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Effect of low dissolved oxygen concentrations on behavior and predation rates on red sea bream *Pagrus major* larvae by the jellyfish *Aurelia aurita* and by juvenile Spanish mackerel *Scomberomorus niphonius*

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Abstract A shift in outcomes of predator-prey interactions in plankton community may occur at sublethal dissolved oxygen concentrations that commonly occur in coastal waters. Laboratory experiments were conducted to investigate how a decline in dissolved oxygen concentration alters the predation rate on fish larvae by two estuarine predators. Behavior and consumption of larval fish by moon jellyfish *Aurelia aurita* (103.1 ± 12.4 mm in bell diameter) and by a juvenile piscivore, Spanish mackerel *Scomberomorus niphonius* (30.1 ± 2.1 mm in standard length: SL), were observed under four oxygen concentration treatments (1, 2 and 4 mg l⁻¹ and air-saturated: 5.8 mg l⁻¹). Larvae of a coastal marine fish species, red sea bream *Pagrus major* (7.21 ± 0.52 mm SL), were used as prey for the experiment. Bell contraction rate of the jellyfish did not vary among the oxygen concentrations tested, indicating a tolerance to low oxygen concentration. Gill ventilation rate of the Spanish mackerel increased and swimming speed decreased as the oxygen concentration decreased, indicating that oxygen concentrations ≤ 4 mg l⁻¹ are physiologically stressful for this species. The number of larvae consumed in 15 min. by jellyfish increased whereas those consumed by Spanish mackerel decreased with the decrease in oxygen concentration. Low oxygen concentrations that are commonly observed in coastal waters of Japan

during summer have the potential to increase the relative importance of jellyfish as predator of fish larvae and to change the importance of alternative trophic pathways in estuarine ecosystems.

Introduction

Low dissolved oxygen concentrations induced by anthropogenic, physical and/or biological factors commonly occur in many aquatic habitats such as estuaries, lakes, fjords, coastal waters, and in the deep sea (Renaud 1986; Suzuki and Matsukawa 1987; Nixon 1988). Occurrence of low dissolved oxygen in stratified waters of shallow marine systems during summer can cause lethal effects on benthic and pelagic organisms (Officer et al. 1984; Aoki 1999). Even though the effect is not lethal, oxygen concentrations in the range of 1–4 mg l⁻¹ (moderate levels of hypoxia) are physiologically stressful (Rombough 1988) and disturb growth and survival of many fish species (van der Veer and Bergman 1986; Kramer 1987). Fish larvae would be more vulnerable to mortality when oxygen concentration declines to a stressful level since they are less tolerant of low dissolved oxygen concentration due to undeveloped physiological function (Rombough 1988). Declines in dissolved oxygen to moderate levels of hypoxia, which is not lethal during short-term exposure, can reduce larval ability to escape from predators and increase vulnerability to predation (Breitburg et al. 1994). However, there is much less information on the effects of low dissolved oxygen on larval survival compared to those on adults and immature fishes.

The Seto Inland Sea is the largest area with reduced salinity water in Japan and has many industrialized areas along its coast. Excess nutritional loading from the land exacerbates the depletion of oxygen concentration in the coastal waters (Okaichi et al. 1996). In the Sea of Hiuchi, the central Seto Inland Sea, dissolved oxygen concentration commonly declines to < 1 mg l⁻¹ during

