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Effects of turbidity on survival of larval ayu and red sea bream exposed to predation by jack mackerel and moon jellyfish

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Abstract We conducted laboratory experiments to examine the effects of turbidity on the survival of red sea bream *Pagrus major* and ayu *Plecoglossus altivelis altivelis* larvae when exposed to either visual (jack mackerel juveniles) or tactile (moon jellyfish) predators. The experiments were conducted in 30-l tanks with three different levels of turbidity obtained by dissolving 0, 50, or 300 ppm kaolin. Predators were introduced to the experimental tanks followed by larvae of either red sea bream (mean ± standard deviation 6.1 ± 0.3 to 11.4 ± 2.1 mm standard length) or ayu (6.6 ± 0.3 and 24.4 ± 1.8 mm). When exposed to jack mackerel, the mean survival rate of larvae was significantly higher in 300 ppm treatments compared with the other turbidity levels. When exposed to moon jellyfish, however, there was a less marked difference in the survival rates among different turbidity treatments. Survival rates of ayu larvae exposed to moon jellyfish were generally lower than those of red sea bream. Our study indicates that anthropogenic increases of turbidity may increase the relative impact of jellyfish predation on fish larvae.

Keywords Antipredatory strategy · *Aurelia aurita* · *Pagrus major* · *Plecoglossus altivelis altivelis* · *Trachurus japonicus* · Turbidity

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Introduction

In general, fishes suffer massive mortality during the relatively limited period of early life history [1]. Therefore, the number of fish that survive this period is a reliable predictor of year-class strength [2]. It is widely accepted that predation is a major cause of mortality in larval fish [1, 2]. Thus, detailed investigation of predator–prey interactions is a priority for understanding the recruitment mechanisms and conservation strategies of fishery resources.

A large proportion of important fishery species spend their larval and juvenile stages in coastal and estuarine regions where the physical environment is relatively unstable. Such a dynamic environment is due to both natural and anthropogenic causes; for example, freshwater river flow can decrease salinity and increase turbidity after heavy rains. High turbidity can also result from eutrophication and increased input of fine sediments induced by anthropogenic activities, as reported in Hiroshima Bay [3] and the Baltic Sea [4, 5]. Larval fishes, such as ayu *Plecoglossus altivelis altivelis*, anchovy *Engraulis japonicus*, red sea bream *Pagrus major*, and seabass *Lateolabrax japonicus*, often utilize such turbid coastal areas as nursery habitat [6–12]. Ayu larvae have a *shirasu* (i.e., an elongate and transparent form of) larval period, and their densities tend to be higher in turbid areas than in clear waters [13]. Japanese anchovy larvae often aggregate in turbid areas and form the so-called *shirasu* fishery grounds [9]. Turbid environments are likely to be utilized by ayu and other *shirasu* larvae because these areas decrease the risk of predation by visual predators. Indeed, predation capability has been reported to decline with increased turbidity in several species of piscine predators [14]; for instance, the reaction distance of juvenile Chinook salmon

Oncorhynchus tshawytscha to prey items decreased with increased turbidity [15]. Hecht and van der Lingen [16] found that a visual piscivorous predator, the tenpounder *Elops machnata*, was more affected by an increase in turbidity than a macrobenthic feeder, the spotted grunter *Pomadasys commersonnii*. There are, however, predators for which vision is much less important, such as jellyfish. Titelman and Hansson [17] revealed that there was no significant difference in the feeding rate by jellyfish on yolk-sac larvae of cod between light and dark conditions. For such tactile predators, turbid waters may not serve as a refuge for larvae. Furthermore, some jellyfish such as the helmet jellyfish *Periphylla periphylla* are reported to be more abundant in highly turbid and low-light-intensity areas compared with areas with the opposite condition [18]. The laboratory experiments of our study included multiple combinations of different prey and predators within the same study framework.

Jellyfish populations are increasing worldwide [19]. Uye and Ueta [20] reported that, in the Seto Inland Sea in Japan, moon jellyfish *Aurelia aurita* populations have substantially increased since the 1980s. Fish larvae are common prey items for jellyfish [21, 22]. Moon jellyfish are reported to consume large amounts of yolk-sac larvae of herring *Clupea harengus* [23] and capelin *Mallotus villosus* [24]. Because both herring and capelin have a *shirasu*-type larval period, it is likely that certain characteristics of *shirasu* make them particularly vulnerable to predation by moon jellyfish.

