Behavioral Ontogeny of Marine Pelagic Fishes with the Implications for the Sustainable Management of Fisheries Resources

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Abstract
Behavioral ontogeny of marine pelagic fishes is reviewed in the context of sustainable fisheries resource management. In carangid fishes, development of sensory organs corresponds with their basic behavior such as phototaxis and optokinetic response, whereas the onset of schooling requires the development of the central nervous systems (CNS). Because docosahexaenoic acid (DHA) is indispensable for the development of CNS, quality as well as quantity of prey is important for the development of behavior and thus survival. Among common pelagic fishes, chub mackerel, *Scomber japonicus*, had the best growth performance and their cruise swimming speed was remarkably fast. Japanese anchovy, *Engraulis japonicus*, were slow both at cruise and burst swimming speeds, and were extremely vulnerable to predation by jellyfish. Jack mackerel were slow at cruise swimming speed, but they can make use of jellyfish as a refuge and as a prey collector. Each biotic and abiotic environmental factor, such as water temperature, the amount of phytoplankton, copepods and jellyfish, may work in a positive or negative way for each species, and this can be a driving force for the replacement of predominant fish species. Considering that there are always competition and predator–prey relations among different pelagic fish species, ecosystem based management is indispensable for the sustainable utilization of pelagic fishes.

1. General introduction

Research related to fish early life history has been one of the major subjects in marine science for various reasons. The practical driving force of studying fish early life history is the concern about the management of fisheries resources (Fuiman and Werner 2002). Although a single parental fish provides a large number of offspring, fish eggs and larvae generally suffer a high mortality rate. As a result, modest differences in daily mortality results in orders of magnitude difference of recruitment in the long run (Houde 2002).

In this monograph, I review research on the ontogeny of anti-predator behavior and concurrent developmental changes in pelagic fishes with emphasis on my own work. In Chapter 2, morphological development of a carangid fish, striped jack, *Pseudocaranx dentex*, was described,
then the ontogenetic changes of behavior in this species, described in Chapter 3, were compared to these morphological changes. Because developmental timing of schooling behavior (Chapter 3) was posterior to the morphological development of sensory organs (Chapter 2), development of the central nervous system was speculated to be the limiting factor for the onset of schooling. To test this hypothesis, feeding experiments using docosahexaenoic acid (DHA) enriched or deficient diets were conducted so that development of the brain was manipulated (Chapter 4). Chapter 5 focuses on the association behavior of jack mackerel, *Trachurus japonicus*, with jellyfishes, the ecological functions of which were revealed based on laboratory experiments and field underwater observations. Chapter 6 deals with ontogeny of behavioral characteristics such as swimming speed, schooling, and antipredator performance against jellyfish in common pelagic fishes (jack mackerel, chub mackerel *Scomber japonicus* and anchovy *Engraulis japonicus*). Emphasis was on the understanding of population fluctuation and replacement of predominance among these species which occurs in about a decade of a cycle in Japanese coastal waters. The final chapter provides perspectives towards the sustainable management of fisheries resources.

In this monograph, fish body length was expressed either in total length (TL) or in standard length (SL) depending on the original data. SLs were about 83, 84, 86 and 88% of TL in early juveniles of striped jack, jack mackerel, chub mackerel and anchovy, respectively (Masuda R, unpublished data).

2. **Morphological development of sensory and swimming organs and the central nervous system in the striped jack**

2-1. Introduction

The early life history of fishes is characterized by substantial and dramatic changes in structure that take place over a relatively short period when the larvae encounter a complex and dynamic environment (Fuiman 1996). Such morphological changes provide bases of the performance directly related to survival. Fish morphological changes have been studied both from ecological and aquacultural perspectives. Atlantic herring, *Clupea harengus*, is perhaps the most intensively studied marine fish for its life history, because this species was once extremely abundant and commercially important, then dramatically declined (Blaxter 1985). Red drum is also an intensively studied species in the United States (ex. Fuiman et al. 1999) probably because of its importance for recreational fishing. Behavioral study is also prosperous in coral reef fish larvae, mainly in the context of conservational interest (Leis and McCormick 2002). In Japan, red sea bream, *Pagrus major*, and Japanese flounder, *Paralichthys olivaceus*, are two major fish species intensively studied with their morphology and ecology in early life history (ex. Tanaka 1985; Kawamura and Ishida 1985), due to that they are the two major species of aquaculture and stock enhancement in this country (Masuda and Tsukamoto 1998b). In the temperate north Pacific, northern anchovy *Engraulis mordax* has been a good model species for studying interaction between morphological development and behavioral ontogeny (Hunter and Coyne 1982). Less attention has been paid on the morphological and behavioral development in carangid fishes in temperate waters.

The primary goal of this chapter was to describe morphological changes of sensory and swimming organs in striped jack, *Pseudocaranx dentex*, a carangid fish. Although it is not a common species in Japanese coastal waters, striped jack is highly appreciated as a material of sushi and sashimi in the Japanese market. Therefore, demands from economic aspect are substantial. My interest was to relate morphological changes to the ontogeny of schooling behavior described in the following chapter. Schooling is essentially a form of swimming behavior. Therefore swimming organs are expected to develop prior to the development of schooling. Because vision and lateral line systems are considered to be two major sensory bases for schooling, the developments of these organs were studied (Masuda and Tsukamoto 1996). Information from sensory organs has to be processed in the central nervous system to enable each individual to perform as a member of a highly organized school. A histological study to reveal the development of the brain was also conducted.
2-2. Materials and methods

2-2A. Materials

Materials for studying morphological development (Chapter 2) and ontogeny of taxis and behavior (Chapter 3) were obtained in the hatchery of the Kamiura branch of the Japan Sea-Farming Association (JASFA: presently National Center for Stock Enhancement, Fisheries Research Agency) (Fig. 1). Larvae of striped jack, *Pseudocaranx dentex*, were reared in a 25 m³ outdoor concrete rearing tank. They were fed rotifers beginning on 2 days post hatching (dph) and switched to *Artemia* nauplii and artificial pellets on 20 dph. Both rotifers and *Artemia* were enriched with commercial DHA emulsion before being fed to the fish larvae. Wild copepods collected in adjacent waters by light trap were also provided after 27 dph. The surface light intensity was about 40,000 lux when the weather was clear, and 3,000 to 10,000 lux when it was cloudy. Rearing water temperature ranged from 22 to 25°C. Juvenile fish were transferred to a net pen in a coastal area on 36 dph.

Approximately 100 individuals were collected every 1 to 2 days until 50 dph for morphological and histological analysis. Larvae were fixed in 10% formalin for morphological analysis, skeletal specimen preparation, and lateral line observation. Fish were also fixed by Bouin’s solution for histological analysis and by Karnovsky solution for scanning electron microscopy.

2-2B. Morphology

Preserved larvae and juveniles were observed under a binocular microscope. Total length (TL), pectoral-fin length, dorsal-fin length, caudal-peduncle height and anal and pectoral body height of randomly chosen 43 individuals were measured with an ocular micrometer (Fig. 2). The relationship between total length and each body part was plotted on logarithmic coordinates.

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Fig. 1. Patchy distribution of striped jack larvae (9 dph) in a hatchery tank.
to analyze relative growth. There seemed to be a major inflection point at about 9 mm TL and a minor inflection at about 20 mm TL in all the parameters. Larvae and juveniles were therefore divided into three groups: smaller than 9 mm, between 9 and 20 mm and larger than 20 mm. The measurements of these three groups were fitted to the power equation ($Y = \beta X^\alpha$) separately.

When the constant $\alpha$ of the power equation is close to 1, growth is considered to be isometric (Gould 1966).

The shape of the caudal fin was measured by its aspect ratio, which was the square of the caudal fin height divided by the fin area (Lindsey 1978). To measure the caudal fin area, a caudal fin was traced under a binocular microscope on cardboard. The trace was then cut out, weighed and divided by the unit weight of the cardboard. This procedure was conducted on 20 fish and was repeated three times for each individual to estimate the caudal fin area.

### 2-2C. Histology of eye, lateral line, muscle, bone and the central nervous system

Three to five transparent fish-skeletal specimens were prepared for each sampling date by a standard double staining method (Potthoff 1984). Cartilage was stained with Alcian Blue 8GX, muscles were digested by trypsin and bones and scales were stained with Alizarine Red S. For the histological analysis of body muscle, eye and cephalic lateral lines, 4 mm paraffin sections were prepared from more than three larvae on each sampling date and stained with hematoxylin-eosin. For the observation of cephalic and trunk canal formation, two to three individuals on each sampling date were stained with cyanine. Lateral line and neuromast formation were also observed with scanning electron microscopy. Development of brain and nervous system was also observed histologically based on 6 mm paraffin sections.

### 2-3. Results

#### 2-3A. Morphology

Morphological development in striped jack is as follows. At 3.3 mm TL (1 dph), the body was elongated and larvae had fin folds. Although the lenses were already formed, the retina was not yet pigmented. The anus was open, but the mouth was not. Pectoral fins were round and not well developed. At 3.5 mm (3 dph), the mouth was open and the retina was pigmented. At 4 mm (7 dph), spines developed on the opercles and gas appeared in the swim bladder. At 5 mm (14 dph), the larval fin fold regressed. Flexion of the notochord and development of caudal fin rays began. The bases of the dorsal and anal fins appeared. At 8 mm (20 dph), flexion of the notochord was completed and the caudal fin changed from a round to truncate shape (Fig. 3). Rays of the

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**Fig. 2.** Morphological measurements. ABH: anal body height (body height through anus), CH: caudal fin height, CPH: caudal peduncle height (height of caudal peduncle at narrowest part), D: dorsal fin length (length of the third dorsal fin spine, when formed), PBH: pectoral body height (body height at base of pectoral fin), S: area of caudal fin.
pectoral, first and second dorsal and anal fins were developed. At 12 mm (25 dph), the shape of the caudal fin changed to emarginated. The shape of pectoral fins changed from wide to elongated (Fig. 3). At 15 mm (30 dph), the relative proportion of the head decreased and the caudal peduncle narrowed.

2-3B. Relative growth

Relationships between total length and body part measurements are plotted in Fig. 4 together with power functions for three different stages. The pectoral fin showed remarkable positively allometric growth until 9 mm with \( \alpha \) equal to 1.893 (Figs. 3A, 4A). From 9 to 20 mm, it showed weaker allometry (\( \alpha = 1.577 \)), and beyond 20 mm there was still slight positive allometric growth. Measurements of other body parts showed similar trajectories of growth; strong allometry until 9 mm, weaker allometry from 9 to 20 mm, then almost isometric growth thereafter. The aspect ratio increased from 1.0 in 5 mm fish to 3.1 in 97 mm fish (Figs. 3B, 4F). Before reaching 12 mm in total length, the increase in aspect ratio of the caudal fin was steep. It increased gradually from 12 to 25 mm TL and grew rapidly again thereafter.

2-3C. Ossification

At 5 mm (14 dph; Fig. 5A), ossification of vertebrae began anteriorly and proceeded in the posterior direction. At 8.6 mm (20 dph; Fig. 5C), vertebrae were completely ossified, and ossification of the spines and rays of the pectoral, dorsal, anal and caudal fins was almost complete. Parts of the pelvic fin rays and spine were also ossified at this size. The first dorsal fin had eight spines and the second dorsal fin had one spine and 26 rays, reaching the typical number for adults. At 9.8 mm (23 dph), anal and pelvic fin ray formation were complete and ossification of the shoulder girdle began. At 12 mm (25 dph), ossification of the shoulder girdle was complete. Bone formation in the pterygiophores was also complete, except in some of the posterior parts. Caudal fin rays formed branches. At 23 mm (30 dph), ossification of all pterygiophores was complete and scale formation started from the posterior end. Scale formation was completed at 30 mm.

2-3D. Muscle

At 3.5 mm (3 dph; Fig. 6A), lateral muscle was composed of white muscle in a vague bundle of muscle fibers. A single layer of superficial cells covered the white muscle fiber zone. At 4.3 mm (10 dph; Fig. 6B), one or two layers of red muscle were confirmed on the surface near the horizontal septum. Superficial red muscle layers increased to five or six layers at 8 mm (20 dph; Fig. 6C) and to more than 10 layers at 12 mm (25 dph; Fig. 6D).

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Fig. 3. Developmental changes in the shape of (A) pectoral fin and (B) caudal fin. (i) 5.1 mm TL (14 dph), (ii) 8.3 mm TL (20 dph), (iii) 14.9 mm TL (30 dph) and (iv) 23.6 mm TL (35 dph).
2-3E. Eye

At 3.4 mm (2 dph; Fig. 7A), the lens and ganglion cell layer, inner plexiform layer, inner nuclear layer and outer nuclear layer were developed. Pigmentation of the retina was slight. At 3.5 mm (3 dph; Fig. 7B), the inner plexiform layer was thickened and the visual cell layer and pigment epithelium developed. The retina and iris were strongly pigmented. At 4.3 mm, vitreous humor developed and the distance between the lens and retina increased (Fig. 7C). After 8.0 mm, the thickness of the visual cell layer and the density of visual cells increased. After 12.4 mm, the density of nuclei in the outer nuclear layer increased.
2-3F. Cephalic and trunk lateral lines

Free neuromasts were present at 3.5 mm (3 days) in the supraorbital area. By 5 mm, free neuromasts were present on the supraorbital, infraorbital, and mandibular areas. At 6 mm, cephalic canal formation began in the supraorbital area. At 8 mm, neuromasts in the supraorbital area were covered by epidermis and the development of the supraorbital canal started (Fig. 8A). Canal formation also started in the preopercular and mandibular areas. At 10 mm, development of the supraorbital canal was almost complete with a pit at its center. At 12 mm, the preopercular canal was complete and the development of the otic and supratemporal canal had also progressed. The supraorbital canal was branched and the supratemporal and temporal canals were connected at this size. At 15 mm, all the cephalic canals excepting the infraorbital canal were complete. The infraorbital canal was complete at 18 mm. At 30 mm (50 dph), all the cephalic lateral line canals were deeply buried. Trunk lateral line formation began on the posterior area at 23 mm and was complete by 30 mm (Fig. 9).