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summer (Ochi et al. 1978). Recently, an increase in the moon jellyfish *Aurelia aurita* population has led to significant impacts, ecologically on the plankton community through its predation on zooplankton in the Seto Inland Sea and economically on industries, by hampering fishery activities and by preventing power plants from taking cooling water (Uye and Ueta 2004; Yasuda 2003). Uye et al. (2003) observed moon jellyfish aggregated at a mean abundance of 250 m⁻² and which consumed almost 100% of mesozooplankton in coastal waters of southwestern Japan in summer. An increase in the moon jellyfish population would have significant effects on the recruitment of coastal fishery resources in the Seto Inland Sea through increasing the predation impact and/or compensation. In addition, predation on fish larvae by moon jellyfish would be more important during summer hypoxia if moon jellyfish are tolerant to moderate hypoxia, a decline in oxygen concentrations to 1–4 mg l⁻¹ that commonly occurs in the central Seto Inland Sea during summer. Investigation on the effect of dissolved oxygen concentration on larval predation mortality in relation to prey-predator interactions would lead to a better understanding of how changes in environmental conditions directly and indirectly affect larval survival in estuarine ecosystems. However, there is no information on predation on fish larvae by moon jellyfish in coastal waters of Japan, although the jellyfish's life history (Toyokawa et al. 2000) and predation on invertebrate zooplankton (Ishii and Tanaka 2001; Uye et al. 2003) have been well documented.

In the present study, we describe results from experiments conducted to examine how low dissolved oxygen concentrations affect the predation on fish larvae by two predators, moon jellyfish and a juvenile piscivore, Spanish mackerel *Scomberomorus niphonius*. Behavior and consumption rates of the predators under low oxygen concentrations were observed under laboratory conditions.

Larvae of red sea bream *Pagrus major* was used as prey in the predation experiments. The red sea bream is widely distributed and is one of the most important fishery resources in coastal waters of Japan. Pelagic larvae and juveniles are abundant from March to May in Shijiki Bay, Nagasaki (Tanaka 1980), and in May and June in the Seto Inland Sea (Shoji et al. 2002). Late larvae and early juveniles migrate from coastal open waters in May and June to settle in shallow waters of bays (Azeta et al. 1980).

The moon jellyfish is widely distributed in coastal waters of the world (Yasuda 2003) and is reported to have recently increased in abundance in coastal waters of Japan such as Tokyo Bay (Ishii 2001) and the Seto Inland Sea (Uye and Ueta 2004). Moon jellyfish has been considered as an important predator of zooplankton (Bailey and Batty 1984; van der Veer and Oorthuysen 1986; Sullivan et al. 1994; Matanoski et al. 2004) because of its high consumption rates. Möller (1984) observed that 68 Atlantic herring *Clupea harengus* larvae were eaten by a moon jellyfish 42 mm in bell diameter (BD) in Kiel Fjord. Nakayama et al. (2003) described that more than 110 red

sea bream larvae were consumed by a moon jellyfish 66–80 mm BD under laboratory conditions.

The Spanish mackerel is widely distributed in southwestern coastal waters of Japan and spawns in May and June (Kishida and Aida 1989) in the Seto Inland Sea, one of the major spawning area of the species. Young-of-the-year Spanish mackerel inhabit the central Seto Inland Sea throughout the summer until the wintering migration out of the Seto Inland Sea (Kishida 1989). Larvae and juveniles exhibit strong piscivory (Shoji and Tanaka 2001) and high consumption of fish larvae (90–127% body weight day⁻¹; Shoji et al. 2001). The Spanish mackerel is considered to be the most important predator in the summer ichthyoplankton community since no other pelagic juvenile fish has been reported to be piscivorous in the area.

Materials and methods

Rearing of prey larvae

Red sea bream eggs naturally spawned and fertilized at the Kyoto Prefecture Sea-Farming Center (KPSFC) were transported to the Maizuru Fisheries Research Station (MFRS), Kyoto University Field Science Education and Research Center, and were maintained in 500-l tanks with aerated seawater. Larvae were fed with rotifer *Brachionus plicatilis* and *Artemia* spp. at 16.1–19.5°C under natural light conditions. Age and mean ($\pm$ SD) standard length (SL) of larvae used for the experiments were day 23 and 7.21 ($\pm$ 0.52) mm (post-flexion stage).

Rearing and husbandry of predators

Moon jellyfish were collected at the pier of MFRS using a 10-l plastic bucket and were kept in 100-l tanks with filtered sea water. Considering the size of moon jellyfish abundant in the Seto Inland Sea during summer (Uye 2004), moon jellyfish in mean BD ($\pm$ SD) of 103.1 ($\pm$ 13.1) mm ($n=24$) were used for the predation experiments. The moon jellyfish were fed with *Artemia* spp. and were starved for overnight before the experiments.