We hypothesized that survival of fish larvae would increase with increased turbidity when exposed to visual predators but not when exposed to tactile predators. We conducted laboratory experiments to examine the effects of turbidity on prey–predator interactions, using red sea bream and ayu larvae as prey and jack mackerel and moon jellyfish as visual and tactile predators, respectively. Red sea bream is a commercially important species in Japan, spawning in offshore reefs in spring, then migrating to shallow (5–10 m depth) coastal sandy areas to start demersal life after a 30–40-day planktonic larval period [10]. Recruitment of red sea bream juveniles to coastal reefs shows strong yearly fluctuation [25]. Presettlement larvae move from offshore to coastal areas, where they are likely to encounter patches of moon jellyfish. Shoji et al. [26] revealed experimentally that red sea bream larvae are easily captured by moon jellyfish, and as many as 110 individuals were preyed upon by a single moon jellyfish [27]. Ayu is an important amphidromous fish for both commercial and recreational fisheries in Japan. Ayu have an annual life cycle, and after adults spawn upstream in autumn, hatched larvae drift downstream, remain in estuarine and coastal habitats during winter, then ascend the rivers from early spring to summer [6–8]. Ayu larvae are presumed to have a higher mortality rate when they are in estuarine or coastal waters than when they migrate upstream as juveniles [28]. Recently, more and more moon jellyfish are overwintering in temperate waters, presumably due to the global warming trend [29]. Therefore, it is highly likely that ayu larvae are preyed upon by moon jellyfish. For sustainable management of ayu populations, we need to identify the major causes of mortality during the coastal life phase. Jack mackerel *Trachurus japonicus* were examined as the visual predator for comparison with moon jellyfish. Jack mackerel juveniles can be the most dominant fish species in a coastal area; juveniles ranging from 40 to 120 mm standard length (SL) are the most dominant fish in our research field in Maizuru Bay [30]. Jack mackerel juveniles often feed on larvae of anchovy and other fishes [31, 32]. Both predator and prey species used in the present study live abundantly in Maizuru Bay, where turbidity exceeds 50 ppm after heavy rain (Ohata R, unpubl. data, 2010).

Materials and methods

Rearing and husbandry of fish larvae and predators

Fertilized red sea bream eggs were provided by the Ishikawa Prefectural Fisheries Research Center on 3 June 2008. Eggs were transferred to the Maizuru Fisheries Research Station (MFRS) of Kyoto University and were stocked in two 500-l transparent circular polycarbonate tanks. Eggs hatched the following day. Larvae (22–35 days old) of four different size groups [mean ± standard deviation (SD) 6.1 ± 0.3 to 11.4 ± 2.1 mm SL] were examined in the experiment (Table 1). Larvae were provided with rotifers *Brachionus plicatilis*, *Artemia* spp. nauplii, and formulated food (Kyowa N400; Kyowa Hakko Kogyo, Tokyo, Japan) depending on their developmental stage. Rotifers and *Artemia* were enriched with commercial highly unsaturated fatty acid (HUFA) oil (Marine Gloss; Nisshin Marinetech, Kanagawa, Japan).

Two size groups of ayu larvae, 6.6 ± 0.3 mm SL (yolk-sac larvae) and 24.4 ± 1.8 mm SL (post-larvae), underwent predation trials. The ayu yolk-sac larvae were collected by a plankton net (mouth opening: 45 cm, mesh size: 333 μm) set in the Yura River (35°23′N, 135°09′E) and Isazu River (35°26′N, 135°20′E), both in Kyoto Prefecture, on ten different nights between 8 and 27 November 2008. After sampling, the larvae were kept in a cooler box and were transferred to MFRS. The larvae were acclimatized overnight with aeration, and fully recovered and actively swimming larvae were used in predation trials the next morning. The post-larvae were obtained from the Fisheries Cooperative Association of Hidakagawa in

Wakayama Prefecture on 24 January 2009. They were third-generation individuals from local origin broodstock. Approximately 1500 larvae were transferred to MFRS and were reared in 500-l black circular polycarbonate tanks. Because the larvae had been reared at low-salinity water conditions of approximately 30% seawater, natural filtered seawater was introduced gradually, and after 1 day all the water in the tank was replaced by seawater. The temperature of the water was kept at 15°C, and commercial pellets (Kyowa N250; Kyowa Hakko Kogyo, Tokyo, Japan) were provided three times a day. Random sampling of 10–20 larvae per species was conducted on each experimental day with SL measured after MS222 anesthesia.