Fig. 5. Development of cartilage and bone in striped jack larvae and juveniles. Their total lengths and days after hatching were (A) 4.2 mm (10 dph), (B) 4.9 mm (14 dph), (C) 8.6 mm (20 dph), (D) 9.8 mm (23 dph), (E) 12.0 mm (25 dph), and (F) 23.6 mm (35 dph). All scale bars equal 2 mm. Note that scales began to be formed in the posterior part of trunk in (F). Reprinted by permission of Taylor & Francis, Ltd., http://www.tandf.co.uk/journals, after Marine and Freshwater Behaviour and Physiology, 28, Masuda and Tsukamoto. Morphological development in relation to phototaxis and rheotaxis in the striped jack, Pseudocaranx dentex. 75–90, Figure 4, © 1996, Taylor & Francis.
Fig. 6. Development of muscles in striped jack larvae and juveniles. (A) 3.4 mm, (B) 4 mm, (C) 8 mm, and (D) 12 mm TL. (E)–(H) represent higher magnifications of arrowed area in (A)–(D), respectively. R: red muscle, W: white muscle.

Fig. 7. Light microscopic images of the eye of (A) 3.4 mm (2 dph), (B) 3.5 mm (3 dph) and (C) 4.3 mm (10 dph) larvae of striped jack. C: cornea, G: ganglion layer, I: Iris, IN: inner nuclear layer, IP: inner plexiform layer, L: lens, ON: outer nuclear layer, PE: pigment epithalium, V: vitreous humor. Scale bars show (A) 20 mm, (B) and (C) 50 mm.
Fig. 8. Development of cephalic lateral lines in the striped jack. (A) 8.3 mm (20 dph), (B) 12.1 mm (25 dph), (C) 14.9 mm (30 dph) and (D) 33.4 mm (50 dph).

Fig. 9. Development of trunk lateral line canals in the striped jack. (A) 14.9 mm (30 dph), (B) 23.0 mm (35 dph), (C) 26.2 mm (37 dph) and (D) 30 mm (50 dph).
2-3G. The central nervous system

Within the observed stages of fish (i.e. from 5.2 mm at 18 dph to 17.6 mm at 30 dph), the relative size of the brain gradually decreased. At 5.2 mm (18 dph), optic tectum was already developed, although olfactory bulb was not. At 8.5 mm (20 dph), olfactory bulb differentiated. At 12.4 mm (25 dph), cerebellum became larger. At 17.6 mm (30 dph), the superficial white and gray zone increased substantially especially in the area of optic tectum (Fig. 10).

2-4. Discussion

2-4A. Morphological development related to swimming ability

Definition of larvae and juveniles in relation to metamorphosis is controversial. Kendall et al. (1984) defined the juvenile period starting with the completion of fin-ray counts and the beginning of squamation, a definition generally accepted among marine fishery biologists. As all the teleosts have calcified bone and the developmental timing is relatively conservative (Mabee et al. 2000), the staging by bone formation is a useful criterion especially for the inter-specific comparison.

Striped jack at 8.6 mm had not developed the final number of spines and rays in the anal fin. However, all fin rays were complete by 9.8 mm. Therefore, fish larger than 9 mm are considered to be juveniles. This timing of metamorphosis corresponded well with the first and major inflection point in the relative growth (Fig. 3).

In juveniles larger than 20 mm, dorsal-fin length showed almost isometric growth ($\alpha = 1.0$). This suggests that the maneuvering ability of the dorsal fin (Lindsey 1978) reaches its stable maximum at this stage. On the contrary, caudal peduncle continues to be narrower ($\alpha = 0.785$) corresponding with the growing aspect ratio. This result was consistent with growth studies in sculpins (Strauss and Fuiman 1985) and tuna (Webb and Weihs 1986), showing that the aspect ratio does not reach a maximum value in the larval stage but continues to grow through the juvenile stages.

Pectoral fins of striped jack continue slight allometric growth after 20 mm ($\alpha = 1.1$). Lindsey (1978) pointed out that paired fins function little in conventional forward swimming and are reserved for maneuvering, reduced head yaw and as a brake. The allometric growth of pectoral fins in juveniles might therefore be to increase braking ability for the continuous increase in propulsion from the caudal fin through the juvenile stage.

Matsuoka and Iwai (1984) reported that red muscle of red sea bream, Pagrus major, appears in the larvae at 7 mm TL, and even early juveniles of 11.2 mm had only 3–4 layers of red muscle. In the striped jack, however, red muscle appeared in much smaller larvae (about 4 mm), and larvae of 12.4 mm had more than 10 layers of red muscle fibers. The relatively early development of red muscle fibers in striped jack may suggest an adaptation for sustainable swimming in the larval and early juveniles of this species. It is well known that white (fast) muscle is for burst swimming, and red (slow) muscle for low-speed cruise swimming (Bone 1978). In the larval stages of striped jack, as in other species, burst swimming for feeding on zooplankton and avoiding predators is probably essential. In juveniles, cruise swimming might be required for onshore migration in addition to schooling. Early development of red muscle in the striped jack suggests that they would swim actively for the recruitment to reach favorable nursery habitat rather than they would just be transported passively.

2-4B. Development of sensory organs

Vision of the striped jack is considered to be functional only when they attain 3.5 mm (3 dph) when the visual cell layer is differentiated and retina is pigmented. At this size, however, larvae should be extremely short sighted, since vitreous humor is not yet developed. In 4 mm larvae, now with fully developed vitreous humor, a longer focal distance may be attained. From 8 to 12 mm, the nuclear density of the outer nuclear layer increased; this may reflect the development of rods in the retina (Blaxter and Jones 1967). Fish juveniles at this stage are still short sighted and night-blind, because visual acuity and vision at low light intensity are directly dependent on the diameter of the eye, even when rod cells have developed (Miyazaki et al. 2000).
Fig. 10. Development of brain in striped jack. (A) 5.2 mm (18 dph), (B) 8.5 mm (20 dph), (C) 12.4 mm (25 dph), (D) 17.6 mm (30 dph). CC: corpus cerebelli, DC: diencephalon, MO: medulla oblongata, OB: olfactory bulb, OL: olfactory lobe, OT: optic tectum. All scale bars equal 2 mm.
Free neuromasts were present in the larvae of 3.5 mm. According to Blaxter (1988), all newly hatched larvae have free neuromasts on the head and trunk and the number of neuromasts increases during development. Striped jack should also have free neuromasts in newly hatched larvae. Formation of lateral-line canals occurred fairly late. Cephalic lateral lines were completed at about 18 mm and trunk lateral lines at 30 mm, both later than the onset of schooling behavior (see Chapter 3). Cahn et al. (1968) related innervation of neuromasts to the development of schooling behavior in Menidia, whereas Blaxter and Fuiman (1989) suggested that lateral line canals provide protection for the neuromasts when friction in the boundary layer increases with improvement in swimming ability.

2-4C. Development of the central nervous system

Toyoda and Uematsu (1994) conducted a detailed study on the development of brain in the red sea bream. According to their observation, the relative volume of the optic tectum rapidly increases after hatching until 8 dph (3.5 mm TL), suggesting the importance of the visual sense for the first feeding, which begins on 4 dph. I observed that striped jack at 5.2 mm already had a relatively large optic tectum. This may lead to the conclusion that 5.2 mm larvae are heavily dependent on visual sensory both for feeding and anti-predator performance. Indeed, larvae of carangid fishes at this stage become motionless at night and stay near the surface, as was observed in jack mackerel Trachurus japonicus (Masuda 2006), striped jack, and yellowtail Seriola quinquemaculata (pers. obs.). The relative volumetric increase of cerebellum was observed from before and after the transition from larvae to juvenile (Figs. 10B and C). This may correspond with the rapid growth of swimming capability represented by the completion of fins and development of red muscle. The superficial white and grey zone increased in the juvenile stage (Figs. 10C and D). Because dendrites constitute the main element of this area (Northcutt 1983), the increase of the superficial white and grey zone may represent that nervous cells in the brain extended dendrites to form a network via synapses connection at this stage.

3. Ontogeny of schooling behavior and other behavioral traits in the striped jack

3-1. Introduction

Schooling is a ubiquitous anti-predator behavior in marine organisms found from sea skaters, squids, fishes and marine mammals (reviewed by Kraus and Ruxton 2002). Because of its omnipresence, schooling is considered to have evolved in parallel in various groups of animals and different families of fishes. Function and mechanism of fish schools are well documented both in marine and freshwater fishes (Pitcher and Parrish 1993). Ontogenetic studies on schooling behavior, however, have been limited to species where rearing from eggs and during larval stage is relatively easy. Recent advances of larval fish rearing technology brought out a great opportunity to study the ontogeny of behavior in captivity, the outcomes of which will be applicable to help understand the fish’s survival strategy in a natural environment.

Rearing technology is well advanced for striped jack because of the demand from the aquaculture side, whereas ecological data of this species is scarce as the wild population level is relatively low. We therefore studied the ontogeny of behavior such as schooling (Masuda and Tsukamoto 1998a) and association with floating objects (Masuda and Tsukamoto 2000) using hatchery-reared individuals. An ecological survey was also conducted (Masuda et al. 1993, 1995) and combining these with morphological changes, some of the unrevealed part of their early life ecology was speculated (Masuda and Tsukamoto 1999).

3-2. Materials and methods

3-2A. Phototaxis

Developmental changes in phototaxis were observed in 2–35 dph larvae and juveniles (3.4–23.5 mm TL). Eighty (2, 3, 10 and 20 dph), 40 (23 dph) or 20 (25, 30 and 35 dph) individuals were used in each stage of the experiment. A long rectangular aquarium (100 × 10 × 7 cm)
was divided into four blocks, with the light intensity equal (10³ lux) in all blocks. The fish were released at the center of the aquarium and were acclimated for 5–10 minutes. Then the light intensity in each block was changed to be about 10², 10³, 10⁴, or 10⁵ lux using two 40 W fluorescent lights and three 300 W video lights. Light intensity was adjusted by an illumination meter. Another aquarium with the same dimension was prepared as a control and illuminated with 10³ lux, fish were added and the numbers were counted as in the test. The numbers of fish appearing in each block were compared by the G-test. The water temperature of the experimental aquaria was kept to that of the rearing tank by a heater and a thermostat in a water bath.

3-2B. Rheotaxis
Thirty-eight fish (4.3–11 mm; 9 to 29 dph) were transferred singly to a round raceway aquarium (17.5 cm in diameter and 4.3 cm for the width of the raceway; Fig. 11A) with flowing water. The water was siphoned into the aquarium from a water pool, the surface of which was 6 cm higher than that of raceway aquarium, through three nozzles of transparent vinyl tube. The constant speed of water flow was thus attained, which was 1.7 ± 0.5 cm s⁻¹. Black and white stripes along the inner cylinder and the bottom of the aquarium were drawn as a reference to help the fish stay in position. For the measurement of rheotaxis, a fish was given a score of 1 when it swam or kept position against the direction of the water flow. The score was tallied 50 times, at 5 s intervals, and the total of all scores was recorded as the rheotaxis index. This index was expected to be 50 when a fish always swam against the water flow and to be zero when it always swam with the water flow. If it swam in a random direction at each time interval, the index would be 19–31 at a 95% reliability limit (χ² test). Rheotaxis was thus regarded to be significant when the index was 32 or above (P < 0.05, χ² test).

3-2C. Optokinetic response
The optokinetic response (OKR) was measured by using a transparent aquarium (20 cm in diameter and 10 cm in depth) surrounded by a black-and-white (6 and 8 mm width, respectively) striped screen, the screen being rotated at 10 revolutions per min. When a larva was put into this aquarium, it rotated about the vertical axis in the center of the aquarium so that it continued to face the screen. This behavior was defined as rotatory OKR. In the other experiments, a columnar mirror (PVC pipe, 5 cm in diameter, covered with aluminum foil) was positioned in the center of the aquarium, and a fish was put in the annular channel (Fig. 11B). The fish circled the center column following the screen and its mirror image on the center column. This behavior was defined as circular OKR.

To analyze rotatory OKR, the number of the rotations of a fish per minute was counted three times, and the total was divided by the number of revolutions of the screen (30); this was
defined as the rotation rate. If a fish always faced the screen, the rotation rate was 1, and if it never reacted to the screen, rotation rate was 0.