Artificially fertilized eggs were obtained from a pair of adults of Spanish mackerel fished by a gill net in the Sea of Harima, eastern Seto Inland Sea. The eggs were transported from the Yashima Branch, Japan Sea Farming Association (JASFA), to MFRS and were maintained in 500-l tanks with aerated seawater. Larvae were fed with yolk-sac red sea bream larvae (day 0–3) under natural light conditions with water temperature ranging from 15.8 to 19.5°C. Early juveniles (30.1 $\pm$ 2.1 mm SL, day 28) were used as the predators for the predation experiment. The juveniles were starved overnight before the experiment.

Table 1 *Aurelia aurita* and *Scomberomorus niphonius*. Mean $\pm$ SD dissolved oxygen concentrations (mg l^{-1}) in the tanks with moon jellyfish (MJ) and juvenile Spanish mackerel (SM) as predator of red sea bream larvae. Four oxygen concentrations (1, 2 and 4 mg l^{-1} and air-saturated) were set for the predation experiments

Oxygen level desired	Predator	
	MJ	SM
1 mg l^{-1}	1.02 ± 0.04	1.04 ± 0.06
2 mg l^{-1}	1.96 ± 0.11	1.97 ± 0.10
4 mg l^{-1}	3.94 ± 0.05	3.97 ± 0.08
Air-saturated	5.75 ± 0.01	5.78 ± 0.09

Predation experiment

Observations on the behavior of the predators and measurements of predation rates on fish larvae were conducted under four oxygen concentration treatments (1, 2, 4 mg l^{-1} and air-saturated: 5.8 mg l^{-1}). Water temperature, salinity, and oxygen concentration were recorded with an Environmental Monitoring System (YSI 650 MDS, YSI, USA). Water temperature ranged between 19.5 and 20.3°C and salinity between 33.2–33.5 psu both in the stocking and experimental tanks. The desired oxygen concentrations were obtained by bubbling filtered seawater with nitrogen and air. Oxygen concentrations within $\pm 4\%$ of the desired concentration were obtained (Table 1).

Either of 1 moon jellyfish or 1 Spanish mackerel with 30 red sea bream larvae were introduced to a 10-l circular experimental tank surrounded with a black plastic sheet to minimize the effect of the influence of the observer. A relatively shallow depth of the water (14 cm) prevented the moon jellyfish from vertical distribution. The tank was sealed and the behavior of the predators was videotaped. Observations on the behavior of the predators were started 5 min after the beginning of the experiments. The number of contractions of the moon jellyfish bell was counted for 3 min by direct observations. Cruise swimming speed (cm sec^{-1}) and gill ventilation rate (no. min^{-1}) of the Spanish mackerel were measured using the videotaped records. The number of red sea bream larvae predated on by the two predators for 15 min was counted at the end of each experiment. The larvae ingested or captured on the umbrella surface and with tentacles by moon jellyfish were defined as predated. The moon jellyfish were measured in BD and the Spanish mackerel in SL. The predators were not reused. Six replicates were made for each predator and oxygen treatment. All experiments were conducted from 0900 to 1500 hours.

Results

Moon jellyfish behavior and consumption rate

The bell contraction rate of moon jellyfish did not vary among the oxygen concentrations tested (Fig. 1). Mean bell contraction rate ($\text{no. min}^{-1} \pm \text{SD}$) ranged between

