pr(\log(F_t)).$$

12.3.3 Simulation Test

We conducted a simulation test to examine the performance of the ecosystem model. We assumed three species ($S = 3$) and used the Gompertz–Fox ecosystem model, as previously mentioned. We used $q_s = 1$ for all species, assuming that the biomass for each species was known, for simplicity. The parameters in the simulation model were established, as listed in Table 12.1.

The 100-year time-series data were generated, and the last 50 years were subsequently employed for the parameter estimation (Fig. 12.2). The populations for each species were assumed to be at equilibrium without fishing when the simulation started. Thus, we did not assume that $P_{s,0} = K_s$ in the estimation model. The parameter estimation was conducted using WinBUGS (Meyer and Millar 1999). We ran two Markov chain Monte Carlo (MCMC; Gelman et al. 2003) simulations with 20,000 iterations for each simulation and discarded the first 10,000 iterations as burn-in samples. We retained every fifth draw for each chain and discarded the remaining draws to save computer storage. The convergence of Markov chains was

Table 12.1 True values of parameters set in the simulation and the prior distributions of hyperparameters in estimation

Parameter	Value			Estimated	Prior distribution
$\log(A_r)$	0.2			Yes	$\log(A_r) \sim \mathrm{U}(-4,1)$
B_r	−0.25			Yes	$B_r \sim \mathrm{U}(-2,2)$
σ_r	0.1			Yes	$\sigma_r^2 \sim \mathrm{IG}(0.01,0.01)$
$\log(A_K)$	1000			Yes	$\log(A_K) \sim \mathrm{U}(4,11)$
B_K	0.25			Yes	$B_K \sim \mathrm{U}(-2,2)$
σ_K	0.1			Yes	$\sigma_K^2 \sim \mathrm{IG}(0.01,0.01)$
	Sp1	Sp2	Sp3		
W	0.1	1.0	20.0	No (fixed)	NA
Q	1.0	1.0	1.0	No (fixed)	NA
diag(Q)	0.1	0.1	0.1	Yes	$Q \sim \mathrm{IW}(E_4)$
τ	0.1	0.1	0.1	Yes	$\tau^2 \sim \mathrm{IG}(0.01,0.01)$
η	0.1	0.1	0.1	Yes	$\eta^2 \sim \mathrm{IG}(0.01,0.01)$
ξ	0.1	0.1	0.1	Yes	$\xi^2 \sim \mathrm{IG}(0.01,0.01)$
Correl					
Sp1		0.7	−0.5	Yes	$Q \sim \mathrm{IW}(E_4)$
Sp2			−0.6	Yes	

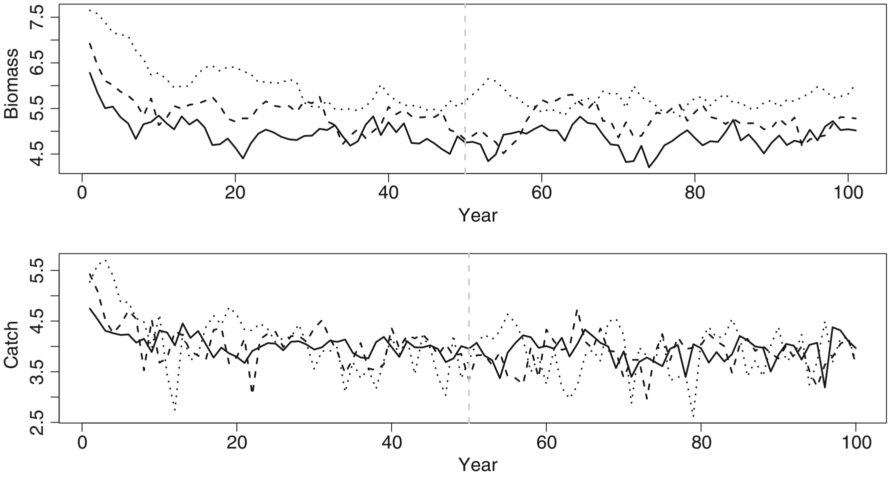

Fig. 12.2 Example of simulated data

based on whether the $\widehat{R}$ calculated from the two chains was close to one for all estimates (Gelman et al. 2003). The prior distributions for hyperparameters are listed in Table 12.1.

We repeated the simulations 100 times and evaluated the relative bias of F_{MSY}, B_{MSY}, and MSY using the single- and multispecies models. The multispecies model corresponds to the model with the previously mentioned specification and is the same as the data-generation model. The single-species model has no correlation among the population dynamics of the species, that is, all components other than the diagonal in the Q matrix are set to zero.

The median values of the estimated biological reference points (MSY, F_{MSY}, and B_{MSY}) for single- and multispecies models were similar (Fig. 12.3). However, the variance of B_{MSY} for the single-species model is conspicuously larger than the variance of B_{MSY} for the multispecies model. The root mean square errors (RMSE $= (\mathrm{Bias}^2 + \mathrm{Var})^{0.5}$) were 0.37 (MSY), 0.53 (F_{MSY}), and 1.35 (B_{MSY}) for the single-species model and 0.21 (MSY), 0.57 (F_{MSY}), and 0.76 (B_{MSY}) for the multispecies model. Thus, the multispecies model is expected to provide more precise biomass estimates than the single-species model.

12.3.4 Application to Real Data

Matsuda et al. (1992) demonstrated the phenomenon that is referred to as the species replacement in the North Pacific Ocean. Pacific sardines were the dominant species in the landed catch of pelagic fish around Japan in the 1930s. They declined to lower levels until the 1950s. During this time, catches of horse mackerel, Pacific saury, and

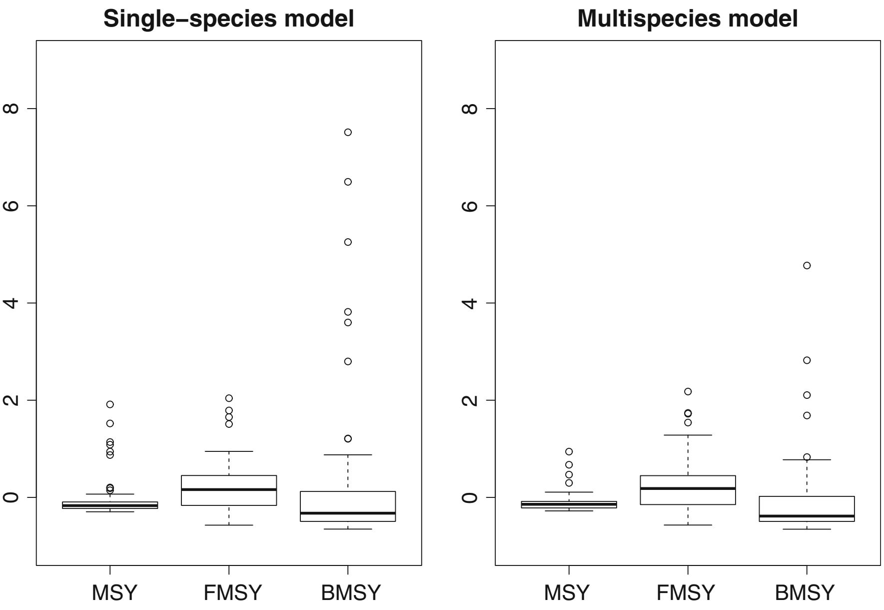

Fig. 12.3 Boxplot of bias between estimated biological reference points and true biological reference points

anchovy increased. They showed signs of decline, at which point chub and spotted mackerel increased and became the dominant species. In the 1980s, Pacific sardine rapidly increased and became the most dominant species (Matsuda et al. 1992).