The analysis of circular OKR was basically same as that of rheotaxis. A fish was scored 1 point when it swam or kept position with the screen. Fifty measurements were taken at 5 s intervals, and the total count of the fish was recorded as the circular OKR index. This index was expected to be 50 when a fish always swam following the movement of the screen. The index was considered to be significant when it was 32 or above based on the $\chi^2$ test. As a control the rotatory and circular OKR index of some individuals was recorded when the screen was stationary.

3-2D. Schooling behavior

Separation angle, nearest neighbor distance and a mutual attraction index were measured from one group (20 individuals) from several different age groups. Three transparent aquaria ($30 \times 20 \times 20$ cm, 7 cm depth of water) were placed side by side. Twenty fish were placed in the middle aquarium and acclimated for 10 min before commencement of video recording. Twenty minutes later, 20 fish of the same age and similar size were put into either of the neighboring aquaria for the analysis of mutual attraction. During this treatment, the movement of fish in the middle tank was video recorded from above (Fig. 12).

To analyze separation angles, video recording of the first 20 min was utilized. Separation angle from the nearest neighbor was measured for all individuals in a video frame, and the mean of 20 angles was calculated. One frame was sampled every 10 s, from which separation angles were calculated. This was repeated until 10 frames had been sampled. This value was expected to be close to zero if the fish always swam parallel to one another, or to be $90^\circ$ if they were located at random. Nearest neighbor distances were measured in the same video frames as those used for the separation angle analysis. The distance to the nearest neighbor was measured for each individual and the average for 20 individuals was calculated.

To measure mutual attraction index, the middle tank was divided into three sections and each section was given different scores as follows: +1 for neighboring fish’s side, –1 for opposite side and 0 for the middle block. The number of fish in each block was multiplied by the

![Fig. 12.](image-url)  
*Fig. 12. Apparatus to measure mutual attraction with vision. For the measurement of mutual attraction, the experimental tank was divided into three sections, and each section given a score of +1, 0, –1. The number of fish in each section was multiplied by the score, summed and then divided by 20 to give the mutual attraction index.*
score for the corresponding section, summed and then divided by 20 to give the mutual attraction index (MAI). MAI is expected to be close to +1 if the fish are always attracted to the fish in the neighboring aquarium, and near 0 if the fish move at random.

3-2E. Association with floating objects

Some pelagic fishes, especially carangids, are known to show an association with floating objects (flotsam) (Kingsford 1993). Since the habits of schooling and of association may be related, ontogeny of association behavior was studied (Masuda and Tsukamoto 2000). Four different flotsam conditions were tested; a transparent acrylic object (transparent flotsam), a gray PVC pipe (grey flotsam), a shadow of a gray PVC plate (shadow flotsam), and a control without any flotsam (Fig. 13). Twelve 30 L tanks were put in one water bath, each with one of the above flotsam conditions suspended above the tank, and 10 fish were released in each tank. The distribution of fish in each tank with flotsam was observed every 4 h for the following 24 h.

3-3. Results

3-3A. Phototaxis

At 3.5 mm (2 dph) larvae showed no phototaxis and dispersed equally in all areas (Fig. 14A). At 3.5 mm (3 dph), they showed strong phototaxis and most chose the brightest area (10^2 lux) (Fig. 14B). A similar tendency was observed in fish at 4.4 mm (10 dph), 8.7 mm (20 dph),

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Fig. 13. Schematic drawings of experimental tanks with each type of flotsam. (A) transparent flotsam, (B) gray flotsam, (C) shadow, and (D) control. Redrawn after Fishery Bulletin, 98, Masuda and Tsukamoto. Onset of association behavior in striped jack, Pseudocaranx dentex, in relation to floating objects. 2000, 864–869, Figure 1, with permission from NMFS Scientific Publication Office.
and 10 mm (23 dph) stages (Fig. 14C). Fish at 12 mm (25 dph) tended to appear in the second brightest area (10^4 lux), as did the 16 mm (30 dph) and 24 mm (35 dph) juveniles (Fig. 14D).

3-3B. Rheotaxis

The smallest individual showing positive rheotaxis was 4.5 mm TL. Although we did not test larvae smaller than 4 mm, five out of eight individuals showed positive rheotaxis in the larvae ranging from 4 to 5 mm, suggesting that this size range is the early stage of the development of rheotaxis. Fish larger than 5 mm showed stronger and more consistent rheotaxis (Fig. 15).

3-3C. Optokinetic response

Larvae smaller than 4 mm showed little rotatory OKR, whereas fish larger than 4 mm showed a strong reaction (Fig. 16A). Circular OKR was absent below 6 mm TL but present at 6 mm TL or larger fish (Fig. 16B).

![Fig. 14. Development of phototaxis in striped jack. A column with an asterisk was significantly different from others (P < 0.05, G-test). (A) 3.4 mm (2 dph), (B) 3.5 mm (3 dph), (C) 10.1 mm (23 dph), (D) 12.3 mm (25 dph).](image-url)
Both separation angle (SA) and nearest neighbor distance (NND) decreased in fish from 12 to 16 mm TL, showing that schooling behavior appeared between these sizes (Figs. 17A, B). Average SA (± SD) in 10 and 12 mm TL fish were 78 ± 13.5° and 82 ± 9.5°, respectively, which
were not significantly different from 90° (Student’s $t$-test). In juveniles of 16 mm TL, SA was $57 \pm 13.1°$, which was significantly smaller than 90°. NND also decreased with the growth of fish and showed a significant decrease between 12 and 16 mm TL. The NND/TL ratio decreased from 12 until 30 mm TL; the NND/TL ratio of 30 mm fish was $0.79 \pm 0.15$. For the mutual attraction index, there was no difference between test and control at 10 mm TL. At 12 mm TL, they showed slight but significant mutual attraction, and this value increased with growth (Fig. 17C).

**Fig. 17.** Development of (A) separation angle, (B) nearest neighbor distance (NND) in absolute value (black circles, left Y axis) and NND–TL ratio (white circles, right Y axis), (C) mutual attraction (black circles: fish in neighboring tank, white square: no fish in neighboring tank) and (D) association with flotsam. Lines in (A) and (C) represent the value expected in random orientation and position, respectively. In (A) and (B) difference among stages were compared by Student’s $t$-test, and in (C) and (D) tests and controls were compared by $t$-test. NS, not significant; *$P < 0.05$; **$P < 0.01$. Redrawn after *Journal of Fish Biology*, 52, Masuda and Tsukamoto. The ontogeny of schooling behaviour in the striped jack. 483–493, Figure 2, © 1998, The Fisheries Society of the British Isles, with kind permission of Wiley-Blackwell.
3-3E. Association behavior

The association behavior was observed in fish at 12 mm, both with transparent and gray flotsams (Fig. 17D). Fish larger than 20 mm showed a very strong association to the gray flotsam, and a weaker association to the transparent one (Fig. 18). They tended to show a stronger association at night. Association to the shadow was never observed.

3-4. Discussion

3-4A. Development of taxis in relation to sensory and swimming organs

Phototaxis first appeared in fish at 3.5 mm TL (3 dph). This coincided with the pigmentation of the eye, which should greatly enhance vision. At this stage, however, their focal distance must be short because of the undeveloped vitreous humor. In 4 mm larvae, with now fully-developed vitreous humor, a longer focal distance may be attained. This should then enable them to show the rotatory OKR (Fig. 16A). Circular OKR develops at a later stage (6 mm). During rotatory OKR, a fish faces an object from the frontal position with both eyes (Koyama and Ueda 1984). This behavior is therefore likely to be related to feeding. Circular OKR requires behavior to follow the image on a single side of the eye. This may be related to the association behavior with drifting objects (Chapter 5).

Rheotaxis was present in fish at 4.5 mm. Montgomery et al. (1997) revealed through pharmacological blocking test that superficial neuromast plays the major role in the rheotaxis in three different fish species. As free neuromasts are present in hatched out larvae, in general (Blaxter 1988), they may likely to have rheotaxis even in an early stage of larvae.

From 8 to 12 mm, the nuclear density of the outer nuclear layer increased; this may reflect the development of rods in the retina (Blaxter and Jones 1967). The shift of a preferred light intensity of $10^4$ to $10^5$ lux coincides with this period, strongly suggesting a role of rod development in this behavior. Champalbert et al. (1991) reported that sole, Solea solea, shows drastic changes in phototaxis during metamorphosis, and they related this to cone twinning and rod acquisition at this stage.

Onset of schooling behavior represented by decreased SA and NND occurred between 12 and 16 mm TL, and right before this, an increase of the mutual attraction index was observed from 10 to 12 mm TL. Therefore, at an early stage of schooling, they first recognize conspecifics, then approach each other and gradually start to form parallel orientation represented by decreased SA. The appearance of schooling did not correspond to any change of sensory organs, although completion of cephalic and trunk lateral line canals (18 and 30 mm, respectively) is

![Fig. 18. Typical association behavior of striped jack at night observed in 20 mm juveniles; (A) transparent flotsam, (B) gray flotsam.](image_url)
likely to improve their capability of fine-tuning inter-individual distances. An increased layer of red muscle may also provide a better cruise swimming capability and thus continuous schooling would be possible. Brain development histology revealed that cerebellum became larger and the superficial white and gray zone of the optic tectum increased volumatically from the larval to juvenile stage. The development of cerebellum may correspond improved motor performance (Toyoda and Uematsu 1994), and the qualitative improvement of the optic tectum may represent that their processing capability of visual information is improving in this period.

3-4B. Ecological speculations on survival strategy and migratory behavior
Based on behavioral ontogeny and information on wild jack mackerel, their life history is speculated (Fig. 19). Matured female striped jack are often caught off the Ryukyu Islands (Kanashiro and Ebisawa 1993) and Yakushima Island (Masuda 1995), both southern islands of Japan. Lack of the report of matured female in Honshu mainland suggests that the spawning ground of this species is offshore from the southern island of Japan (Harada et al. 1984).

Laboratory experiments revealed that they are strongly phototactic at 3.5 mm TL (3 dph). In hatchery tanks, they form patchiness starting from 3 dph (Fig. 1). Under natural condition, they probably remain near the ocean surface and drift with currents. Climax of morphological changes in the swimming organs was at 9 mm TL, when the fin ray counts were completed and relative growth changed from strong to weak allometry or almost isometry. These changes should be the preparation for following events, such as association with flotsams and schooling.
At 12 mm TL, light intensity preference changed, and fish began choosing areas of lower illumination. At the same time, association with floating objects and mutual attraction using vision appeared. At this size, they might aggregate with floating objects such as drift wood and jellyfishes. Association with jellyfish is observed in many other carangid fishes (Kingsford 1993; also see Fig. 32). Striped jack also showed mutual attraction at 12 mm TL. Therefore, fish attracted with flotsam would easily find conspecifics and then gradually form a school. At this stage, striped jack juveniles have relatively weak vision at night, because juvenile fish in general have limited capability of collecting light on the retina (Miyazaki et al. 2000). Association with floating objects therefore may work to prevent the dispersion of a school once formed.

Sample collection from a set net and underwater visual census revealed that striped jack recruit to coastal areas at 40 mm TL (Masuda et al. 1993, 1995). They remain there until reaching 150–200 mm TL, then migrate to sandy areas. After growing to 200 mm TL or larger, striped jack migrate to offshore reefs in deeper areas (Masuda et al. 1993). When they mature they are supposed to return to the southern spawning site. Dispersion of the ranched striped jack after certain period (Suzuki et al. 2003) may be partly attributable to this southward spawning migration.

4. Critical involvement of the central nervous system for the development of schooling behavior revealed by docosahexaenoic acid deficiency experiments

4-1. Introduction

Development of sensory and swimming organs (Chapter 2) corresponded with the ontogeny of some basic behavior such as phototaxis and rheotaxis, whereas onset of schooling behavior was not necessarily in coincidence with the development of sensory and swimming organs. One possible explanation is that the development of the central nervous system is the critical factor for the ontogeny of schooling.

To test this hypothesis, dietary contents of docosahexaenoic acid (DHA) were manipulated so that the ontogenetic timing of schooling was experimentally controlled (Masuda et al. 1999). This experiment was originally planned with the striped jack, but they were too vulnerable to DHA deficiency and their survival and activity were too low to compare the behavior between DHA provided and deficient fish (Takeuchi et al. 1996). Brain morphology of striped jack fed with or without DHA was morphologically compared (Masuda 1995). Behavioral comparisons between DHA enriched and deficient fish were conducted using yellowtail, Seriola quinqueradiata, another carangid species (Masuda et al. 1998). Incorporation of dietary origin DHA was confirmed using radioisotope-labeled DHA (Masuda et al. 1999).