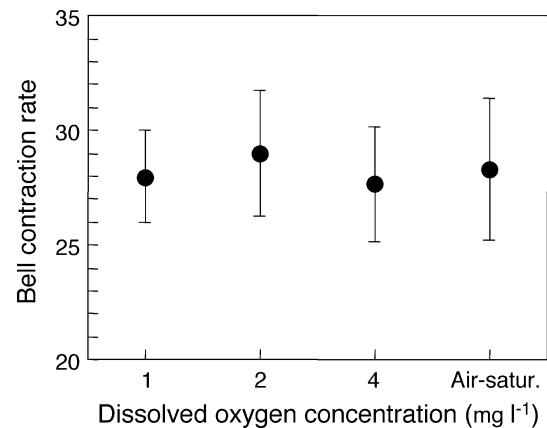


Fig. 1 *Aurelia aurita*. Bell contraction rate (no. min^{-1}) of moon jellyfish *Aurelia aurita* under reduced and air-saturated (5.8 mg l^{-1}) oxygen concentrations. Six replicates were conducted at each oxygen concentration. Vertical bars indicate SD

27.7 ± 2.5 at 4 mg l^{-1} and 29.0 ± 2.8 at 2 mg l^{-1} during the experiment. There was no significant effect of the oxygen treatment on the bell contraction rate (Kruskal-Wallis test, $P=0.86$). Overall mean ($n=24$) of bell contraction rate was 28.3 ± 2.4 .

Consumption rate by moon jellyfish was higher under the two lowest oxygen concentrations (Fig. 2). More than 80% of red sea bream larvae were predated on by moon jellyfish at oxygen concentration of 1 and 2 mg l^{-1} . About half of the larvae survived under the two highest oxygen concentrations. Effect of the oxygen concentration treatment on consumption rate was significant (Kruskal-Wallis followed by Dunnett test, $P<0.05$).

Spanish mackerel behavior and consumption rate

The gill ventilation rate of juvenile Spanish mackerel increased with the decrease in dissolved oxygen concentration (Fig. 3). Mean gill ventilation rate ($\pm \text{SD}$)

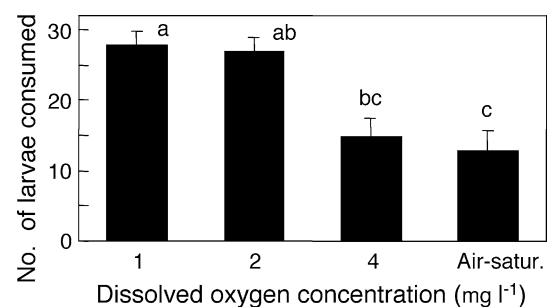


Fig. 2 *Aurelia aurita*. Number of red sea bream larvae predated on in 15 min by one moon jellyfish under reduced and air-saturated (5.8 mg l^{-1}) oxygen concentrations. Six replicates were conducted at each oxygen concentration. Different letters indicate significant differences among oxygen concentration treatments (Kruskal-Wallis followed by Dunnett test, $P<0.05$). Vertical bars indicate SD

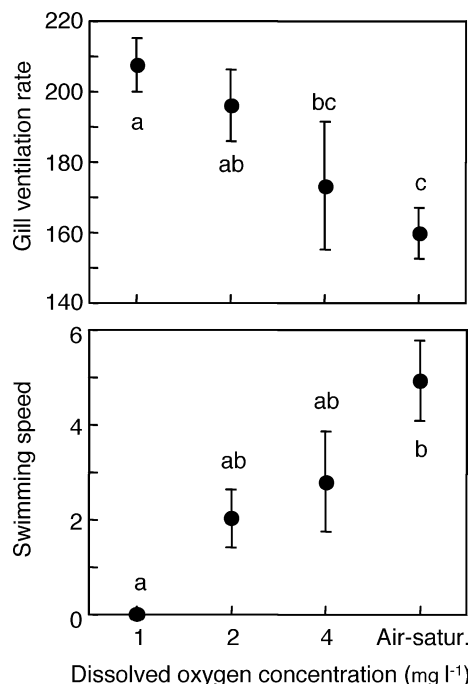


Fig. 3 *Scomberomorus niphonius*. Gill ventilation rate (no. min⁻¹) and cruising swimming speed (cm s⁻¹) of juvenile Spanish mackerel under reduced and air-saturated (5.8 mg l⁻¹) oxygen concentrations. Six replicates were conducted at each oxygen concentration. Different letters indicate significant differences among oxygen concentration treatments (Kruskal-Wallis followed by Dunnett test, $P < 0.05$). Vertical bars indicate SD

ranged from 207.8 ± 7.7 at 1 mg l⁻¹ and 159.8 ± 7.3 under the control condition. There was a significant effect of oxygen concentration on the gill ventilation rate (Kruskal-Wallis followed by Dunnett test, $P < 0.05$).