The importance of species interaction, environmental factors, or fishing pressure as a driver of multispecies population dynamics is an interesting topic. Although Matsuda et al. (1992) provided a hypothetical model to explain species replacement, they did not fit their model to the data in a statistical manner. In this article, we applied our multispecies model to data for three of these species in the western North Pacific Ocean that were considered to have shown species replacement: chub mackerel, sardine, and anchovy (Matsuda et al. 1992). The biomass and catch for each species were extracted from the stock assessment reports of the Fisheries Agency of Japan (chub mackerel, Kawabata et al. 2013b; sardine, Kawabata et al. 2013a; and anchovy, Watanabe et al. 2013). We added the Pacific Decadal Oscillation (PDO) index for winter as an environmental factor (http://jisao.washington.edu/pdo/). Because the catch statistics of anchovy begin in 1978 and end in 2012, we extracted the data for this period from all species (Fig. 12.4) and the PDO index.

We fitted three models to the data: (1) full model, (2) species interaction-only model, and (3) environmental effect-only model. In the full model, the population dynamics of the three species followed the Gompertz–Fox model, and the PDO index was described by the first-order random walk model. All components of the variance–covariance matrix Q were estimated. In the species interaction-only model,

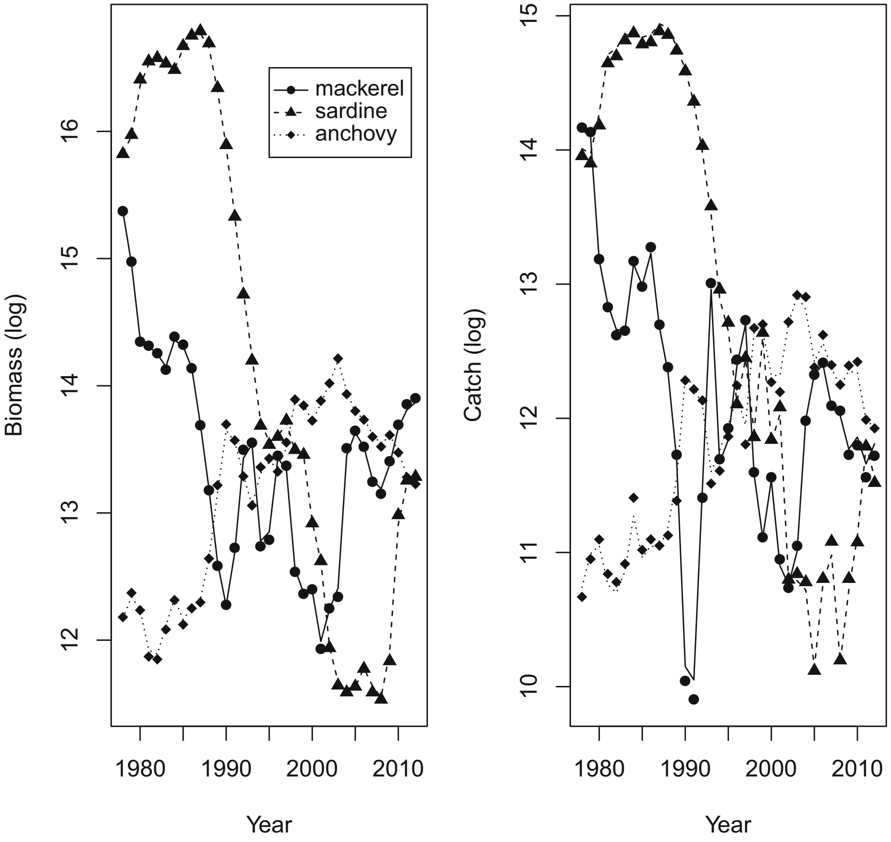

Fig. 12.4 Observed catch (dots) and predicted (lines) catch and biomass of three species (chub mackerel, sardine, and anchovy) from the western North Pacific

the model was equal to the full model, with the exception that the components of the interactions between each species and the PDO index in the Q matrix were set to zero. In the environmental effect-only model, the model was equal to the full model, with the exception that the interaction components among the species in the Q matrix were set to zero.

We employed a Bayesian approach to estimate the parameters. We ran two MCMC simulations with 200,000 iterations for each simulation and discarded the first 100,000 iterations as burn-in samples. We retained every 50th draw for each chain and discarded the remaining draws to conserve computer storage. The convergence of the Markov chains was determined by whether the $\widehat{R}$ that was calculated from the two chains was close to one for all estimands. The prior distributions are provided in Table 12.2. Because we had biomass estimates in this case, we fixed $q_s = 1$ for all species.

Table 12.2 Prior distributions of the hyperparameters in real data application

Parameter	Prior distribution
$\log(A_r)$	$\log(A_r) \sim \mathrm{U}(-4,1)$
B_r	$B_r \sim \mathrm{U}(-2,2)$
σ_r	$\sigma_r{}^2 \sim \mathrm{IG}(0.01,0.01)$
$\log(A_K)$	$\log(A_K) \sim \mathrm{U}(10,20)$
B_K	$B_K \sim \mathrm{U}(-2,2)$
σ_K	$\sigma_K{}^2 \sim \mathrm{IG}(0.01,0.01)$
Q	$Q \sim \mathrm{IW}(\mathrm{E}_4)$
τ	$\tau^2 \sim \mathrm{IG}(0.01,0.01)$
η	$\eta^2 \sim \mathrm{IG}(0.01,0.01)$
ξ	$\xi^2 \sim \mathrm{IG}(0.01,0.01)$

The median posterior trajectories of the predicted catch and biomass were superimposed on the observed data on a logarithmic scale; they revealed a good fit (Fig. 12.4). The median posterior estimates of the correlation between chub mackerel and sardine, between chub mackerel and anchovy, and between sardine and mackerel were 0.17, 0.32, and –0.17, respectively. The median posterior estimates of the correlations between chub mackerel and the PDO index, between sardine and the PDO index, and between anchovy and the PDO index were 0.079, 0.13, and –0.02, respectively. Thus, the correlations between each species and PDO seem to be substantially weaker than the correlations among the species. The deviance information criteria (DICs; Gelman et al. 2003) were –44.89 for the full model, –70.64 for the species interaction-only model, and –61.75 for the environmental effect-only model. These results indicate that species interactions are more influential than the environmental effect.