4-2. Materials and methods

4-2A. Effect of dietary DHA on the growth, survival, and brain development in the striped jack

Striped jack fertilized eggs were obtained from the Komame branch of JASFA (Japan Sea-Farming Association; presently National Center for Stock Enhancement, Fisheries Research Agency) on 22 February 1994 then transferred to and reared at the Kamiura branch. They were kept in a 100 m³ hatchery tank until required for starting the rearing experiment. On 22 dph, 5000 individuals of larvae (7.0 mm TL) were transferred to five 500 L tanks, 1000 individuals each. The fish were fed with Artemia nauplii with different enrichment conditions as follows: OA (oleic acid), 1/2 EPA (eicosapentaenoic acid) (OA:EPA = 1:1), EPA, 1/2 DHA (OA:DHA = 1:1) and DHA enrichment. Each fatty acid was emulsified by adding egg yolk and water, which was then added to the Artemia incubation tank so that Artemia enriched with each condition was available. At the end of 12-day-feeding trials with different diets, an activity test measured by the survival rate during 30 or 60 s air exposure was conducted. Growth and survival were compared between groups. Development of the brain was also compared with different dietary conditions.
4-2B. Effect of dietary condition on behavior

Yellowtail larvae hatched out on 9 May 1993 in the Komame branch of JASFA, were transferred to the Kamiura branch, and were raised under routine procedures (Sakakura and Tsukamoto 1996). Larvae were reared for 12 days (6.6 mm TL) then reared with four different dietary conditions: oleic acid (OA), 1/2 EPA (EPA:OA = 1:1), 1/2 DHA (DHA:OA = 1:1), and DHA. The fish were fed with each condition of Artemia from 13 to 22 dph. Growth, survival, activity test (survival after air exposure), circular OKR (Fig. 11B), and mutual attraction (Fig. 12) were investigated.

4-2C. Incorporation of DHA into the central nervous system

To show if DHA is incorporated into the central nervous system, tracer experiment was conducted by using radioisotope (RI) labeled DHA. One hundred and fifty yellowtail larvae at 17 dph were divided into three aquaria and reared for 10 days under three different dietary regimes. In incubation beakers, Artemia nauplii were enriched with either 14C labeled DHA (thus ‘hot’ Artemia) or non-radioactive DHA (‘cold’ Artemia). In aquarium 1, fish were fed with ‘hot’ Artemia nauplii for 10 days. In aquarium 2, ‘hot’ Artemia were fed for 8 days and then unlabeled or cold Artemia were fed for 2 days. In aquarium 3, only cold Artemia were fed for 10 days. After 10 days, 3–4 individuals from each aquarium were dissected and radioactivity in the eyes, brain, gill rakers, liver, gut and other bone and muscles, was measured with a liquid scintillation counter. Whole body autoradiography was also conducted using specimens on the fourth and eleventh days (10 days feeding trial and one day starvation) in each tank. Frozen sections with 10 µm thickness were prepared, dried and then exposed to imaging plates (Fuji Film Co.) and the radioactivity measured by a bioimaging analyzer (BAS 1000 Mac, Fuji Film Co.). The conventional method of autoradiography with X-ray sensitive film was also conducted.

4-3. Results

4-3A. Effect of dietary DHA on the growth, survival, and brain development in the striped jack

Fish fed the OA-Artemia showed low growth and a poor survival rate (Table 1). After 7 days of the feeding experiment, most of the fish in the OA group displayed swimming disorders and their survival rate was zero in the activity test. Fish in the EPA or DHA groups showed better growth and survival, but comparing these two groups, the latter had slightly better growth and survival. The survival rate of activity test in EPA groups were zero.

The basic brain structure was not different among fish in experimental groups. Fish in the DHA group had a much thicker superficial white and gray zone in the optic tectum compared to those from the OA or EPA groups (Fig. 20).

4-3B. Effect of dietary condition on the schooling behavior of yellowtail

On the twelfth day of rearing, total survival rate of OA group was 44%, whereas the 1/2 DHA group showed the highest survival rate (94%), followed by 1/2 EPA (90%) and DHA (86%) groups (Table 2). The DHA group showed the highest growth rate, followed by the 1/2 DHA

<table>
<thead>
<tr>
<th></th>
<th>OA (Total length (mm) ± SD)</th>
<th>1/2 EPA</th>
<th>EPA</th>
<th>1/2 DHA</th>
<th>DHA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total length</td>
<td>9.6 ± 1.5a</td>
<td>12.7 ± 1.6b</td>
<td>12.3 ± 1.5b</td>
<td>13.2 ± 1.9c</td>
<td>13.1 ± 1.6c</td>
</tr>
<tr>
<td>Survival rate</td>
<td>37</td>
<td>71</td>
<td>82</td>
<td>90</td>
<td>95</td>
</tr>
<tr>
<td>30 s air dive</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>96</td>
<td>100</td>
</tr>
<tr>
<td>60 s air dive</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>88</td>
<td>96</td>
</tr>
</tbody>
</table>

Table 1. Total length (mean ± SD) of fish, survival rate during the rearing period, and the results of activity tests (% survival) in the striped jack reared with five different dietary enrichment groups. Total length with different letters represent significant difference (P < 0.01, Tukey’s test).
Fig. 20. Brain of striped jack reared with three different dietary conditions as (A) oleic acid (OA), (B) eicosapentaenoic acid (EPA), and (C) docosahexaenoic acid (DHA). Note that brain fed with DHA enrichment had thicker superficial white and gray zone in the optic tectum (arrow).
and 1/2 EPA groups, whereas the OA group had the lowest growth rate. In the activity tests, the DHA group showed the greatest survival rate both in the 30 and the 60 s air exposure, and the OA group had the smallest. The inferiority of the OA group was obvious, while differences among the other three groups were only slight.

In the circular OKR, most fish from each rearing condition showed a positive response and there was no significant difference among the average of the tests in all the groups (Fig. 21). Mutual attraction appeared on the ninth day of the experiment in the 1/2 DHA and DHA groups, when the average total lengths were 11.3 and 12.1 mm, respectively (Figs. 22C, D). In the 1/2 EPA and OA groups, however, mutual attraction had not appeared by 11.1 and 13.4 mm, respectively (Figs. 22A, B).

4-3C. Incorporation of DHA into the central nervous system in the yellowtail

Fish from aquarium 1 contained consistently high amounts of radioactivity in each organ (Fig. 23A). Fish in aquarium 2 contained a significantly higher amount of radioactivity in the brain compared to other organs (Fig. 23B). Both image analyzer and conventional methods of autoradiography revealed that the brain and the entire body were already radioactive from the fourth day of the rearing experiment. On the eleventh day, the distribution of radioactivity in the fish from aquarium 1 was basically same as on the fourth day. In the eleventh day sample from aquarium 2, however, only brain and nerve tissue showed strong radioactivity (Fig. 24). This shows that DHA used in brain nerve tissue is retained for 2 days or longer, whereas DHA used in other parts of the body has been metabolized. These results suggest that the fish use DHA to form brain and nerve tissue.

4-4. Discussion

Yellowtail reared with a DHA-free diet cannot develop schooling behavior, even though they developed OKR. This suggests that development of OKR is not sufficient in the ontogeny

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**Table 2.** Fish total length (mean ± SD), survival rate during rearing, and the results of the activity tests (% survival) in the yellowtail reared with four different dietary enrichment groups. Total length with different letters represent significant difference (P < 0.01, Tukey’s test).

<table>
<thead>
<tr>
<th></th>
<th>OA</th>
<th>1/2 EPA</th>
<th>1/2 DHA</th>
<th>DHA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total length (mm)</td>
<td>11.1 ± 2.0a</td>
<td>13.4 ± 2.2b</td>
<td>13.7 ± 2.7b</td>
<td>15.1 ± 2.1c</td>
</tr>
<tr>
<td>Survival rate (%)</td>
<td>44</td>
<td>90</td>
<td>94</td>
<td>86</td>
</tr>
<tr>
<td>30 s air dive (%)</td>
<td>40</td>
<td>66</td>
<td>48</td>
<td>92</td>
</tr>
<tr>
<td>60 s air dive (%)</td>
<td>14</td>
<td>64</td>
<td>60</td>
<td>76</td>
</tr>
</tbody>
</table>

**Fig. 21.** Circular optokinetic response of yellowtail reared with four different dietary conditions. Dotted lines show 95% reliability limits of χ² test. Reproduced from *Journal of Fish Biology, 53*, Masuda et al., Critical involvement of dietary docosa-hexaenoic acid in the ontogeny of schooling behaviour in the yellowtail. 471–484, Figure 3 © 1998, The Fisheries Society of the British Isles, with kind permission of Wiley-Blackwell.
Fig. 22. Mutual attraction index reared under four different dietary conditions as (A) oleic acid, (B) EPA, (C) 1/2 DHA, and (D) DHA. Closed circles and open squares represent test and control, respectively (mean ± SE of 30 frames), and asterisks represent a significant difference between test and control (measurement without fish in the neighboring tank) by t-test (*P < 0.05, **P < 0.01). Reproduced from Journal of Fish Biology, 53, Masuda et al., Critical involvement of dietary docosa-hexaenoic acid in the ontogeny of schooling behaviour in the yellowtail. 471–484, Figure 4, © 1998, The Fisheries Society of the British Isles, with kind permission of Wiley-Blackwell.

Fig. 23. Mean (± SE) per gram radioactivity of the different organs after the 10 days of the tracer experiment. Fish from aquarium 1 were fed radio-labeled Artemia for 10 days; those from aquarium 2 were fed radio-labeled Artemia for 8 days and non-labeled Artemia for 2 days. Both were then starved for one day. Reproduced with permission from Brain, Behavior and Evolution, 53, Masuda et al., Incorporation of dietary docosahexaenoic acid into the central nervous system of the yellowtail Seriola quinqueradiata. 173–179, Figure 2, © 1999, S.Karger AG, Basel.
of schooling behavior. Because dietary DHA is incorporated and retained in the brain, the development of the central nervous system (CNS) is more likely to be the limiting factor for the development of schooling. The histology of striped jack reared with different diets revealed that fish fed with DHA had a thicker superficial white and grey zone in their optic tectum compared to EPA- or OA-provided groups. Kishimoto et al. (1969) analyzed different fractions of gray and white matter in rat brains. They observed that fractions of nerve terminals had much more DHA than did those with myelin. This strongly suggests a role of DHA in synapse terminals. Therefore the possible function of DHA in the brain involves the myelination of neurocytes and the construction of synapses; both functions are considered to be essential for the formation of neural networks.

DHA requirements were quantitatively studied in larvae of many species of fish and crustaceans, with the typical amount shown to be 1% DHA dry weight or more in the diet (Takeuchi et al. 1996; Sargent et al. 1999). Although rotifers and Artemia nauplii are commonly used diet species for larval fish culture, efforts to search for alternative diets have been made. Both wild and cultured copepods are known to be superb as a diet (Nanton and Castell 1998). The wild diet of fish larvae generally contains high amounts of DHA (Watanabe et al. 1978). However, this may not always be true. Davis and Olla (1992) demonstrated that the DHA content of wild copepods (Acartia) fluctuated dramatically within as short a period as 12 days in the same open-ocean area, suggesting that fish larvae may encounter DHA deficiency in natural waters.

Production of DHA and other highly unsaturated fatty acids in the marine ecosystem is mostly attributable to phytoplankton and, to a much lesser extent, bacteria (Watanabe et al. 1997). DHA production in phytoplankton is influenced by water temperature and light conditions, with a notable negative impact of UVB (280–320 nm wavelength) light. Wang and Chai (1994) demonstrated that the production of EPA and DHA in algae such as Isochrysis galbana

Fig. 24. Autoradiography of the sagittal section of yellowtail reared in aquarium 2 for 11 days. White areas represent organs with strong radioactivity. Reproduced with permission from Brain, Behavior and Evolution, 53, Masuda et al., Incorporation of dietary docosahexaenoic acid into the central nervous system of the yellowtail Seriola quinqueradiata. 173–179, Figure 4, © 1999, S.Karger AG, Basel.
and *Prorocentrum micans* decreased to 50 and 20%, respectively, after 5–6 days of UV exposure under laboratory conditions.

Most marine copepods and other zooplankton rely on phytoplankton for their DHA source (Breteler et al. 2005). The increase of UV radiation on the ocean surface may therefore have profound effects on the marine ecosystem through the food chain (Fig. 25). UV radiation also has a direct negative effect on copepods (Rodriguez et al. 2000) and fish eggs (Browman et al. 2000). Fukunishi et al. (2006) revealed that UV tolerance differs even among fish species in the same family; larvae of black sea bream *Acanthopagrus schlegeli* are more tolerant to UV than those of red sea bream *Pagrus major*. Increase of UV radiation on the ocean surface may therefore favor fish species that are more tolerant to UV.

Some marine bacteria that produce DHA, EPA and other HUFAs live symbiotically in the intestine of fishes and thus help the physiological DHA requirement of the host (Yazawa et al. 1994). Yazawa (1996) reported that bacteria isolated from the intestinal contents of the chub mackerel synthesize EPA efficiently. Because DHA requirement can be a limiting factor of long-term growth and survival for any marine fishes, such symbiosis may give great advantage to the host. Furthermore, even when the DHA production of marine algae decreases for some reason, such as the temporal increase of UV radiation, those fish species which have HUFA producing bacteria may be relatively secure from the DHA shortage. These inter-specific differences in DHA acquisition routes could also contribute to population changes among pelagic fish species (Masuda 2003). In the west Pacific Ocean, the dominance of jack mackerel, chub mackerel and sardine, *Sardinops melanostictus*, is replaced in a cycle of a few decades (Matsuda et al. 1991; also see Chapter 6), and the interaction between UV and DHA- or EPA-producing symbiotic bacteria may play a role in the replacement of the dominant fish in the pelagic ocean.