Mean cruise swimming speed was higher in the higher oxygen concentration treatments (Fig. 3). All Spanish mackerel were at the bottom of experimental tank having stopped swimming at 5 min after the start of experiment in 1 mg l⁻¹ treatment. There was a significant difference in the swimming speed between 1 mg l⁻¹

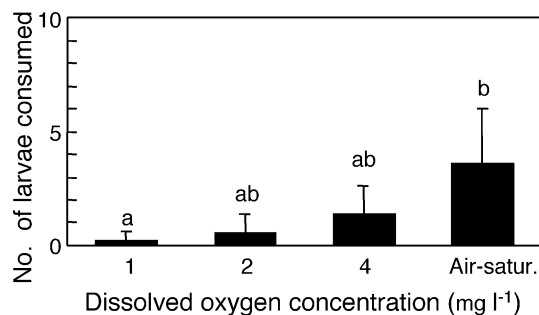


Fig. 4 *Scomberomorus niphonius*. Number of red sea bream larvae predated on in 15 min by one juvenile Spanish mackerel under reduced and air-saturated (5.8 mg l⁻¹) oxygen concentrations. Six replicates were conducted at each oxygen concentration. Different letters indicate significant differences among oxygen concentration treatments (Kruskal-Wallis followed by Dunnett test, $P < 0.05$). Vertical bars indicate SD

and air-saturated oxygen concentration treatments (Kruskal-Wallis followed by Dunnett test, $P < 0.05$).

Consumption rate of larvae by Spanish mackerel juvenile increased with the increase in oxygen concentration (Fig. 4). Only one red sea bream larva was predated on by the Spanish mackerel under the 1 mg l⁻¹ treatment. There was a significant effect of oxygen concentration on the consumption rate (Kruskal-Wallis followed by Dunnett test, $P < 0.05$).

Discussion

The present experiments showed that a decline in oxygen concentration had different effects on the consumption rate by the different predators, moon jellyfish and juvenile Spanish mackerel. Differences in tolerances to low dissolved oxygen concentration between the two predators are attributable to the difference in the pattern of change in consumption under the oxygen concentrations between 1.04–5.75 mg l⁻¹. Bell contraction rate of moon jellyfish did not vary under the oxygen concentrations tested whereas gill ventilation rate of Spanish mackerel increased and cruise swimming speed decreased as the oxygen concentrations decreased. These observations suggest that moon jellyfish has a higher tolerance to low oxygen concentrations (≤ 2 mg l⁻¹) than juvenile Spanish mackerel does.

The increase in consumption on the larvae (7.21 mm SL) by moon jellyfish under oxygen concentrations ≤ 2 mg l⁻¹ supports results from another experiment in which the consumption by moon jellyfish on red sea bream larvae (6.19 and 8.60 mm SL) increased at ≤ 2 mg l⁻¹ (Shoji et al. 2005). Fukuhara (1985) observed under laboratory conditions that the cruising swimming speed rapidly increased in red sea bream larvae > 6 mm SL at which size the development of unpaired fins begins. Nakayama et al. (2003) reported that time to capture by moon jellyfish significantly increased in red sea bream larvae > 7 mm SL in aquaria. These observations suggest that red sea bream larvae > 7 mm SL are less vulnerable to predation by moon jellyfish than smaller larvae are apparently due to their increased swimming ability.