The posterior medians of F_{MSY} and B_{MSY} for the full model were 0.16 and 1,270,499, respectively, for chub mackerel; 0.07 and 11,984,999, respectively, for sardine; and 0.05 and 57,674,951, respectively, for anchovy. These values were similar for the species interaction-only model but considerably differed for the environmental effect-only model, in particular for B_{MSY}. The large differences in B_{MSY} when disregarding species interactions were anticipated from the previous simulation results. These results indicate that the species interactions should be very influential for these three species in the western North Pacific. The relative biomass and fishing rates compared with B_{MSY} and F_{MSY} are shown in Fig. 12.5. In general, the biomasses tend to increase and the fishing rates tend to decrease.

12.4 Discussion and Conclusion

Modeling is an important and indispensable component for ecosystem assessment. We have mentioned a range of ecosystem models from minimum realistic models, such as MSVPA and MULTSPEC, to end-to-end models, such as EwE and Atlantis. Although they have provided essential insights for ecosystem questions and

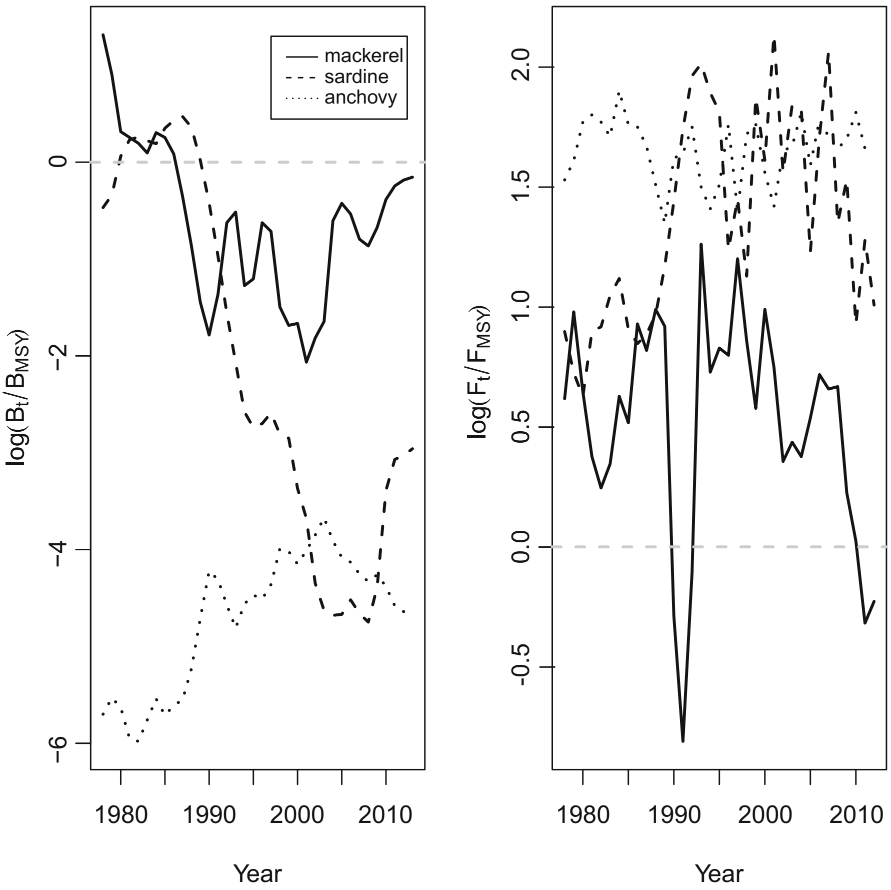

Fig. 12.5 Estimated relative biomasses and fishing rates

hypotheses, they usually require direct information about species interactions, such as diet-composition data from stomach contents. In addition, they are not a statistical model and do not compensate for missing data. They often require unrealistic assumptions, such as equilibrium when fishing started or mass balance in a certain period. Therefore, their application to data-poor situations is difficult. The model that we proposed in this chapter is based on accessible data from fisheries statistics; it does not require diet-composition data and unrealistic assumptions, such as equilibrium when fishing started. Because it is a state-space model, the missing observations are naturally treated. Thus, it can be employed as a model for data-poor situations.

Although we directly estimated a variance–covariance matrix in our example, an increase in the number of species may be problematic. One method is the use of an allometric function relationship, even for species interactions (Woodward et al. 2005). Alternatively, we could use a deterministic functional response form, such as EwE and the Koen-Alonso and Yodzis model. The number of parameters in the species interactions increases as the number of species increases; we would like to know which interactions are strong or weak or if direct and indirect interactions exist. We can employ statistical techniques such as lasso (James et al. 2013), which permits some weak parameters to be exactly set to zero using an L_1 penalty. This operation will help circumvent the overfitting of model to the data. We can use copulas to model flexible multivariate correlations (Hosack et al. 2014). Although we assumed a time-invariant variance–covariance matrix, it should be extended to a time-dependent variance–covariance matrix that should probably include biomass and environmental factors as explanatory variables.

Calculation time is one problem in the applications. We used WinBUGS for our analysis, which required a considerable amount of time for convergence, even for a three-species model. When extending to models that include a larger number of species, we need a refined and advanced calculation algorithm because our model has many random effects that require multiple integrations.

Our model indicated a small influence of PDO on the three species. However, this finding does not suggest that each species was unaffected by all environmental effects. The environmental effects comprise a mix of various components; thus, one index, such as PDO, may be insufficient. In addition, the environmental effects may be diluted with time lags and age effects. Species at a similar trophic level may exhibit similar (nonlinear) trends due to cumulative environmental effects. Therefore, we exercise caution when interpreting the results from the model.

DIC suggested that species interactions were more influential than the environmental effect (PDO). Sugihara et al. (2012) investigated the population dynamics of sardine and anchovy and the time-series data of sea surface temperature to detect causality in the ecosystem. They concluded that the sardine and anchovy had no or little direct interaction and that their dynamics were significantly affected by the environmental effect. This finding seems inconsistent with our results. One reason for the difference is that we only addressed correlations, whereas Sugihara et al. (2012) examined the existence of causality. In addition, the DIC may not be an appropriate index for model selection in this example. Nevertheless, we cannot negate that species interactions in the western North Pacific may be stronger than species interactions in California. Our model will provide a tool for examining species interactions and comparing and combining the results with the results from convergent cross-mapping (Sugihara et al. 2012).

Although the biological reference points were estimated, their use in multispecies management remains uncertain. F_{MSY} and B_{MSY} should only be considered as optimal points when other species are unchanged or in an equilibrium state. Based on the dynamics of nonequilibrium, the best management strategies should probably be examined using simulation trials. Because the multispecies model can provide accurate biomass estimates from our simple simulation exercise, its use as an ecosystem model is assuring and encouraging because biomass information remains important for fisheries management (Punt et al. 2013).

We hope that our new model is useful for solving various ecosystem problems and contributes to a reduction in overfishing and overfished populations (Hilborn and Hilborn 2012) for data-poor situations. Our model can be extensively employed for assessing data-poor ecosystems and as an operating model for MSE.