### 5. Ontogeny of association behavior between jack mackerel and jellyfish

#### 5-1. Introduction

Recent increase of jellyfish including cnidaria and ctenophores is a world-wide problem causing extensive nuisance to local fisheries (Purcell et al. 2007). In Japanese coastal waters,
outbreaks of moon jellyfish *Aurelia aurita* have been common in the latter half of the twentieth century (Uye *et al.* 2003). Recent population explosions of giant jellyfish, *Nemopilema nomurai*, occurring on a yearly basis since 2002 are causing serious damage, especially to fisheries in the coastal areas of the Sea of Japan (Kawahara *et al.* 2006). Brodeur *et al.* (1999) suggested that jellyfish biomass may represent a vast unavailable reservoir of carbon in the pelagic system, although they noted that some fish species such as walleye pollock, *Theragra chalcogramma*, juveniles associate with jellyfish.

A large variety of fish associate with jellyfish, among which fishes from Carangidae are often most dominant (Manuetti 1963; Kingsford 1993; Purcell and Arai 2001). Arai (2005) identified 69 species of fish that feed on jellyfishes. Shojima (1962) revealed that although carangid fishes, scad, *Decapterus maruadsi*, and jack mackerel, *Trachurus japonicus*, associated with jellyfishes such as *Aurelia aurita* and *Aequorea coerulescens*, none of them contained jellyfish parts in their gut contents, suggesting that these carangids use jellyfish for protection against predators rather than as a food source. This was coincident with the study conducted by Hirota *et al.* (2004) who revealed that jack mackerel juveniles almost exclusively feed on copepods. Few researchers, however, seem to have tested the ecological function of the association between fish and jellyfish through experimental approaches.

I therefore tested to see if jack mackerel utilize jellyfish either as prey (Masuda 2006), as a prey collector, or as a refuge from predators (Masuda *et al.* 2008). Ontogenetic changes of such functions were investigated using a predator model and artificial jellyfish (Masuda 2009). Underwater observations were conducted to test speculations deduced from laboratory experiments. Fishery management to deal with jellyfish-bloom problems is also discussed in this chapter.

5-2. Materials and methods

5-2A. Feeding on jellyfish

Jack mackerel eggs were spawned naturally from broodstock kept at Maizuru Fisheries Research Station of Kyoto University on 30 May 2002. They were reared by feeding rotifers, *Artemia* nauplii and pellets according to their growth. Interaction between jack mackerel and moon jellyfish was observed in a two-day trial experiment starting at 5.8 mm SL (17 dph). The aim of this experiment was to see the potential feeding behavior of jack mackerel on jellyfish. Three jellyfish were put in each of two 100 L tanks, and 10 jack mackerel were gently introduced to the tank. Any injury and mortality of both jack mackerel and jellyfish were observed and recorded three times a day. This procedure was repeated at 2–3 days intervals for the following 30 days.

5-2B. Utilization of jellyfish as a prey collector

Fertilized eggs of jack mackerel were obtained from the spawning of broodstock kept in the Kamiura branch of JASFA (presently National Center for Stock Enhancement, Fisheries Research Agency) on 15 June 2005. They were reared as the previous experiment, then used in one of three trials of the feeding experiment and the predation experiment. In addition to these hatchery-reared fish, wild collected jack mackerel juveniles were used in the other two trials. Jack mackerel were kept in 100 L tanks and tanks of the test group contained three individuals of moon jellyfish each, whereas the control group did not. *Artemia* nauplii enriched with DHA emulsion were provided once every day. Rearing was conducted for 60–79 days, depending on the trial. Feeding of jack mackerel in test and control groups was observed. Growth between test and control groups was also compared.

5-2C. Utilization of jellyfish as a refuge from predators

Predation experiment was conducted using three 500 L tanks (Fig. 26). Three moon jellyfish were kept in the first tank (tank A). In the second tank, 10 chub mackerel juveniles (119 ± 9.2 mm SL, mean ± SD) and three moon jellyfish were kept (tank B). The third tank contained 10 chub mackerel juveniles (116 ± 6.8 mm SL) (tank C). Thirty jack mackerel juveniles from the stock tank were divided into three groups with the same size range, released into each tank and
their behavior was observed. Twelve trials were conducted by using different mean sizes of juveniles ranging from 11.8 to 37.3 mm SL.

The survival index was calculated according to Masuda and Ziemann (2003). The number of surviving individuals was counted at 5 min, 1, 3, 6 and 24 h after the release. The number of survivors at each observation time was summed up in each trial and divided by 50. This value, defined as the survival index, ranges from 0 when all the individuals were eaten within 5 min to 1.0 when all the individuals survived up to 24 h after release. The association index was defined as follows. When fish stayed within one fish body length of a jellyfish, this was considered to be associating with a jellyfish. The number of associating individuals was counted 30 times with a 10 s interval at each observation period, i.e., immediately after release and 1, 3, 6 and 24 h after release. The total number of associating individuals in each observation period was divided by the number of observations (30) and the number of surviving individuals. The association index would range from 0 when no individual associated with jellyfish to 1.0 when all the individuals always associated with jellyfish. The survival index was compared among all the three treatment groups, and association was compared between two groups with jellyfish (tanks A and B).

5-2D. Ontogenetic changes in the function of association between jack mackerel and jellyfish

The ontogeny of the ecological function of the association of jack mackerel with jellyfish was also studied experimentally by using jack mackerel juveniles (Masuda 2009). They were wild juveniles collected off Kanmurijima Island, Maizuru. Four different size groups of juveniles were tested as 11, 19, 38 and 55 mm on average SL, respectively. Ten individuals from each size group were put in three 500 L identical tanks each. Two live moon jellyfish and one artificial jellyfish made of silicon were put in each tank (Fig. 27). Association of jack mackerel with both moon jellyfish and artificial jellyfish were counted on the following seven occasions: before presenting a predator model (realistic model of chub mackerel, 14 cm SL), immediately after presenting a predator model, before feeding *Artemia*, immediately after feeding, at 1 and 3 h after feeding, and at night.

**Fig. 26.** Schematic drawing of the experimental design to reveal the association with jellyfish as anti-predator behavior. Jack mackerel juveniles were released in (A) a tank with moon jellyfish, (B) a tank with both jellyfish and predators (chub mackerel) and (C) tank with predators. Survival was compared among three tanks focusing on tanks B and C, and association with jellyfish was compared between tanks A and B.
5-2E. Underwater observation of fish assemblages associated with jellyfish

Underwater observations of jack mackerel and other fishes associated with giant jellyfish *Nemopilema nomurai* were conducted by SCUBA and snorkeling divers from August to December in 2005, 2006 and 2007 off Kanmurijima, Maizuru, Kyoto Prefecture, Japan. Observation was also conducted in September, November and December 2006 at Tsushima, Nagasaki Prefecture, Japan. All the observation sites were near the shore of isolated islands at 30 m depth or shallower, and were exposed to the offshore ocean. Fish species, body length and the number of individuals associating with jellyfish were recorded on waterproof paper for each giant jellyfish encountered.

Visual censuses of fish assemblages were also conducted by SCUBA in both areas using a modified strip transect method. Transects (50 × 2 m) were established at 54 locations around the Tsushima Islands on 30 November and 1 December 2006, and at 43 locations around the Kanmurijima Islands, Maizuru on 20 October and 7 December 2006, respectively. The length of each transect was estimated by the number of fin kicks (55 kicks) based on a preliminary measurement made by swimming along a known distance. All the fish encountered during SCUBA dives along each transect were recorded with their species, number and visually estimated SLs. The total number of fish species, fishes, jack mackerel, pelagic predators, and benthic predators were compared between Tsushima and Maizuru using *U*-tests (Masuda 2009).

5-3. Results

5-3A. Feeding on jellyfish

Among 19 trials, each duplicated, of two days observation covering 17 to 47 dph of jack mackerel larvae and juveniles, I did not see any occasion where jack mackerel directly fed on moon jellyfish. There were, however, four occasions where moon jellyfish were partially damaged (Masuda 2006).
5-3B. Utilization of jellyfish as a prey collector

When *Artemia* were provided in experimental tanks, jack mackerel first fed on the free-swimming *Artemia*. After approximately 3 min, however, as moon jellyfish started to accumulate *Artemia* in their tentacles and gut cavity, some jack mackerel individuals started to feed on the *Artemia* in the gut cavity as well as those on the tentacles of the jellyfish (Fig. 28A). When jack mackerel fed on the *Artemia* that had been captured by jellyfish, they usually did so as a group rather than single individuals. This way, even when one individual jack mackerel was trapped by a jellyfish, the trapped individual was released by the feeding activity of the other individuals.

Jack mackerel held with jellyfish showed better growth compared to those held without jellyfish (Fig. 29). Only a few individuals associated with jellyfish before and immediately after feeding, whereas significantly more individuals associated with jellyfish at 1 and 3 h after feeding.

5-3C. Utilization of jellyfish as a refuge from predators

When there were no predators, jack mackerel stayed away from the jellyfish and dispersed in the tank (Fig. 28B). When there were both predators and jellyfish, jack mackerel often hid behind a jellyfish (Fig. 28C); however, the chub mackerel attacked and ate both the jack mackerel and jellyfish. Therefore, there was no difference in survival index between the presence and absence of jellyfish (Fig. 30A; *P* > 0.05, ANOVA). The association index was significantly higher when predators were present compared to the absent (Fig. 30B; *P* < 0.05, Tukey’s test).

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**Fig. 28.** (A) Jack mackerel juveniles feeding on *Artemia* collected by moon jellyfish. Note that all the juveniles were attacking one of two jellyfish as a group. (B) Jack mackerel in tank A of the predation experiment, where association with jellyfish was hardly observed. (C) Jack mackerel in tank B of the predation experiment hiding behind moon jellyfish to avoid predators. (D) Jack mackerel in tank C of the predation experiment aggregating near the water surface to avoid predators.
5-3D. Ontogenetic changes of the function of association between jack mackerel and jellyfish

Jack mackerel at 11 mm associated with both live and artificial jellyfish (Figs. 27, 31A) and without any systematic tendency depending on the condition of treatment. Fish at 19 mm associated only with live jellyfish and had significantly higher association when the predator model was presented (Fig. 31B). Fish at 38 and 55 mm also showed association only with live jellyfish but under different conditions; they associated with jellyfish only at 1 and 3 h after prey organisms (Artemia) were provided (Figs. 31C, D).
Eleven fish species were confirmed to associate with giant jellyfish, among which jack mackerel was the most abundant both in the total number and frequency, followed by scad, *Decapterus maruadsi*, both carangid species (Fig. 32A). Three monacanthid species were also frequently observed as filefish, *Thamnaconus modestus* (Fig. 32B), thread-sail filefish, *Stephanolepis cirrhifer*, and pygmy filefish, *Rudarius ercodes*. Medusa fish, *Psenopsis anomala*, was also commonly observed. Filefish and thread-sail filefish were often seen voraciously feeding on giant jellyfish. Striped knifejaw, *Oplegnathus fasciatus*, was also observed to feed on the jellyfish. Striped knifejaw and striped poison-fang blenny, *Petroscirtes brevianomala*, were observed along with giant jellyfish drifting near the coast, whereas pilot fish, *Naucrates doctor*, and dolphin fish, *Coryphaena hippurus*, and remora, *Echeneis naucrates*, were observed with those drifting off the coast, apparently because the former fishes are more associated with shore reefs.

The smallest and the largest jack mackerel found with giant jellyfish were 6 and 65 mm SL, respectively, but a more typical size was between 10 and 45 mm SL. Jack mackerel associated with jellyfish in Tushima tended to be larger than those in Maizuru. The ratio of giant
Fig. 32. (A) Jack mackerel juveniles associating with giant jellyfish. (B) Filefish feeding on giant jellyfish. Both taken in November 2007 off the Kanmuriijima Islands, Maizuru.

Jellyfish associated with jack mackerel increased from 33 to 96% in the three consecutive years of observation in Maizuru (Fig. 33A). The average number of jack mackerel associating per giant jellyfish also increased during the same period (Fig. 33B).

A total of 60 fish species and 2,565 individuals and 30 species and 4,383 individuals were recorded in the visual censuses in Tsushima and Maizuru, respectively. Although the fish assemblage in Tsushima included more species, the number of species per transect was not significantly different between these two areas (Fig. 34A; P = 0.19, U-test). The number of individuals
was higher in Maizuru, largely due to the presence of many jack mackerel (Figs. 34B, C). No jack mackerel was found in reef areas in Tsushima. Tsushima had more numbers of large-sized (>15 cm) benthic predators such as the groupers, *Epinephelus chlorostigma* and *E. bruneus*, and lionfish, *Pterois lunulata*, whereas pelagic predators such as yellowtail, *Seriola quinquergadiata*, predominated in Maizuru (Figs. 34D, E).

### 5-4. Discussion

#### 5-4A. Ontogeny of function in the association behavior of jack mackerel with jellyfish

In the laboratory experiment, neither jack mackerel larvae nor juveniles fed on moon jellyfish, but they fed on *Artemia* captured by jellyfish. They also utilized jellyfish as a refuge from predators. These results suggest that the association of jack mackerel with jellyfish is multifunctional and parasitic.