Fish larvae are considered more vulnerable to physiological stress by a decline in the oxygen concentration since they are less physiologically developed (Rombough 1988). Dissolved oxygen concentrations ≤ 2 mg l⁻¹ are not considered lethal for short-term exposure, but reduce the ability of fish larvae to react to and escape from jellyfish predators and to recover from contact with jellyfish (Breitburg et al. 1994). Therefore, the vulnerability of fish larvae to predation by jellyfish predators increases under low dissolved oxygen concentrations that are not lethal during short-term exposure. We conclude that red sea bream larvae > 7 mm SL are highly vulnerable to predation by moon jellyfish under dissolved oxygen concentration ≤ 2 mg l⁻¹ in nature; at oxygen concentrations ≥ 4 mg l⁻¹ they are potentially able to avoid moon jellyfish.

Costello and Colin (1994) examined the mechanisms of prey capture by moon jellyfish under laboratory conditions and suggested that moon jellyfish can capture prey organisms with slower escape speeds than flow velocity at the bell margin of moon jellyfish. In the present study, bell contraction rate did not vary under oxygen concentrations between 1.04 and 5.75 mg l⁻¹. This result indicates that the volume of water filtered by moon jellyfish and their ability to capture prey did not decrease under oxygen concentrations ≤ 2 mg l⁻¹. Moon jellyfish survival was 100% at 1 mg l⁻¹ in 3-h experiments (Shoji, unpublished data). We conclude that the moon jellyfish is highly tolerant to low dissolved oxygen concentrations and under these conditions there would be enhanced flow from ichthyoplankton to moon jellyfish.

In contrast to the consumption by moon jellyfish, consumption by juvenile Spanish mackerel decreased as dissolved oxygen concentration decreased. Early life stages of scombrid fishes (including *Scomberomorus* fish) are considered to have a high oxygen requirement due to the high swimming and metabolic rates (Hunter 1981). The increase in gill ventilation rate and decrease in swimming speed of juvenile Spanish mackerel with the decline in oxygen concentration to 4 mg l⁻¹ in the experiments indicate that the oxygen concentration ≤ 4 mg l⁻¹ was physiologically stressful for juvenile Spanish mackerel.

Juvenile Spanish mackerel are considered to be affected by oxygen concentrations ≤ 4 mg l⁻¹ in nature. Summer hypoxia causes a decline in oxygen concentration of the bottom water to ≤ 1 mg l⁻¹ in the central Seto Inland Sea (Ochi et al. 1978). Juvenile Spanish mackerel were caught by bottom trawls that target flatfish and shrimp in the central Seto Inland Sea in summer (Shoji, unpublished data). Young fishes of congeners, *S. cavalla* and *S. maculatus*, were also collected by shrimp trawls in the southeastern United States (Collins and Wenner 1988). It is likely that juvenile Spanish mackerel inhabit the bottom water of the central Seto Inland Sea during summer when hypoxia most frequently occurs.

A decline in consumption under low dissolved oxygen concentrations has also been reported in other estuarine juvenile piscivores. In juvenile striped bass *Morone saxatilis*, a decline in dissolved oxygen concentration to 2.5 mg l⁻¹ caused a decrease in the consumption to 50% of that under the control condition (Breitburg et al. 1997). In the Patuxent estuary, Chesapeake Bay, the ctenophore *Mnemiopsis leidyi* was reported to be abundant where oxygen concentration was 1.3 mg l⁻¹ (Keister et al. 2000). These observations and our results indicate that juvenile fish are less tolerant to low dissolved oxygen concentrations than jellyfish.

Uye (2002) pointed out that a change in the trophic interactions between zooplankton and their predators, including jellyfish, have occurred since the moon jellyfish increased in abundance in the Seto Inland Sea. Pelagic planktivorous fish which were the dominant predators of

zooplankton have been replaced by moon jellyfish in the food web since the moon jellyfish biomass increased in the Seto Inland Sea. The excess nutritional loading from land is considered as one of the major factors that caused the dominance by moon jellyfish in the summer plankton community in the Seto Inland Sea since it promotes production of small zooplankton which is a major prey organism of the moon jellyfish (Mills 2001; Uye and Ueta 2004). We suggest, based on present results, another possible mechanism for the increase in abundance of the moon jelly fish: the excess nutritional loading has contributed to the increase in abundance of moon jellyfish through exacerbating the depletion in oxygen concentration which is advantageous to feeding of the moon jellyfish.