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Part IV
Perspectives

Chapter 13
Toward Sustainable Fisheries in the Eternal Ocean

Takashi Yamakawa, Ichiro Aoki, and Akinori Takasuka

Abstract The contributions of all the chapters in this book are integrated to give a perspective on the requirements for realizing the sustainable fisheries of dynamic resources. A comprehensive overview of the whole process of data gathering, analyzing, and decision-making for fisheries assessment and management is presented in a sequential adaptive way as a plan-do-check-act (PDCA) cycle and illustrated in a schematic diagram. The process is a loop of sequential information updates and adaptive decision-making in the actual world parallel with the corresponding virtual world. Some points along the panoramic diagram are discussed with reference to discussions in previous chapters. Issues discussed are (1) diversity of management objectives and performance measures: multidisciplinary approach; (2) development of harvest control rules (HCRs); (3) revealing dynamics of stocks, communities, and ecosystems: mechanistic approach; (4) value of monitoring for adaptive management: empirical approach; (5) assessment models vs. operating models: to what extent should they be complex?; and (6) social institution and organization for fisheries management. The ocean is eternal in its existence; however, its components are never static but dynamic. Since fish communities dynamically change with climate-induced ocean regime shifts, we humans have no choice but to adapt to the nature of ecosystems. The benefits of the ocean will be eternal for us only if we successfully achieve such an adaptation.

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Keywords Adaptive management · Ecosystem approach · Eternal ocean · Fisheries management · Monitoring · PDCA cycle · Population dynamics · Regime shift · Stock assessment · Sustainability

13.1 Sustainable Fisheries of Dynamic Resources

So far, we have discussed individual issues in each discipline regarding the urgent problems affecting the sustainable and effective utilization of fisheries resources. These resources are finite but reproducible (feature (1)), with inherent variability and uncertainty in space and time (feature (2)), and without ownership in nature (feature (3)) as mentioned in Chap. 1 (Fig. 1.2). We have given several perspectives for each aspect concerning "dynamics of fish stocks in marine ecosystems" (Part I), "monitoring systems" (Part II), and "management models" (Part III) (Fig. 1.3). In the present chapter, we will integrate the contributions of all chapters and give a perspective on requirements for realizing sustainable fisheries for dynamic resources.

To this end, it is necessary to review all aspects from a goal-oriented, complementary, and synergistic view in a multidisciplinary, integrated approach, enabling sustainable fisheries. Here, we will present an overview of the entire process in a comprehensive schematic diagram including data gathering, analyzing, and decision-making for fisheries assessment and management in a sequential adaptive way as a plan-do-check-act (PDCA) cycle. Then, we will discuss some issues in the panoramic diagram with reference to discussions in previous chapters. Our main objective is to provide an overview of the entire process of fisheries assessment and management as a loop of sequential information updates and adaptive decision-making in the actual world parallel with the corresponding virtual world and to give a perspective of sustainable fisheries in light of the loop structure. For an overview of the current status and perspectives of each issue, please refer to each previous chapter for details.

13.2 Fisheries Assessment and Management as a Loop of Sequential Information Updates and Adaptive Decision-Making

An overview of the entire process of fisheries assessment and management is shown in a comprehensive schematic diagram (Fig. 13.1). This figure is similar to Fig. 11.1, overviewing the process of basic management strategy evaluation (MSE), but is more comprehensive including additional detailed aspects such as the dynamics of stocks, communities, and ecosystems in actual and virtual worlds and the external environmental effects. The main topic of each chapter is also specified in this diagram.

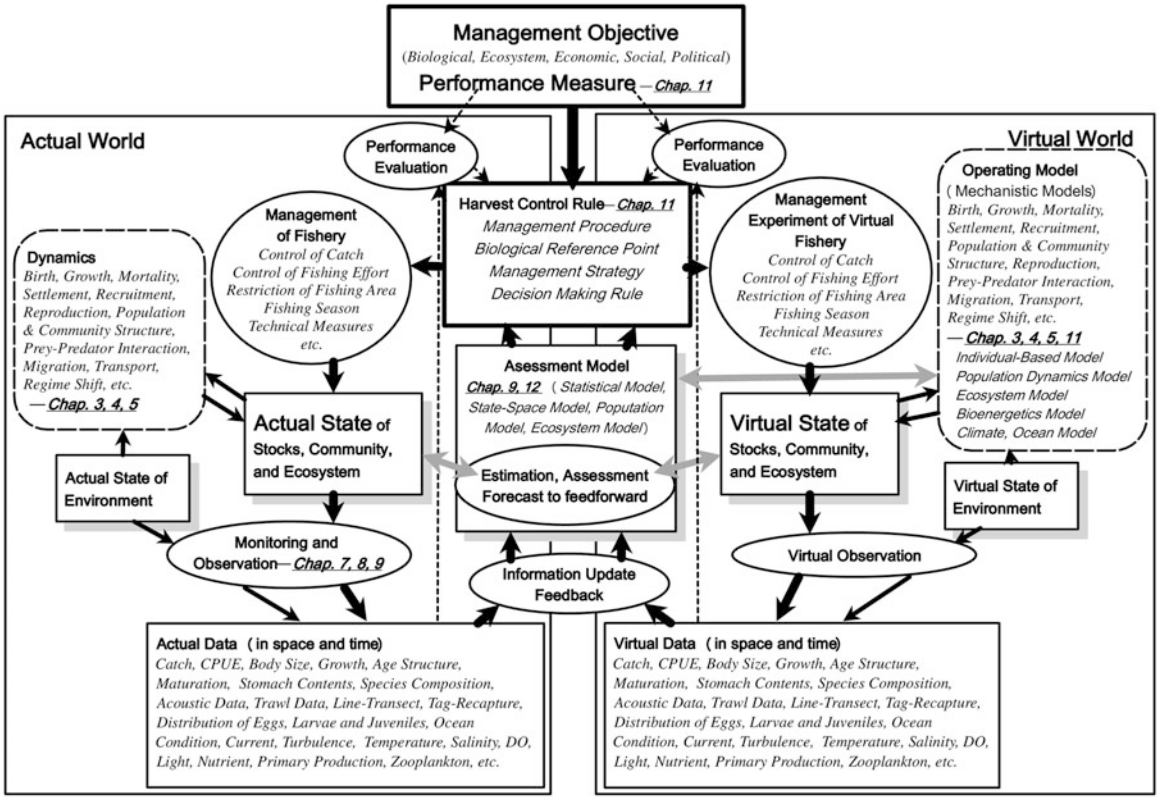

Fig. 13.1 A schematic diagram overviewing the entire cycle of adaptive fisheries management by using concurrent feedback loops in actual and virtual worlds. Elements and actions in the management process are enclosed in rectangles and ellipses, respectively. "Dynamics" and "operating model" are enclosed in dashed rectangles with rounded corners to emphasize their symmetric properties. Arrows indicate information flow (black) and comparisons (gray). Black thick arrows: the main loop. Dashed arrows: flow for performance evaluation. The loop structure is identical to the plan-do-check-act (PDCA) cycle, which is an iterative management method used in business for the control and continuous improvement of processes and products