In underwater observations, the smallest jack mackerel larvae associated with giant jellyfish were 6 mm SL. Larvae of this size are estimated to be about 15 dph based on hatchery-rearing data. Sassa et al. (2006) reported that a major spawning area of jack mackerel occurs in the central part of the East China Sea in spring (Fig. 35). The relatively slow speed of the Tsushima Current (i.e., 7 cm s\(^{-1}\); Hase et al. 1999) would place the spawning site of the 6 mm larvae found in Maizuru only 90 km southwest of the sampling area.

In the experimental tank, jack mackerel juveniles of 11 mm SL associate with both living and artificial jellyfish, but did not show a change in their strength of association in relation to the presence of a predator model or provision of prey items. This suggests that they associate with jellyfish for reasons other than predator avoidance or prey collection. In the wild, small larvae or juveniles (6–20 mm SL) associated with giant jellyfish tended to have large variation in size, whereas juveniles, at 20–40 mm SL, tended to have less size variation. This may reflect that a solitary larvae or juvenile might have been attracted to a jellyfish after some period of drifting in the ocean, where they met conspecifics and then formed schools. Fréon and Dagorn (2000) suggested that among 16 hypotheses proposed for the ecological function of association behavior with fish attracting devices (FADs), ‘meeting point hypothesis’ is most persuasive. The association

![Fig. 33. (A) The number of giant jellyfish observed that were associated with (gray) or without (white) jack mackerel juveniles in each year in the study area. (B) The average number of associating jack mackerel per giant jellyfish. Note that both the ratio of giant jellyfish accompanying jack mackerel (A) and the average number associated (B) increased from 2005 to 2007 in Maizuru.](image-url)
of 6 mm jack mackerel larvae with giant jellyfish fits well with this hypothesis, because finding jellyfish would be much easier than finding a small conspecific in the open ocean.

Fish at 19 mm showed association with moon jellyfish in the presence of a model predator, whereas this response was not observed in larger juveniles. Absence of an anti-predator response in larger juveniles may be partly due to the relatively small size of the predator model (140 mm SL) as well as the small size of the moon jellyfish (102 mm diameter) used in this experiment. In the underwater observations, jack mackerel at 40 mm or smaller often associated with giant jellyfish with the presence of a diver. However, larger juveniles tended to swim away from the jellyfish towards the sea bottom when they were disturbed. Leis et al. (2006) observed the swimming behavior of the larvae and juveniles of giant trevally Caranx ignobilis released in the ocean and found that individuals at 9–13.5 mm SL showed no particular interest in high-relief coral reefs when they encountered these structures. Larvae and juveniles of carangid fishes

**Fig. 34.** The number of fish species, fish individuals, jack mackerel, and pelagic and benthic predators larger than 150 mm BL found along 100 m² census transects. Means ± SE of 54 and 43 replicates in Tsushima and Maizuru study sites were presented, respectively. Values in two locations were compared by U-test. Redrawn after, with kind permission from Springer Science+Business Media: *Hydrobiologia*. Ontogenetic changes in the ecological function of the association behavior between jack mackerel *Trachurus japonicus* and jellyfish. 616, 2009, 269–277, Masuda, Figure 5, © 2009, Springer.
Fig. 35. Ecological function of the association behavior between jack mackerel and jellyfish is suggested to change ontogenetically from meeting place among conspecifics to refuge from predators and feeding place. *1 and *2 represent locations of Tsushima and Maizuru study sites, respectively. All the inserted pictures were taken in Maizuru. Seeding area of giant jellyfish (Kawahara et al. 2006) and spawning area of jack mackerel (Sassa et al. 2006) were shaded.

in pelagic stage perhaps prefer to stay in pelagic life even when they are under a threat, whereas those at 40 mm or larger are ready to shift to reef-associated life so that they would swim down to avoid the disturbance.

Jack mackerel at 38 and 55 mm SL showed strong association with moon jellyfish at 1 and 3 h after introducing Artemia to the tank; this was apparently to feed on the Artemia from the gut
cavity of moon jellyfish. Although there are many species that feed on jellyfish, jack mackerel juveniles prefer to feed on smaller zooplankton such as copepods in the wild (Hirota et al. 2004) or Artemia and mysids in captivity (Masuda 2006). In natural waters, however, they are likely to use jellyfish as a prey collector.

Based on the laboratory and field observations, the function of association with jellyfish in jack mackerel is suggested to change gradually from a meeting place with con specifics, to a hiding place from predators, then to a prey collector of zooplankton while migrating in the oligotrophic offshore environment (Fig. 35). There are several other untested hypothetical functions of association behavior. Since they also associate with jellyfish at night, early juveniles may make use of jellyfish to prevent dispersion of their once formed school, although we know little about the fish–jellyfish interaction at night, except that the relatively large size of jack mackerel can be predated by jellyfish at night and this does not occur during the day (Masuda 2006). Jack mackerel may utilize jellyfish as a shelter from UV radiation in the open ocean, since UV radiation should be detrimental for small larvae, especially in offshore areas with less dissolved organic matter to diffuse UV (Zagarese and Williamson 2001). Small larvae may be able to swim faster by utilizing eddies formed by jellyfish rather than swimming by themselves. Such possibilities should be tested in laboratory experiments and field observations.

5-4B. Ontogeny of mechanisms in associating with jellyfish

Striped jack started to show association with both transparent and gray floating objects at 11.9 mm TL (ca. 10 mm SL), whereas this behavior was absent in smaller larvae (5.5, 8.3, or 10.3 mm TL) (Chapter 3). The discrepancy between the laboratory experiment with striped jack and the field observation showing the presence of 6 mm SL jack mackerel larvae associating with giant jellyfish, is attributable to the relatively early development of optokinetic responses. The circular OKR (Fig. 16) first appeared at 6 mm TL in the striped jack, whereas the transparent and gray flotsams were fixed objects, which are likely to be less attractive for carangid fish larvae. Perhaps the optokinetic response to moving objects in the ocean is the primary mechanism for jack mackerel larvae to associate with jellyfish. Alternatively, it may be a difference between the two carangid species in behavior.

Jack mackerel larvae at 6 mm do not have scales and thus should be vulnerable to the nematocysts of jellyfish. Indeed, I occasionally encountered injured jack mackerel associated with giant jellyfish. Nevertheless, juvenile jack mackerel seem to be relatively immune to jellyfish nematocysts compared with other fish such as red sea bream, chub mackerel, and Japanese anchovy (Masuda 2006; also see Chapter 6). This may guarantee a relative advantage for jack mackerel larvae in associating with jellyfish rather than associating with abiotic floating objects or drifting singly. It should be noted that jack mackerel and other carangid larvae and juveniles are most commonly found associated with poisonous jellyfishes such as giant jellyfish, Pelagia noctiluca and Chrysaora melanaster but less often with less poisonous species such as moon jellyfish (Mansueti 1963; Sassa et al. 2006; Masuda pers. obs.).

Scales were formed from 20 to 30 mm TL in the case of striped jack (Masuda and Tsukamoto 1996; also see Fig. 5F in the case of striped jack). Scales of jack mackerel juveniles are completely formed at 27 mm SL. This should increase their protection against nematocysts and thus it is not surprising that they would associate with jellyfish more often, especially when threatened with a predator model (Fig. 31B) or when disturbed by an observer in the vicinity of a jellyfish. Jack mackerel has tight scales compared with other pelagic fishes; this may sacrifice cruise-swimming capability (Masuda 2006), but is likely to be adapted for protection against nematocysts. Association with jellyfish become less strong as jack mackerel grow beyond 40 mm SL, perhaps due to a decreased dependence on jellyfish as an anti-predator strategy; a highly-organized, large school with matured capability of social communication (Nakayama et al. 2007) is likely to be the major anti-predator behavior at this stage.

The utilization of jellyfish by jack mackerel is likely to be dependent on the environmental context such as the availability of other habitat, prey, and the presence of predators. Underwater observation comparing fish assemblages between Maizuru and Tsushima supports some of these possibilities. The visual censuses suggested that the rocky reefs in Maizuru have more pelagic,
but fewer benthic predators compared with the upstream locations in the Tsushima Current (Figs. 34, 35). The predation pressure from pelagic predators may cause jack mackerel to abandon giant jellyfish as a vehicle for migration and shift to a reef-associated habitat. It is notable that the smallest size of jack mackerel found in the rocky shore habitat along Maizuru Fisheries Research Station was 40 mm SL (Masuda et al. 2008). This habitat shift from pelagic and jellyfish-associated to reef-associated may represent an increased food requirement as well as improved anti-predator performance with a large school during the ontogeny.

6. Behavioral ontogeny of common pelagic fishes with reference to the population replacement

6-1. Introduction

It is well known that the abundance of the population of certain marine pelagic fishes fluctuate with a cycle of decades, even without the interference of the anthropogenic effect. Yet fishing pressure is reported to increase the magnitude of fluctuations especially because commercial fisheries selectively harvest large individuals with high fecundity (Anderson et al. 2008). In Japanese coastal waters, the catch of sardine had two peaks in the twentieth century, one in the 1930s and the other in the 1980s (Watanabe 2002; Fig. 36A). During the years when sardine had been scarce, populations of other species such as chub mackerel, jack mackerel and anchovy filled this vacant niche (Figs. 36B–D). Matsuda et al. (1991) proposed a mathematical model to predict this replacement, suggesting that the sequence of predominance would be sardine, followed by anchovy and jack mackerel, then chub mackerel. Takasuka et al. (2007) analyzed the growth trajectories of sardine and anchovy in different eras through otolith analysis and found that the optimal growth rate for anchovy larvae occurred at 22.0°C, whereas that for sardine larvae occurred at 16.2°C. They concluded that because ambient temperature has historically fluctuated between these optima, this simple mechanism could potentially cause the shifts between the warm anchovy regime and the cool sardine regime in the western North Pacific. Kawai (1994) suggested that during the rapid decline of sardine population, the abundance of piscivorous plankton such as jellyfishes and Chaetognatha such as Sagitta spp. were unusually abundant, suggesting the mortality of eggs and larvae of sardine by these piscivorous plankton. Solar activity represented by sunspot is also speculated to govern the pelagic fish abundance (Guisande et al. 2004; plotted in Fig. 36E), because solar irradiance is higher when the number of sunspot is higher (Wilson and Hudson 1991).

Although circumstantial evidence from extensive field research is accumulating, relatively few experimental works have been conducted to reveal the mechanism of population replacement, partly due to the difficulty in rearing marine pelagic fishes for long periods. The goal of the research presented in this chapter was to reveal the biological characteristics of three major pelagic fishes, jack mackerel, chub mackerel and Japanese anchovy through rearing experiments. Emphasis was on the anti-predator strategy such as swimming speed, schooling behavior and avoidance from the capture of moon jellyfish. Life history traits of the pelagic fishes such as growth and reproduction were also compared to elucidate life history characteristics of each pelagic fish species and to relate them to population fluctuation.

6-2. Materials and methods

6-2A. Fish husbandry

Three common pelagic fishes, jack mackerel, chub mackerel and anchovy, were reared from eggs to juveniles and behavioral ontogeny was observed in each species. Jack mackerel eggs were either spawned naturally from broodstock kept in tanks in MFRS, or provided from the Kamirua branch of JASFA (presently National Center for Stock Enhancement, Fisheries Research Agency). Anchovy eggs were spawned naturally from broodstock kept in MFRS for about 2 months. Chub mackerel eggs were either provided from Kinki University or purchased from a private hatchery company (Nichimo Marifarm, Kumamoto, Japan). They were raised
Fig. 36. The catch of four common pelagic fishes in Japanese coastal waters (A–D: Fisheries Agency Japan), and the number of sunspot (E: data from ftp://ftp.ngdc.noaa.gov/STP/SOLAR_DATA/SUNSPOT_NUMBERS/MONTHLY/PLT).
using conventional methods by feeding rotifers and *Artemia* nauplii, both enriched by commercial enrichment oil (Masuda et al. 2002; Masuda 2006).

6-2B. **Swimming speed**

Cruise swimming speed of larvae and juveniles were measured in these three species. A single fish was transferred to a glass container covered with a black vinyl sheet and its movement was recorded from above for 90 s using a digital video recorder. Sound stimuli were provided three times releasing a string-hung metal nut three times at 10 s intervals. Frame-by-frame video analysis was conducted to calculate cruise swimming speed and burst swimming speed. Cruise speed was estimated based on the 10 s video recording from 30 s after the recording was started. The movement of the fish was traced on a TV monitor, and this distance was divided by the time taken (10 s). The burst speed was measured when the fish made a burst start in response to the sound stimuli. The fish’s movement was traced for four consecutive video frames, and the distance was divided by the time taken (4/30 s). Both cruise and burst speeds were divided by the SL of each individual. Cruise speed was thus equivalent to routine speed (Leis 2006).

6-2C. **Anti-predator performance**

Survival capability in fish larvae against predation by jellyfish was visually observed. Three actively pulsating moon jellyfish were put in a 10 L plastic container covered by a black vinyl sheet. A larva was gently put in this container, then observations were conducted to measure how long it took for the larva to be captured by the jellyfish. The observation was conducted for 5 min, then if the larva was not eaten, it was removed and replaced by another larva.