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References

- Aoki N (1999) Mechanism for establishment of hypoxic water and its movement. *Kaiyo Monthly* 31:477–485
- Azeta M, Ikemoto R, Azuma M (1980) Distribution and growth of demersal 0-age red sea bream, *Pagrus major*, in Shijiki Bay. *Bull Seikai Reg Natl Fish Res Inst* 54:259–278
- Bailey KM, Batty RS (1984) Laboratory study of predation by *Aurelia aurita* on larvae of cod, flounder, plaice and herring: development and vulnerability to capture. *Mar Biol* 83:287–291
- Breitburg DL, Steinberg N, DuBeau S, Cooksey C, Houde ED (1994) Effects of low dissolved oxygen on predation on estuarine fish larvae. *Mar Ecol Prog Ser* 104:235–246
- Breitburg DL, Loher T, Pacey CA, Gerstein A (1997) Varying effects of low dissolved oxygen on trophic interactions in an estuarine food web. *Ecol Monogr* 67:489–507
- Collins MR, Wenner CA (1988) Occurrence of young-of-the-year king, *Scomberomorus cavalla*, and Spanish, *S. maculatus* mackerels in commercial-type shrimp trawls along the Atlantic coast of the southeast United States. *Fish Bull* 86:394–397
- Costello JH, Colin SP (1994) Morphology, fluid motion and predation by the scyphomedusa *Aurelia aurita*. *Mar Biol* 121:327–334
- Fukuhara O (1985) Functional morphology and behavior of early life stages of red sea bream. *Bull Jap Soc Sci Fish* 51:731–743
- Hunter JR (1981) Feeding ecology and predation of marine fish larvae. In: Lasker R (ed) *Marine fish larvae*. University of Washington Press, Seattle, pp 33–77
- Ishii H (2001) The influence of environmental changes upon the coastal ecosystems, with special reference to mass occurrence of jellyfish. *Bull Plank Soc Jap* 48:55–61
- Ishii H, Tanaka F (2001) Food and feeding of *Aurelia aurita* in Tokyo Bay with an analysis of stomach contents and a measurement of digestion times. *Hydrobiologia* 451:311–320
- Keister JE, Houde ED, Breitburg DL (2000) Effects of bottom-layer hypoxia on abundances and depth distributions of organisms in Patuxent River, Chesapeake Bay. *Mar Ecol Prog Ser* 205:43–59