The first step toward realizing sustainable fisheries is identifying an adequate management objective (i.e., goal, target, expected output) and the corresponding performance measure (i.e., success metrics) (Chap. 11). Next, a management strategy and harvest control rule (HCR) (or decision-making rule) comprising adequate biological reference points (BRPs) are planned to effectively attain the management objective (Chap. 11). The actual management of the fishery is implemented through control of catch, effort, etc., by following the predetermined HCR. As a result of fishing activity and natural dynamic processes (Chaps. 3, 4, and 5), including external environmental effects (disturbance), the state of fisheries stocks and the status of the surrounding community and ecosystem will change. In the following step, data are collected from the stocks, community, and ecosystem through sequential monitoring and observation (Chaps. 7, 8, and 9), which are utilized to assess their status. In the assessment process (Chaps. 9 and 12), information (data) is updated and inputted into the assessment models, to estimate the parameters representing the past and present resource status and to predict the future status. The HCR performance is then evaluated by the predetermined performance measure, and the validity of the management strategy is reviewed. By integrating the knowledge generated thus far from the entire learning process, the management strategy (HCR) can be adapted to improve the performance, and the management objective can be reformulated when necessary. Thereafter, the management cycle enters the next cycle, and the steps are repeated for continual improvement.

This cycle of fisheries assessment and management is identical to the PDCA cycle (Shewhart and Deming 1939, Deming 1986), which is an iterative management method used in business for the control and continuous improvement of processes and products, also known as the Deming/Shewhart cycle, plan-do-study-act (PDSA) cycle, or observation-plan-do-check-act (OPDCA) cycle. In the above cycle of fisheries assessment and management, setting a management objective, performance measure, and HCR is identical to "plan" in the PDCA cycle; implementation of the fisheries management is equivalent to "do"; monitoring, data observation, assessment, and performance evaluation correspond to "check"; and adaptive adjustment of management strategy (HCR) and management objective is "act (adjust)." Thus, the cycle is used as a systematic series of steps for learning valuable information and knowledge for continual and adaptive improvement of the process. Such an adaptive framework through sequential information updates is essential to fisheries management since the target fisheries resources show inherent variability and uncertainty as mentioned in Chap. 1.

One of the reasons for difficulties in fisheries resource management, other than the variability and uncertainty of stocks, is that we are not able to prove the validity of models, assumptions, and HCRs by repetitive experiments using natural stocks, communities, and ecosystems. To overcome this problem, we can create a virtual reality (i.e., virtual world in Fig. 13.1) to model the dynamics of the actual world using an operating model (OM) and perform repeated experiments in the virtual world to reproduce the whole process of fisheries assessment and management along the PDCA cycle. In computer simulation, it is possible to evaluate the performance of the entire management system since we are allowed to determine the failure/

success of the assessment and management, as the true status of the virtual resource is known. Moreover, by assuming a wide range of scenarios corresponding to various uncertainties in the virtual reality and repeating thousands of computer simulations, it is possible to develop a robust process to adequately consider the uncertainties. Figure 13.1 includes the framework to improve the management system by using the virtual world, where assessment models and the HCRs play a key role in bridging the actual world and the virtual world.

From the next section, the elements in the loop structure in Fig. 13.1 are traced individually, to provide perspectives for sustainable fisheries following the contributions of previous chapters.

13.3 Diversity of Management Objectives and Performance Measures: Multidisciplinary Approach

The management objectives can be biological, ecological, economic, social, and political (Hilborn 2007), as discussed in Chap. 11. In Fig. 13.1, only biological and ecological elements are incorporated in the diagram for simplicity. However, elements related to bio-economic or socioeconomic issues such as cost function, price-formation mechanisms based on a balance between demand and supply, employment numbers, marketing processes, etc., can also be incorporated in the same framework if economic, social, and political management objectives are targeted. Makino (2011), Makino et al. (2014), and Makino and Sakurai (2014) presented a figure overviewing the entire "fisheries system"—from where the target species hatch and develop at sea to being fished, distributed, processed, and served onto consumer plates—and assigned corresponding management measures to each step. They emphasized the need for integrated management through *integrated research*, which they defined as "interdisciplinary research for society and human well-being which deals with the sustainability of dynamic fisheries systems, taking various knowledge, values, and needs into account." Such multidisciplinary approaches are required to attain a management objective to pursue diverse values in the real society.

Once the management objective is established, the performance measure to correctly evaluate the performance of the management strategy and HCR is defined. For example, if the management objective is defined by the biological production in yield base, trade-offs among average yield, year-to-year variability of yields, minimum stock size, etc., should be incorporated in the performance measure with appropriate weighting on each objective to include the trade-offs among different objectives. If the management objective is socio-ecological, then the performance measure should be devised to include the trade-offs among socio-ecological indices.

As stated in Chap. 1, if large population variability and species alteration are inevitable in natural systems, it would be necessary to manage total fish productivity based on multispecies integration at the fish community level rather than the single-species approach. Establishment of clear management objectives for adaptive multispecies/ecosystem utilization is required by multidisciplinary interactions. Appropriate definitions of ecosystem indicators should be included in the performance measures to maintain a healthy balance and function of the fish community and ecosystem. Macroscopic analysis, such as body-size spectrum and species abundance distribution (SAD) of the overall community/ecosystem, might aid in investigating the balance and function of the system.

For a multidisciplinary approach, the spatiotemporal scales of information in the "loop" should match the common standards according to the management objectives and actions. For example, information explaining the fluctuation of fisheries resources based on events in a small local spatial scale, e.g., such as per each individual and/or patch of larval and/or juvenile fish, cannot be applied in their original scale to the management of the entire stock. Similarly, information on events in time scales in minutes and/or hours cannot be applied to actual management in annual scales. Thus, it is important to specify the target spatiotemporal scales of information to be applied to management actions in advance and to aggregate all information from each sector toward the common scale. Additional errors can emerge in varying degrees, when scaling information up and down, and all participants (scientists) from different sectors should acknowledge this in advance.

13.4 Development of Harvest Control Rules (HCRs)

In Chap. 11, necessary developments of HCRs were discussed as follows: (1) incorporating the effect of changes in climate and fish stock productivity, (2) improvement from simple HCRs which only control catch quotas into comprehensive HCRs combining other effective measures (e.g., the establishment of closed areas such as marine protected areas (MPAs), control of fishing season, etc.) to manage highly fluctuating and vulnerable species, (3) HCRs that can be applied to ecosystem-based fisheries management (EBFM), and (4) HCRs including socioeconomic objectives involving multiple stakeholders.

Thus, diverse management objectives and measures will be included in future HCRs, and it is critical to optimize each HCR to adapt to the differences in management objectives and measures. Optimal HCRs will be developed by iterating the PDCA cycle with intensive computer simulations in the virtual world parallel with information updates in the actual world as discussed above.