The development of schooling behavior was observed in chub mackerel and anchovy by recording the behavior of the fish in the rearing tanks. Two semicircular white reflecting boards were put on the tank before recording images. The video camera was set above the tank so as to record approximately one-quarter of the tank. Separation angle and nearest neighbor distance were measured in anchovy with the same method as in the striped jack (Chapter 3), except that the separation angle was calculated from two individuals, and NND was from five individuals, and the video frame was sampled 30 times with 20 s intervals. A separation swimming index (SSI) was developed to quantify the tendency of parallel swimming behavior that is typical in the early stages of schooling (Masuda et al. 2003; Nakayama et al. 2007). For the measurement, a fish close to the center of the video frame was focused (focal fish), then the fish close to the focal fish was defined as the neighboring fish on the video frame (Fig. 37A). The video frame was then advanced for 1 s and the movement of fish was expressed as a speed vector for each fish. After the starting point of one vector is parallel-translated to that of the other (Fig. 37B), the SSI was calculated as

$$\text{SSI} = \frac{2d}{v_1 + v_2},$$

where \(d\) is distance between two vector endpoints and \(v_1\) and \(v_2\) are the magnitudes of the vector for the focal and neighboring fish, respectively. The SSI represents how far the two neighboring individuals are separated from each other in a given time. The value of SSI ranges between 0 and 2; 0 when two individuals show perfect parallel swimming with the same speed and direction, and about 1.49 when the swimming speed and directions of two individuals are at random (Nakayama et al. 2007). The SSI can be calculated without parallel translation of the vectors by measuring the angle between two vectors (\(\theta\)) and transforming \(d\) in the function as follows:

$$\text{SSI} = \frac{2(v_1^2 + v_2^2 - 2v_1v_2 \cos \theta)^{0.5}}{v_1 + v_2}.$$  

6-3. **Results**

6-3A. **Growth**

The average notochord length of jack mackerel, chub mackerel and Japanese anchovy were 2.7, 3.3 and 2.8 mm at hatching. The slight differences of body lengths were extended after 10 days of rearing (Fig. 38). Jack mackerel attained 10.3 ± 0.7 (mean ± SD) mm in SL by 30 dph and 26.6 ± 1.8 mm at 48 dph. Chub mackerel grew much faster, attaining 11.9 mm on 11 dph.
The growth of anchovy was intermediate, attaining \(23.4 \pm 4.1\) mm SL at 30 dph and \(36.0 \pm 6.1\) mm at 50 dph. The relationship between SL and age during the rearing period was expressed by the following exponential equations:

- **chub mackerel**: \(SL = 3.29 \times e^{0.0956d}\) \((R^2 = 0.995)\),
- **anchovy**: \(SL = 3.06 \times e^{0.0655d}\) \((R^2 = 0.982)\),
- **jack mackerel**: \(SL = 2.47 \times e^{0.0502d}\) \((R^2 = 0.974)\).

**Fig. 37.** Measurement of separation swimming index (SSI). Movements of the focal fish and the neighboring fish in 1 s were expressed as vectors \((v_1\) and \(v_2\)). The latter vector was then parallel-translated to give the separation distance \((d)\) of two vectors. SSI was defined as \(2d(v_1 + v_2)\). Reproduced with permission from *Fisheries Science*, 69, Masuda et al., Development of schooling behavior in Spanish mackerel *Scomberomorus niphonius* during early ontogeny. 772–776, Figure 2, © 2003, the Japanese Society of Fisheries Science.

**Fig. 38.** Growth of chub mackerel, anchovy and jack mackerel reared under the conventional feeding protocol.
6-3B. Swimming speed and anti-predator performance

Cruise swimming speed of jack mackerel was consistently low (1.05–2.37 SL/s), whereas that of chub mackerel showed a remarkable allometric development, increasing from 1.58 SL/s in the larval stage to 5.39 SL/s in the juvenile stage (Fig. 39A; Masuda 2006). The cruise swimming speed of anchovy was intermediate with a slight ontogenetic change, from 1.2 SL/s in the larval and 3.51 SL/s in the juvenile stage.

Jack mackerel showed a remarkably fast burst swimming speed, even in the larval stage range of 10.3–23.4 SL/s (Fig. 39B). Chub mackerel showed a slower burst speed in the larval stage (4.4 SL/s), then showed a faster burst speed in juveniles (5.4–18.5 SL/s). The burst speed of anchovy showed a similar ontogenetic change to chub mackerel from larvae (3.4 SL/s at 6.2 mm SL) to juveniles (18.6 SL/s at 25.9 mm SL).

Anti-predator performances against jellyfish were similar in jack mackerel and chub mackerel; all fish at 5.8 mm (jack mackerel) and 6.0 mm (chub mackerel) or larger successfully escaped predation from jellyfish (Fig. 40A). In the case of anchovy, however, larvae as large as 23 mm still suffered from jellyfish predation (Fig. 40B).

Both separation angle and inter-individual distance decreased from 18 to 23 mm SL in anchovy (Figs. 41A, B). A significant decrease of SSI was observed at the earlier stage, already at 18 mm SL (Fig. 41C). In the case of chub mackerel, the decrease of SSI was observed at 10 mm SL (14 dph; Nakayama et al. 2007).

6-4. Discussion

6-4A. Growth performance of hatchery-reared pelagic fish larvae and comparison to wild conspecifics

Daily specific growth rates obtained in the present research were 0.0502, 0.0956 and 0.0635 in jack mackerel, chub mackerel and anchovy, respectively. Xie et al. (2005) estimated the growth...
rate of wild jack mackerel using daily otolith increments and found that it takes 25 days to attain 12 mm BL, which is slightly more rapid than the results of my rearing experiment. They estimated the specific growth rate of jack mackerel as 0.056. Kanaji et al. (2009) reported that growth trajectories differ significantly among different cohorts of juveniles collected in Kunda Bay, Kyoto. Their estimated SL at 30 dph ranged from 5 to 18 mm, and the cohort spawned in June and July attained 10 mm SL at 30 dph, which was very close to the result in the present work. Shoji et al. (2003) analyzed the growth rate of wild chub mackerel using otolith and found that the specific growth rate of chub mackerel was 0.097. Takahashi and Watanabe (2004) estimated that it takes about 30 days for Japanese anchovy to attain 20 mm BL, which is slightly slower than the present result. Overall, the growth trajectory of the present work matched well with those reported in wild collected larvae and early juveniles.

Fig. 40. Development of anti-predator performance against jellyfish in (A) jack mackerel, chub mackerel and (B) Japanese anchovy.

Fig. 41. (A) Ontogenetic changes of separation angle (SA), (B) nearest neighbor distance (NND), and (C) separation swimming index (SSI) in Japanese anchovy. Dotted lines in (A) and (C) represent random direction and movement, respectively; values below the line are significant.
6-4B. Swimming speeds in the context of feeding ecology

Swimming speed measured in an experimental tank with still water (cruise speed in this paper, or routine speed in Fuiman et al. (1999)) tends to be slower than the one measured in a chamber in current (critical speed) or in the open ocean (Clarke et al. 2005; Leis 2006). Therefore, we need to be careful in applying results of the swimming speed measured in the laboratory in the ecological context. Comparison among species under the same condition is less problematic.

The cruise swimming speed was fastest in chub mackerel, intermediate in anchovy and slowest in jack mackerel in the present work. Hunter and Kimbrell (1980) reported the cruise swimming speed of chub mackerel larvae being expressed as the following power function: \( S = 2.780 \times L^{1.753} \) (\( S \): cruise speed, \( L \): SL). Hunter (1972) also reported the cruise swimming speed of northern anchovy \( Engraulis mordax \) larvae as ca. 1 SL/s (\( S = -0.215 + 1.038 \times L \)). Their values are slightly slower than the present results, perhaps partly due to the temperature during measurement (19°C in their study and 22°C in my work). Hunter (1980) pointed out that northern anchovy swim more slowly than mackerel larvae at all stages of development, and he attributed this difference to the planktivorous and piscivorous feeding habits in anchovy and chub mackerel, respectively.

Sakakura and Tsukamoto (1996) studied the ontogeny of swimming speed in the yellowtail \( Seriola quinqueradiata \) and reported that the cruise speed (relative swimming activity in their paper) of this species ranging from 0.5 to 1.7 TL/s in 6–38 dph (5–24 mm TL). This value is close to the value found in the present work in jack mackerel. Leis et al. (2006) reported the critical speed and \textit{in situ} speed of giant trevally \( Caranx ignobilis \) to be 15–28 SL/s and 4.5–13.0 SL/s, respectively. Their value of critical speed is close to the burst speed of jack mackerel (10.3–23.4 SL/s) in the present work.

Chub mackerel spawn in the open ocean (Yamada et al. 1998; Hwang and Lee 2005). Their predation is highly opportunistic and they feed on copepods, appendicularians, mysids and fish larvae including conspecifics, with preference for fishes as they grow (Lipskaya 1982; Castro and Del Pino 1995; Sánchez-Velasco and Shirasago 2000). Because of the relatively long distance of their migration and feeding on highly mobile prey, they may require the highest capability of cruise swimming or it may be a characteristic of scombrids. Anchovy spawn in both coastal and offshore areas (Imai and Tanaka 1994; Takahashi and Watanabe 2004) and their larvae prefer turbid water, especially near river estuaries (Uotani et al. 2000). The migration in the larval and juvenile stages is within relatively limited coastal areas (Hwang et al. 2006). In the case of jack mackerel, although they have local populations along the coast, Sassa et al. (2006) reported that there is a large spawning area in the South China Sea from which juveniles are recruited to the coastal area in Japan (Fig. 35). Carangid fishes are generally adapted to rocky reefs as is represented by the flattened form with high maneuverability, in contrast to fusiform fish such as chub mackerel (Webb 1984). They also have less red muscle so that they are likely to be less adapted to cruise swimming (Xu et al. 1993). Therefore, they may utilize floating objects to help them transport themselves to a suitable habitat with less effort.

Shirota (1970) reported the mouth size of first feeding larvae in chub mackerel, jack mackerel and Japanese anchovy as 0.622, 0.390 and 0.250 mm, respectively. The large mouth of chub mackerel supports voracious feeding and requires consistent food searching, resulting in relatively fast cruise swimming. Yokota (1961) compared the gut contents of fish larvae collected off Kyushu, Japan, and he reported the prey size of chub mackerel, jack mackerel and anchovy at 5–7 mm TL to be 0.15–1.05, 0.15–1.05 and 0.15–0.35 mm, respectively. Therefore, anchovy adapts to a relatively small size of prey. Omori et al. (1995) pointed out that the relatively large size of copepods was replaced by a small size of species from 1950 to 1960 in Tokyo Bay, and suggested that this change is unfavorable to planktivorous fish but favorable to jellyfish. Considering the small mouth size, reduced zooplankton size in the environment is likely to be advantageous to anchovy rather than other fishes.

6-4C. Inter-specific difference of the ontogeny of anti-predator performance

Larvae of anchovy suffered very high predation mortality from jellyfish (Fig. 40B). Since larvae of clupeoid fishes are transparent underwater, they may be more adapted to avoiding...
visual predators such as piscivorous fishes (Fuiman and Magurran 1994). Turbidity in a local environment may enhance this efficiency of crypticism. This speculation is supported by the fact that Japanese anchovy shows a strong preference to turbid water both in experimental tanks and in the wild (Uotani et al. 1993). Because the moon jellyfish is a tactile feeder with selective feeding of slower and larger zooplankton (Costello and Colin 1994; Sullivan et al. 1994), the anchovy should be more vulnerable to this predator. Major fishes upon which jellyfish predate include other transparent species such as Atlantic herring and capelin (reviewed by Purcell and Arai (2001)). In contrast, jack mackerel performed best against predation by jellyfish. This may be partly because they have a high burst swimming capability so that they can escape, even when they are captured by a jellyfish. A relatively tough skin surface structure may also make them less vulnerable to nematocysts.

Both separation angle and nearest neighbor distance in anchovy significantly decreased from 18 to 23 mm SL, whereas the separation swimming index decreased slightly earlier, from 15 to 18 mm SL. This may be because SSI can detect the earliest stage of schooling behavior. Among other Clupeiformes, Hunter and Coyne (1982) reported that northern anchovy Engraulis mordax start to form schools at 12 mm, while herring begin to form school at 35–40 mm (Gallego and Heath 1994). Although the size at which school formation differs among species, most of these start to form schools at the earliest stage of juveniles starting with the completion of fin ray counts and the beginning of squamation.

Once the schooling behavior was established, the nearest neighbor distance in the anchovy schools was narrow (0.74 × SL and 0.72 × SL in 27 mm and 31 mm SL groups, respectively) compared to Spanish mackerel Scomberomorus niphonius (1.2–1.4 × SL; Masuda et al. 2003). The difference of NND may represent the difference of feeding ecology and the function of schooling between these two fishes. The anchovy juvenile is a planktivore and the Spanish mackerel juvenile is a piscivore. Therefore, Spanish mackerel juveniles always suffer the risk of cannibalism from other members in the same school, resulting in a higher value of NNDs. In addition, the function of schooling in anchovy juveniles should be mostly for reducing predation mortality, whereas schooling of Spanish mackerel may have other functions such as improving the feeding efficiency as well as exchanging information on prey items.