- Kishida T (1989) Distribution and migration of Japanese Spanish mackerel based on the catch and effort data in the central and western Seto Inland Sea. *Bull Nansei Reg Natl Fish Res Inst* 22:13–27
- Kishida T, Aida K (1989) Maturation and spawning of Japanese Spanish mackerel in the central and western Seto Inland Sea. *Bull Jap Soc Sci Fish* 55:2065–2074
- Kramer DL (1987) Dissolved oxygen and fish behavior. *Environ Biol Fish* 18:81–92
- Matanoski JC, Hood RR, Owens RL, Purcell JE (2004) Patterns in swimming by a scyphomedusa: a novel approach to quantifying behavior in individuals. *Mar Biol* 145:303–313
- Mills CE (2001) jellyfish blooms: are populations increasing globally in response to changing ocean conditions? *Hydrobiologia* 451:55–68
- Möller H (1984) Reduction of a larval herring population by jellyfish predator. *Science* 224:621–622
- Nakayama S, Masuda R, Takeuchi T, Tanaka M (2003) Effects of highly unsaturated fatty acids on escape ability from moon jelly fish *Aurelia aurita* in red sea bream *Pagrus major* larvae. *Fish Sci* 69:903–909
- Nixon SW (1988) Physical energy inputs and the comparative ecology of lake and marine ecosystems. *Limnol Oceanogr* 33:1005–1025
- Ochi T, Nishio S, Okaichi T (1978) Anoxic water in the eastern area of Hiuchi Nada. *Bull Agric Dep Kagawa Univ* 29:297–304
- Officer CB, Biggs RB, Taft J, Cronin LE, Tyler MA, Boynton WR (1984) Chesapeake Bay anoxia: origin, development, and significance. *Science* 223:22–27
- Okaichi T, Komori S, Nakanishi H (eds) (1996) Biological resources and environment of the Seto Inland Sea. Koseisha-koseikaku, Tokyo
- Renaud ML (1986) Hypoxia in Louisiana coastal waters during 1983: implication for fisheries. *Fish Bull* 84:19–26
- Rombough PJ (1988) Respiratory gas exchange, aerobic metabolism, and effects of hypoxia during early life. In: Hoar WS, Randall DJ (eds) *Fish physiology XI. The physiology of developing fish. A. Eggs and larvae*. Academic Press, San Diego, pp 59–161
- Shoji J, Tanaka M (2001) Strong piscivory of Japanese Spanish mackerel larvae from their first feeding. *J Fish Biol* 59:1682–1685
- Shoji J, Maehara T, Aoyama M, Fujimoto H, Iwamoto A, Tanaka M (2001) Daily ration of Japanese Spanish mackerel *Scomberomorus niphonius* larvae. *Fish Sci* 67:238–245
- Shoji J, Maehara T, Takichi A, Tanigawa T, Murata N, Tanaka M (2002) Larval fishes collected in Hiuchi-nada, the central Seto Inland Sea, Japan. *Bull Jap Soc Sci Fish* 68:835–842
- Shoji J, Masuda R, Yamashita Y, Tanaka M (2005) Predation on fish larvae by moon jellyfish *Aurelia aurita* under low dissolved oxygen concentrations. *Fish Sci* 71:748–753
- Sullivan BK, Garcia JR, Klein-MacPhee G (1994) Prey selection by the scyphomedusan predator *Aurelia aurita*. *Mar Biol* 121:335–341
- Suzuki T, Matsukawa Y (1987) Hydrography and budget of dissolved total nitrogen and dissolved oxygen in the stratified season in Mikawa Bay, Japan. *J Oceanogr Soc Jap* 43:37–48
- Tanaka M (1980) The ecological studies on the larvae and juveniles of the red sea bream in Shijiki Bay-I The horizontal distribution of the pelagic larvae and juveniles in and outside the bay. *Bull Seikai Reg Natl Fish Res Inst* 54:231–258
- Toyokawa M, Furota T, Terazaki M (2000) Life history and seasonal abundance of *Aurelia aurita* medusae in Tokyo Bay, Japan. *Plank Biol Ecol* 47:48–58
- Uye S (2002) Chain in coastal pelagic water. *Monthly Kaiyo Spec Publ* 29:137–142
- Uye S (2004) Recent increase of the scyphomedusa *Aurelia aurita* and associated nuisance to fisheries in the Inland Sea of Japan. *Bull Jap Soc Sci Fish* 70, 387–391
- Uye S, Ueta, U (2004) Recent increase of jellyfish populations and their nuisance to fisheries in the Inland Sea of Japan. *Bull Jap Soc Fish Oceanogr* 68:9–19
- Uye S, Fujii N, Takeoka H (2003) Unusual aggregations of the scyphomedusa *Aurelia aurita* in coastal waters along western Shikoku, Japan. *Plank Biol Ecol* 50:17–21
- Veer HW van der, Bergman MJN (1986) Development of tidally related behaviour of a newly settled 0-group plaice (*Pleuronectes platessa*) population in the western Wadden Sea. *Mar Ecol Prog Ser* 31:121–129
- Yasuda T (2003) Biology of jellyfish. In: Yasuda T (ed) *Jellyfish-UFO in the sea: occurrence, ecology, and measure*. Koseisha-koseikaku, Tokyo, pp 1–137