Regarding climate change, Tsuyoshi Kawasaki, who conceptualized regime shifts (Kawasaki 1983), suggested, "the fundamental issues for stock management will be to wisely utilize resources in concert with the rhythms of the regime shift, not so as to destroy them" (Kawasaki 2002). Thus, adjusting fishing pressure flexibly according to the productivity in each regime is desirable (MacCall 2002). Regime shifts can be detected by monitoring fisheries resources and environments, but it is necessary to react to the shift a posteriori since prediction of regime shifts is difficult at present. Therefore, management actions in preparation of important incidents such as the occurrence of prominent year classes, and abrupt decreases in stock productivity, should be agreed among stakeholders as HCRs beforehand. Thus, HCR development to contend with regime shifts is an urgent matter.

13.5 Revealing Dynamics of Stocks, Communities, and Ecosystems: Mechanistic Approach

Chapters 3, 4 and 5 in Part I illustrated how ecological processes in life histories and biological interactions in fluctuating ocean environments cause fish stock variability in space and time in major fish groups with different life histories: small pelagic fish (Chap. 3), demersal fish (Chap. 4), and sharks (predatory fish) (Chap. 5). Understanding the dynamics of each group explains uncertainty in stock variability and provides an essential biological base in fisheries management. Here we discuss the role of understanding fisheries resource dynamics based on life history patterns, which is a mechanistic approach to improve our understanding of the dynamics of natural ecosystems. In contrast, Sect. 13.6, "Value of Monitoring," discusses an empirical approach that is effective for practical applications in adaptive fisheries management.

Figure 11.4 in Chap. 11 shows the differences in life history traits among fishes in waters around Japan on a continuum from those with short life spans and high r (upper left in the figure) to those with long life spans and low r (lower right in the figure). The former and the latter types are identical to opportunistic and periodic strategists, respectively, as proposed by Winemiller and Rose (1992) and Winemiller (2005). They classified fish life history strategies on a triangular surface with three typical endpoints: periodic, opportunistic, and equilibrium strategies. These strategies are characterized as follows: periodic (long-lived, high fecundity, and high recruitment variation), opportunistic (small, short-lived, high reproductive effort, and high demographic resilience), and equilibrium (low fecundity, large egg size, parental care, low demographic resilience, and better conformation to assumptions of density-dependent recruitment). Among these, the opportunistic and equilibrium types correspond to the classic r- and K-strategists, respectively.

Fishes discussed in Part I in the present book can be classified as follows: small pelagic fishes (Chap. 3) are "opportunistic," walleye pollock (Chap. 4) is "periodic," and sharks (Chap. 5) are "equilibrium." The differences in life history features can lead to differences in population dynamics in terms of stock variability, productivity, resilience, and density dependency; hence, it is important to construct effective measures for stock management depending on each life history type. For example, in Chap. 4, it was proposed that demersal fish should be managed to maintain critical stock levels, whereas small pelagic fish should be managed not to disturb the recovery in favorable environments. For sharks, fishing pressure should be kept low considering their lower demographic resilience, and different management between sexes might be required. We should also consider the effect of fishing pressure on unexpected evolution of life history traits (Garcia et al. 2012).

In actual management, such differences in life history features and population structures (e.g., metapopulation) should be incorporated in the operating and assessment models and HCRs. Detailed understanding of the mechanisms of population dynamics of each life history type would be helpful in developing the models. When detailed information is lacking, species ordination according to life history types provides suggestions on default parameter values, model configuration, and the management actions required.

There are three kinds of values for understanding the dynamics of stocks, communities, and ecosystems: (1) description of dynamics for use in operating models, (2) incorporation of the knowledge into assessment models, and (3) intrinsic values to understand the natural dynamics independently. Among these, for value (1), mechanistic models are utilized to provide underlying virtual realities of the world including the consequences (i.e., future projections) of management actions. Therefore, the "operating model" in Fig. 13.1 in the virtual world (upper right) is located in contrast to "dynamics" in the actual world (upper left) to reflect the mechanism of the dynamics. Regarding value (2), assessment models are not necessarily mechanistic: statistic empirical models might also work effectively as assessment models. However, improved understanding of the dynamics provides valuable suggestions on constructing effective assessment models.

Regarding value (3) from the perspective of fishermen conducting actual fisheries, improving knowledge of the dynamic mechanisms of stock variability and fishery formation of target resources suggests the way to wisely use resources, other than stock management, by using this information to maximize the efficiency of short-term/long-term fishing activities. This is also one of the most important goals of the research on fisheries resources. For example, if information from short-term forecasts is available, fishermen can effectively select daily fishing grounds, fishing gear, and target species and develop strategies for processing and marketing. However, continual information from real-time monitoring would sometimes be more useful than forecasting with uncertainties, as discussed in the next section.

Since the development of the regime shift concept (Kawasaki 1983), fisheries scientists have improved the understanding of mechanisms underlying regime shifts as reviewed in Chap. 3. Consequently, the concept has gained broad acceptance that long-term fluctuations of fisheries resources (and/or species alteration) are inevitable as inherent natural mechanisms, and it has allowed fishermen to develop long-term strategies of investment, vessel design, and vessel equipment, to adapt their fishing operations to natural shifts (e.g., switching target species (Katsukawa 2002) by using multipurpose fishing vessels). For fisheries managers, long-term perspectives on the mechanisms of fish stock variability allow for the development of appropriate management policies and institutions that take possible future events within the scope of the assumptions into account. Scientific advice based on the best available information and hypotheses will allow for effective fisheries management and strategic policy making based on the premise of regime shift and global warming.

13.6 Value of Monitoring for Adaptive Management: Empirical Approach

Chapters 7, 8 and 9 in Part II reviewed the development and current status of advanced technologies and systems that monitor changes in fisheries resources and marine ecosystems: fishery-independent biological sampling (Chap. 7), acoustic surveys (Chap. 8), and fish stock monitoring (Chap. 9). Additionally, technologies for environmental oceanic monitoring have greatly improved through satellite remote sensing. Data observation through continuous monitoring by such technologies and systems is a key element for conducting adaptive management (PDCA cycle as shown in Fig. 13.1) of stocks, communities, and ecosystems that exhibit inherent variability and uncertainty in space and time.

There are two types of approaches in control engineering, which can also be utilized for fisheries management: feedback (closed-loop) control and feedforward (open-loop) control. Feedback control plays a central role in adaptive management. It is an empirical, inductive process that continually adjusts the management while sequentially monitoring the resource state (stocks, communities, and ecosystems) and determines how the resources have responded to the management action. With the premise that future resources deviate from expected predictions, it continues to monitor the output in response to the input of the system and corresponds to the change a posteriori but promptly in the PDCA cycle. Thus, the feedback approach is a goal-derived backward (top-down) process with a macroscopic and pragmatic view of the whole system, where the difference between the present status and the target goal is minimized by the iterative loop.

In contrast, the feedforward control system is a mechanistic, deductive process that manages the input action by following a prediction of the future state of the system forecasted a priori with deductive models. Thus, the feedforward approach is a fact-derived forward (bottom-up) process with a mechanistic and cumulative view of elements that interact, where emergent properties often greatly affect the system dynamics. Such feedforward control systems will be effective if the future prediction is accurate, but there is a risk of having the opposite effect when the prediction exhibits large errors. In control engineering, however, both advantages of the feedback and feedforward processes are often combined in one control system to enhance the performance and stability of the system.