Major functions of schooling are anti-predator performance and improved feeding efficiency and the importance of these functions is different among species and developmental stages (Krause and Ruxton 2002). Nakayama et al. (2007) studied the ontogeny of schooling behavior in chub mackerel and found that, although they start to show schooling defined by the decrease of SSI at 9.6 mm SL, they start to show social transmission mediated by visual stimuli at as large as 25.1 mm SL.

Even though anchovy is vulnerable to gelatinous predators, the population is relatively stable (Fig. 36C). The reason may be because they have high fecundity (Fig. 42). When the batch fecundity of each fish species is represented by the number of spawned eggs per gram of body weight, anchovy has the highest and jack mackerel has the lowest among four common pelagic fishes. Furthermore, anchovy matures in as little as 6 months after hatching (Tsuruta 1992), whereas it takes 1–2 years for sardine to mature (Morimoto 2003), and jack mackerel and chub mackerel usually attain maturation in about 2 years (Nishida 2004; Watanabe and Yatsu 2006). Therefore, the difference of lifetime fecundity among species is even larger than the batch fecundity represented in Fig. 42.

6-4D. Environmental factors as a driving force of population replacement

Life history strategies of four common pelagic fish species are summarized as follows (Fig. 43). When phytoplankton is abundant, sardine receives the benefit, as they can utilize diatoms and other phytoplankton as food (Noguchi et al. 1990). Copepods are the major prey for larvae of most fish species. A high abundance of copepods is likely to be most advantageous to chub mackerel because this species has the highest growth performance among common pelagic fishes when the feeding and temperature conditions are optimal. Chub mackerel can feed on other fish species when they are available (Lipskaya 1982), so that when larvae of other fish species are abundant, chub mackerel again is advantaged. When jellyfish are abundant, jack mackerel is likely to be favored because they utilize jellyfish for both as a refuge and as a prey.
Fig. 42. Fecundity of four common pelagic fish species represented by the number of eggs divided by the body weight. Data from Nishida (2004), Yamada et al. (1998), Aoki (1996) and Tsuruta (1992) on jack mackerel, chub mackerel, sardine and anchovy, respectively.

Fig. 43. A chart to compare the life history strategies among four common pelagic fish species. Each arrow represents the relative level of environmental factor.

collector (Chapter 5). Chub mackerel may also have an advantage because they feed on jellyfish (Masuda et al. 2008). In contrast, anchovy and sardine larvae are likely to be disadvantaged by jellyfish blooms because they are highly vulnerable to jellyfish predation. When the water temperature is high, chub mackerel is likely to have an advantage as their growth is remarkably
temperature dependent (Mendiola et al. 2008). Sardine is adapted to cold water so that they are disadvantageous when the temperature is high (Takasuka et al. 2007). The change of one of these environmental factors can be the driving force to the increase or decrease of certain pelagic fish species and thus the replacement of dominant fish. Although there is no particular environmental factor which would favor anchovy, they do have an advantage in fecundity as discussed before.

On the global scale, however, Peruvian anchovy Engraulis ringens is probably the most abundant single fish species among all the fishes in the world (Chavez et al. 2003). Chavez et al. (2003) pointed out that sardine populations off Japan increase when water temperature is low and the ocean is rich in nutrients, whereas anchovy is the predominant species off California and Peru when those regions are cool and productive. An increase of primary production favors different groups of fish in the east and west of the Pacific for unknown reasons. The temperature of the Japanese sardine spawning ground ranges from 11 to 20°C (Aoki and Murayama 1993) and that of Japanese anchovy ranges from 15 to 28°C (Funamoto et al. 2004). In the East Pacific, sardines spawn at higher temperatures with a wider range (13–25°C) than anchovy (11.5–16.5°C) (Lluch-Belda et al. 1991). Therefore, the optimal temperature for spawning in these two genus is different between the East and West Pacific.

In this chapter, I assumed that the fluctuation of pelagic fish population is driven by biotic and abiotic environmental changes. Some of these environmental changes, however, may originate from an anthropogenic effect. Global warming is apparently caused by human activity and is likely to be inducing replacement of coastal reef fish assemblages (Masuda 2008). The cause of jellyfish bloom is also attributable to anthropogenic factors such as overfishing, eutrophication and global and local warming of the sea water (Purcell et al. 2007).

7. General discussion: Towards the sustainable management of fisheries resources

7-1. Implications of ontogenetic study for the fisheries resource management

Chapter 2 showed that there are two inflection points in the morphological changes in striped jack (9 and 20 mm TL; Fig. 4). Chapter 3 showed that striped jack rely on tactic behavior in the larval stage, then once they attain the juvenile stage, they form schools and their anti-predator performance and migratory behavior is likely to be more active rather than passive. Balon (1990) suggested that the development of fish is often saltatory rather than gradual. It seems to be the case in striped jack, especially with behavioral events such as the onset of OKR (Fig. 16) and schooling (Fig. 17). This may imply that fish suffer high mortality until just before the onset of certain behavioral repertory.

Chapter 4 showed that dietary origin DHA is essential for the development of brain and behavior in fish juveniles. Because behaviorally maladaptive individuals are easy targets for predators, quality and quantity of prey items in natural waters may be essential for the behavioral ontogeny and thus survival of fishes. I also suggested that an increase of UV radiation on the ocean surface might change the population balance in pelagic waters.

Chapter 5 focused on the commensalisms between jack mackerel and jellyfish, and the ecological function of the association is suggested to change ontogenetically. Jellyfish and other floating objects are likely to provide a feeding place as well as a refuge for jack mackerel and other fishes associating with these objects. This association behavior is utilized widely for fisheries such as the collection of young yellowtail Seriola quinqueradiata associated with floating algae for seedlings for aquaculture, and the utilization of fish aggregating devices (FADs) to catch tunas and other pelagic fishes in open seas. Hallier and Gaertner (2008) reported that tunas associated with FADs contain lower gut contents and had inferior growth than those in free schools. Because about 70% of tunas are caught with the association of FADs and surrounded by purse seine, utilization of FADs may be an ecological trap. Natural floating objects such as jellyfish and logs can be an indicator of feeding place for fishes, whereas man-made drifting FADs would rather mislead them in inappropriate habitat selection (Hallier and Gaertner 2008). This may also be the case for other unintended man-made structures such as floating debris, and even the explosive bloom of jellyfish.
It is insightful that the percentage of jellyfish that accompanied jack mackerel increased within the three years of research period (Fig. 33). Blooms of giant jellyfish were rare until the year 2002. It is tempting to speculate that jack mackerel that associated with jellyfish survived better and had more opportunity to spawn, resulting in the prevalence of behavioral genes to associate with jellyfish.

There is, however, no sign of a significant increase in the catch of jack mackerel, as would be expected if jellyfish blooms were advantageous. This is attributable to the overfishing of young individuals of this species. Jack mackerel mature at 20 cm SL and 2 years old, whereas much of the population is harvested before attaining this size.

We can look at this problem from the aspect of preventing jellyfish bloom. If we preserve a large enough population of jack mackerel, they will parasitically associate with jellyfish and thus prevent their growth. Some other fish species such as chub mackerel and filefish feed on jellyfish (Fig. 32). If we can reduce fishing pressure on these fishes especially at juvenile and young stages, I suggest that jellyfish blooms can be substantially mitigated.

7-2. Perspectives for the sustainable management in fisheries resources

Although fish populations fluctuate under natural condition, fisheries in the world are obviously over-exploited (Pauly and Maclean 2003). In the case of Japanese coastal waters, population replacement is partly attributable to the natural fluctuation of oceanic conditions especially sea water temperature (Takasuka et al. 2007). If populations fluctuate naturally, we should be able to adapt our fishery so that we will maximize the utilization and minimize the risk of depletion. The reality, however, seems to be that fisheries as a whole are destroying the slightest opportunity of recovery of the already depleted population. For example, chub mackerel made a successful recruitment in 1992 and 1996, but the cohorts born in these years were heavily fished before the age of maturity and thus failed to recover its population (Kawai et al. 2002). Because small mackerel has very low commercial value, fishermen should definitely delay catching this species until the fish spawn at least once, so that both the population and the commercial value of the catch will be maintained. Chub mackerel can be caught by hook and line, purse seine net or set net, and the commercial value will be by far the highest for those caught by hook and line. Catching immature chub mackerel using purse seine net results in much less commercial value and also it is destructive for population and should be forbidden, at least until the population is fully recovered. In the case of set net fishery, it is difficult to control the species and size of fish caught in certain areas because it is a passive fishing gear (Fig. 44). For example, set net targeting Japanese anchovy may accidentally catch young and immature chub mackerel which followed a school of anchovy. Understanding of species specific behavioral ecology with respect to the response to netting, schooling and migration would help avoid the inappropriate and uneconomical status of such recruitment overfishing.

Pauly and Maclean (2003) made five recommendations to improve the status of overfishing in the North Atlantic, and I think these are also applicable to the Northwest Pacific. Their recommendations are as follows:

1. Fishing effort must be drastically reduced by a factor of three or four in most areas.
2. Large marine reserves, amounting to at least 20% of the ocean must be established by the year 2020.
3. Eco-labeling and other market-based efforts to move the fishing industry toward sustainable practice must be intensified.
4. An effective regime must be designed and implemented to publicly expose deliberately unsustainable and illegal practices, and their perpetrators.
5. Access and property rights in fisheries should favor smaller-scale, place-based operations, operating passive gear to the extent possible.

Although the impact of fishing on marine ecosystems can be detected in prehistoric ages by archaeological records, cascades of negative impacts are noticeable worldwide since the mid-twentieth century (Jackson et al. 2001). For example, Jackson et al. (2001) suggest that eutrophication and hypoxia did not occur in Chesapeake Bay until the 1930s, nearly two centuries
after the clearing of land for agriculture which greatly increased runoff of sediments and nutrients, because there were sufficient oysters to feed on the increased production of phytoplankton. From this perspective, reduced water quality can be the result rather than the cause of overfishing. Pauly et al. (1998) demonstrated that the trophic level of the species groups targeted in world fisheries significantly declined between 1950 and 1994. After over-exploiting coastal waters, people are fishing down the food web and now intensive fishing pressure is targeting fish species living in the deep sea or in the Antarctic waters, the growth of which is slow and thus are extremely vulnerable to exploitation (Clover 2004). One effective way to reduce fishing pressure, as pointed out by Pauly and Maclean (2003), is to abandon subsidies.

Establishment of marine reserves is an efficient way for the recovery and maintenance in reef-associated fishes and benthic fishery resources. Russ and Alcala (1996) demonstrated that the establishment of marine reserves in coral reefs in the Philippines increased the density of the fish population not only inside but also outside the marine reserves. Although it may be less efficient in highly migratory fishes such as sardine, management should be efficient in less migratory pelagic fish such as anchovy. For example, certain river and estuarine systems in an area should be established as marine reserves for pelagic fishes. Highly migratory species also tend to have species-specific habitats for spawning and nursery. Some fish show spawning aggregation at certain times of the year in specific places. In the case of red hind Epinephelus guttatus, spawning aggregation was once over-exploited, then the spawning area was closed for conservation (Beets and Friedlander 1999). With this strategy, the population of red hind dramatically recovered. A similar strategy can be applicable to other migratory species.

Eco-labeling is the efficient way to inform consumers about sustainable fisheries. Informing about unsustainable fisheries is also very important but is sometimes more difficult. There are often some legal gray zones in fishing activities. In Japan, fisheries regulation is under the control of prefectural administrative offices. Even though one prefecture regulates strictly so that fisheries in local area will be sustainable, fishing vessels in other prefectures can intrude and catch these protected fishery resources. Purse seine net equipped with sonar and strong fish attracting lights operated at night will allure fish from protection and can thus easily lead the fish population towards collapse. Such activities should be strictly forbidden under the decisions made by the national government.
Pauly and Maclean (2003) recommended encouraging small-scale fishermen who use passive fishing gears. Operation of set-net is the major fishery along the coast of the Sea of Japan (Fig. 44B). Because fish often escape a set net, this gear is unlikely to capture the whole school of certain species. Even with its relatively low efficiency, there are cases where inappropriate sizes of fish species, such as small sizes of chub mackerel, are unintentionally captured by set net. Understanding of schooling and migration behavior and the responses to underwater structures in each species should be applied to avoid the over-exploitation of these juveniles.

Ecosystem-based approaches for fishery (EAF) is rapidly being adopted by leading institutions in the world, since the value of the whole ecosystem is much greater than the sum of its parts (Browman and Stergiou 2004; Francis et al. 2007). A shift to EAF does not represent the denial of conventional single species-based management of fisheries, because the failure is not the model itself but the lack of governance (Mace 2004). In the context of EAF, I suggest that interaction among fish species should be further studied through both laboratory and field-based approaches, outcomes of which will be applied to proper governance for sustainable fisheries.

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References


Hwang SD, Song MH, Lee TW, McFarlane GA, King JR. Growth of larval Pacific anchovy Engraulis

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Jackson JBC and 18 other authors. Historical overfishing and the recent collapse of coastal ecosystems. Science 2001; 293: 629–638.


Mansueti R. Symbiotic behavior between small fishes and jellyfishes, with new data on that between the stomatode, Peprilus alepidotus, and the Scyphomedusa, Chrysaora quinquecirrha. copea 1963: 40–80.


Behavioral Ontogeny of Marine Pelagic Fishes for Sustainable Management of Fisheries Resources