Walters (1989) assessed the expected improvement in management performance using short-term forecasts (i.e., feedforward control) in comparison to a flexible regulatory system with an in-season monitoring (i.e., feedback control) by using stochastic dynamic programming. Numerical studies on test cases revealed that for unproductive stocks, only modest improvements (5–15%) could be expected from short-term forecasting (i.e., feedforward control), no matter what in-season regulatory system is used. For productive stocks, large (30–50%) improvements would be possible if they were managed with inflexible annual quotas set before each fishing season (i.e., feedforward control), but only if perfect preseason forecasting were practical. For productive stocks, only modest improvements in average yield

(5–10%) could be expected from improved forecasting if managed with flexible in-season systems (i.e., feedback control). Thus, flexible feedback of information through continuous monitoring is very important to maintain the basic performance of the management system, except when accurate forecasts regarding the future state can be utilized.

There are other important monitoring values, in addition to those mentioned above. One is to provide indispensable information (data) to reveal dynamic mechanisms of the natural system as already discussed in Sect. 13.5. The other is to utilize real-time information on fishery and oceanic conditions and fishery ground formations for developing short-term fishing tactics by fishermen (Chap. 8). Such data is useful for selecting fishing grounds, fishing gear, and target species on a daily basis to keep the fishing operation profitable.

As stated in Chap. 1, if fisheries management evolves from individual populations to an ecosystem approach (Garcia et al. 2003, Garcia and Cochrane 2005), monitoring will also require a new framework that corresponds to the evolution. Presently, accurate prediction of the future of ecosystem status through deductive modeling of the dynamic processes of complex species interactions is difficult. Therefore, empirical methods through continual ecosystem monitoring are indispensable for maintaining the balance, function, integrity, and biodiversity of the system and utilizing its productivity as a valuable resource. Development of new technologies and systems (Chaps. 7 and 8) will be helpful to construct an effective framework for such an ecosystem approach.

13.7 Assessment Models vs. Operating Models: To What Extent Should They Be Complex?

To discuss the requirements of models for use in fisheries assessment and management, the classification of models for intended usage would be necessary. In Chap. 4, models were classified into three categories: (1) recruitment reproduction model (RRM), (2) recruitment estimation model (REM), and (3) recruitment forecast model (RFM). RRM reproduces past events and dynamics and is used to understand and explain underlying mechanisms. Therefore, it can also be called a "mechanistic" or "explanatory" model, identical to those discussed in Sect. 13.5. REM estimates the status of events that have already happened, so it can also be called an "assessment model" for past events or an "empirical model" in a broad sense. RFM forecasts future events that have not happened yet, so it can also be called a "future prediction" or "future projection" model. Either "mechanistic" or "empirical" model is utilized for RFM by extrapolating the model into the future. For operating models, RRM and RFM are mainly utilized, while for assessment models, REM is mainly utilized.

To what extent should the assessment and operating models be complex? The "overfitting" problem should be noted when considering the degree of model complexity (Tetko et al. 1995). Even if high correlations are observed to explain fluctuation of past events when using models with excessive parameters and data, the accuracy of predicted values for future events calculated from the models could be unexpectedly low. In these cases, the high correlation observed for past events is a false coincidence (artifact) without causal (mechanistic) relationships regarding the cause and effect; thus, it is not information that can be used for management. Since complex models such as ecosystem models often incur the problem of low accuracy for future prediction (i.e., "overfitting"), it is necessary to reconfirm the prediction accuracy of the entire model before practical use. Moreover, for predicting future events, prediction accuracy including the dynamic processes of the physical environment as driving forces of the system, and the target biological processes, should be confirmed. Thus, further multidisciplinary approaches are necessary for such future predictions, while the accuracy of complex models including all interactive factors together tends to be decreased except for data-rich situations.

To develop robust HCRs for uncertainties, we must consider every possibility for future simulations, so that we can turn as many events, which are *beyond the scope of the assumption,* as possible into those *within the scope of assumption*. Therefore, for operating models, it is important to capture the underlying mechanism adequately and describe a wide range of possible events that could occur in the future, irrespective of whether they are simple or complex. In contrast, for assessment models the accuracy of estimation and/or prediction is the most important prerequisite. Thus, simpler models that are robust to uncertainties are favored for assessment models, although it depends on data availability. As stated in Chap. 9, simpler assessment models are favored for data-poor stock assessments, while more complex models are favored for data-rich stock assessments.

The multivariate state-space model proposed in Chap. 12 as an ecosystem assessment model is a simple linear model that can be applied to data-limited situations. Species interaction can be evaluated using the variance-covariance matrix for the error term in the state equation, so does not require diet composition data. The model successfully reduces the number of parameters estimated by utilizing a Bayesian structure on fishing coefficient F, intrinsic rate of natural increase r, and carrying capacity K, where allometric relationships are assumed for the species-specific r and K against average body mass for each species. It can sequentially update information as a linear state-space model and, thus, can be systematically utilized for adaptive management in the PDCA cycle. It can also introduce environmental terms and has enough extensibility toward a goal-oriented, integrative assessment model and operating model. Additionally, it might be possible to introduce a gradual time-evolving structure on r and K in the state equation to properly reproduce the time-series autocorrelation because of long-term regime shifts.

There may be other approaches for maintaining simplicity and robustness of ecosystem models other than the approach without age and/or body-size structure proposed in Chap. 12: one such approach would be a size-based ecosystem model (e.g., Gislason and Rice 1998, Duplisea et al. 2002, Benoît and Rochet 2004, Andersen and Beyer 2006, Pope et al. 2006, Maury et al. 2007, Yvon-Durocher et al. 2008, Andersen et al. 2009, Blanchard et al. 2009, Law et al. 2009, Andersen and Pedersen 2010, Blanchard et al. 2011, Rochet and Benoît 2012). The processes determining fish stock abundance are part of marine ecosystem dynamics mainly driven by prey-predator interactions. The trophic interactions in food chains in marine ecosystems are composed of chains of activities where larger organisms prey on smaller ones; therefore, body size roughly identifies the organism's trophic level in the ecosystem. Even if species composition changes in the community, the shape of size spectrum, which expresses the relationship between body size and biomass in the size class, exhibits relative stability (Cury et al. 2003). The property of the size spectrum implies that while relative abundance between body size classes is stable, absolute abundance in each size class varies with the change in overall productivity of the ecosystem, which is determined by primary production as a scaling factor (Jennings and Brander 2010). Size-based ecosystem models can be composed of simple structures with fewer parameters than complex species-based models, by tracing the energy and matter flow using size-scaling (allometric) properties. Thus, size-based ecosystem models can provide a robust and useful index of global productivity at the ecosystem level and give a macroscopic, suggestive perspective on ecosystem-based fisheries management. For example, using a size- and trait-based ecosystem model, Kolding et al. (2016) revealed that fisheries using balanced, nonselective harvesting in body size and species could produce the highest sustainable yield while maintaining the fish community structure.

13.8 Social Institution and Organization for Fisheries Management

Among the fundamental features of fisheries resources mentioned in Chap. 1, the third feature is ownerless property (Fig. 1.2), which is identical to the situation allegorized by Hardin (1968) of the "tragedy of the commons." To realize sustainable fisheries for dynamic resources under this property, consideration of social institutions and organization for fisheries management is necessary to accommodate multiple stakeholders by defining the overall management framework of who can utilize what resources and how, when, and where.

In this book, we have discussed fisheries resource management in the context of scientific model-based management, which is primarily catch quota control where quantitative output control is conducted based on the PDCA cycle corresponding to various uncertainties including regime shift. This management is suitable for large-scale commercially operated offshore fisheries. It is a centrally planned, top-down management system, where the national government plays a major role to set the quota. In addition to these aspects, there are other important issues regarding actual fisheries management, following the setting of total allowable catch quota (TAC), on who can utilize the quota and when, where, and how. It is the spatiotemporal and/or among-person allocation of the rights to access to the quota as represented by individual quotas (IQ), individual vessel quotas (IVQ), group-specific quotas

(GQ), individual transferable quotas (ITQ), etc., which are, however, beyond the scope of this book.

In contrast, most fisheries management of the coastal, small-scale fisheries, as in Japan, is a community-based, decentralized bottom-up system, where local stakeholders have priority in the decision-making process to target diversity of fishes, invertebrates, and seaweeds using various gears (e.g., see Makino (2011)). The management process in such systems might seem very different from that shown in Fig. 13.1; however, the same PDCA cycle in the figure can also be applied to coastal fisheries although slight modifications to the figure are required: (1) Fishermen, and not a central fisheries research institute alone, play major roles in monitoring the resources through daily operation of their fisheries. The resources to be monitored are locally distributed and very diverse; hence, real-time monitoring by central research institutes requires considerable effort and cost, which cannot be covered by the central institute alone. Therefore, tight collaborative relationships between fisherman communities and local research institutes are sometimes established. Such a cooperative management systems of fisheries resources by the user groups and the government is called "co-management" (Pomeroy 1995, Sen and Nielsen 1996), where the responsibility for the resource is shared between the user groups and the government, and both the community and the government are involved during the decision-making, implementation, and enforcement processes. (2) Management models (assessment models, operating models) and the virtual world are not always computer-based but often depend on undocumented fishermen's expert knowledge through their experiences in the form of traditional ecological knowledge (TEK) (Freeman 1992). (3) Decision-making rules are not based on quantitative HCRs alone, but on various effective measures including input control and technical measures.

Makino (2011) introduced some local experiences and systems in Japan that have developed their own customs and values to manage fisheries resources. In coastal areas, fisheries cooperative associations have the customary property rights to the resources, as territorial use rights in the zoning arrangements of coastal sea areas play a major role in resource management with the participation of fishermen. The interaction between humans and coastal seascape ecosystems in Japan is called *satoumi* (United Nations University Institute of Advanced Studies Operating Unit Ishikawa/Kanazawa 2011, Duraiappah et al. 2012) (*sato* means community and *umi* means sea). The term originates from *satoyama* (*yama* means forest) which describes mosaic landscapes of different types of ecosystem—secondary forests, farm lands, irrigation ponds, and grasslands—along with human settlements managed to produce bundles of ecosystem services for human well-being. The concept of *satoyama*, long-standing traditions that allow sustainable use of natural resources, has been extended to cover marine and coastal ecosystems—*satoumi*. Thus, the relationship between local fishermen and the coastal sea area in their community has come to be called the *satoumi* system, which is sustained by continual management actions through community-based adaptive processes to conserve the health of the coastal ecosystem. Such decentralized bottom-up systems are suitable for local ecosystem-approach flexibility, since there is no single solution for fisheries management implementation in diverse situations in nature and customs.

Ostrom (1990) identified eight "design principles" of stable local common-pool resource (CPR) management:

1. Clearly defined boundaries (effective exclusion of external un-entitled parties)
2. Rules regarding the appropriation and provision of common resources that are adapted to local conditions
3. Collective-choice arrangements that allow most resource appropriators to participate in the decision-making process
4. Effective monitoring by monitors who are part of or accountable to the appropriators
5. A scale of graduated sanctions for resource appropriators who violate community rules
6. Mechanisms of conflict resolution that are cheap and of easy access
7. Self-determination of the community recognized by higher-level authorities
8. For larger common-pool resources, organization in the form of multiple layers of nested enterprises, with small local CPRs at the base level

These eight design principles can also be applied to the management of local common fisheries resources and ecosystems that we have discussed.

Concerning the second fundamental feature of fisheries resources mentioned in Chap. 1, "variability and uncertainty" (Fig. 1.2), how can we accommodate our management institutions to the premise of regime shift? Aoki et al. (2005) concluded in the postscript of a book (in Japanese) entitled "Regime Shift and Fisheries Stock Management" as follows: In some fisheries, noticeable discrepancies between current fishery activities and desirable fisheries management practices based on BRPs have been revealed. For example, increased exploitation of low stock levels, targeting of immature fish in large amounts, negative target switching to species with lower stock levels, etc., have been occasionally reported. Overinvestment and overcapacity are the primary reasons for these discrepancies. For example, a problem peculiar to regime shifts occurring at a decadal scale: in the 1980s in Japan, many large vessels were constructed in succession for the purse seine fishery following the rapid increase of the sardine (*Sardinops melanostictus*) stock levels; however, the stock dramatically decreased in the 1990s as a consequence of a regime shift. The remaining overcapacity of purse seine vessels then rushed to catch another target species, i.e., chub mackerel (*Scomber japonicus*), to maintain their profit. Therefore, excess fishing effort was concentrated on the mackerel stock, which delayed its recovery. Thus, there was a fundamental problem of mismatch between the duration of the high-level resource phase (10–15 years) caused by regime shift and the durable life period of vessels (20–25 years). Effective social measures to solve such long-term problems are necessary by setting clear long-term management objectives and performance measures and economically motivating fishermen for sustainable fisheries management through the establishment of appropriate institutions.

13.9 Sustainable Fisheries in the Eternal Ocean

Like the aphorism, *Panta rhei* (*everything flows*) by the pre-Socratic Greek philosopher Heraclitus, a passage from a famous old Japanese epic *The Tale of the Heike* (*Hieke Monogatari* in Japanese) about the struggle between the once-prosperous Taira (*Heike*) and the emerging Minamoto clans written in the thirteenth century sings:

> The sound of the Gion Shōja bells echoes the impermanence of all things; the color of the sāla flowers reveals the truth that the prosperous must decline. The proud do not endure, they are like a dream on a spring night; the mighty fall at last, they are as dust before the wind (translated by H. C. McCullough: McCullough (1988)).

The ocean is eternal in its existence; however, its components are never static but dynamic. Since fish communities dynamically change with climate-induced ocean regime shifts, we humans have no choice but to adapt to the nature of ecosystems. The ocean's benefits will be eternal for us only if we successfully adapt.

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