Moon jellyfish were collected at the MFRS pier using a 10-l plastic bucket and were kept in a 200-l transparent polycarbonate tank before use. They were maintained on *Artemia* but were starved overnight before the experiments. Jellyfish were used within 3 days after sampling, and individuals were not used more than once. The mean ± SD bell diameter of moon jellyfish in each experiment was 96.6 ± 6.0 mm ($n = 24$) for red sea bream, 116.8 ± 29.8 mm ($n = 30$) for ayu yolk-sac larvae, and 132.3 ± 6.7 mm ($n = 24$) for ayu post-larvae trials. The size of moon jellyfish in each experiment was significantly different among the three experiments [analysis of variance (ANOVA), $P < 0.05$]. Each size group of jellyfish represented the dominant size in Maizuru Bay when experiments were conducted, and thus the most likely size to be encountered by these fish larvae. The number of bell contractions of moon jellyfish was counted for 30 s by visual observation before the start of each experiment to check the physiological condition of jellyfish. Jack mackerel juveniles were provided from a commercial set net in Tai, Maizuru (35°56′N, 135°45′E) and were kept in a 500-l black polycarbonate tank before use. They were fed pellets (Otohime S2; Marubeni Nisshin Feed, Tokyo, Japan) once a day and were maintained in captivity ~6 months before the initiation of experiments. Individual fish were used in one set of trials only. Jack mackerel SL (mean ± SD) was 66.3 ± 5.7 mm ($n = 24$) for the red sea bream experiment, 73.3 ± 5.7 mm ($n = 36$) for the ayu yolk-sac larvae, and 101.5 ± 3.2 mm ($n = 24$) for the ayu post-larvae trials. The size of jack mackerel used in each experiment was significantly different among the three experiments (ANOVA, $P < 0.05$). The difference in size of these predators reflects the most likely size group to prey upon each species and stage of fish larvae naturally [33]. Our preliminary experiments confirmed their efficient predation. Jack mackerel were starved for 36 h in the experimental tank. Trials were conducted at approximately 2-h intervals.

Experimental procedures

The predation experiment was conducted at MFRS using 30-l transparent circular polycarbonate tanks (water volume: 25 l) equipped with a water pump (Power Box SV4500; Kotobuki Kogei, Osaka, Japan) to circulate seawater. The experimental tank was surrounded by a blue plastic sheet to minimize the effect of observers. Three individual predators (either moon jellyfish or jack mackerel) were introduced to the experimental tank and acclimated to each turbidity for 5 min, and then larvae of either red sea bream or ayu were gently released. Larvae were exposed to predators for 15 min in red sea bream trials and 5 min in ayu trials. Time of predator exposure was determined based on preliminary trials so that some (but not all) larvae would be preyed upon by moon jellyfish under the no-turbidity condition. Predators were then removed and secured in holding tanks. The water in the experimental tank was carefully filtered using a hand net, and the number of surviving larvae was counted to obtain the survival rate. The number of larvae to be exposed to predators (Table 1) was decided based on preliminary feeding trials using live larvae. Three individuals of jack mackerel were introduced

Table 1 Fish standard length, days after hatching, number of fish per trial, number of sets of trials, and survival rates pooled for all turbidity levels in the experiment using red sea bream and ayu as prey species

Prey species	SL ± SD (n) (mm)	Age (days)	No. of fish	No. of sets		Survival rate (%)	
				JM	MJ	JM	MJ
Red sea bream	6.1 ± 0.3 (20)	22	30	2	2	3	26
	8.2 ± 0.9 (20)	32	15	2	2	24	43
	8.4 ± 1.1 (20)	33	15	2	2	5	58
	11.4 ± 2.1 (20)	35	10	2	2	2	83
Ayu							
Yolk-sac larvae	6.6 ± 0.3 (100)	1–3	20	12	10	31	20
Post-larvae	24.4 ± 1.8 (40)	ca. 90	10	8	8	20	50

SL standard length, *SD* standard deviation, *JM* jack mackerel, *MJ* moon jellyfish to the experimental tank and were fed live larvae until satiation. One-third of the number of fish larvae required to reach satiation was used as the number of larvae to be exposed to predators during one trial. Three different levels of turbidity were obtained by dissolving 0, 50, or 300 ppm kaolin (Wako Junyaku Kogyo, Osaka, Japan). A preliminary experiment found that turbidity less than 50 ppm induced no measurable effect on feeding performance in jack mackerel. Therefore, we conducted experiments at 50 ppm and higher turbidities. Turbidity of 50 ppm is the preferred level for European anchovy larvae [34] and has been observed in Suruga Bay, where a major fishery of Japanese anchovy larvae exists [9]. Turbidity of 300 ppm is typical in Ariake Bay, Japan [35], where fishermen catch edible jellyfish *Rhopilema esculenta* [36]. We defined a trial of three kaolin concentration levels as one set, and the same individual predators were used in only one set of trials.

Considering the stress caused by transport and the satiation level of predators, a 2-h interval for jack mackerel and a 3-h interval for moon jellyfish was established between trials. To compensate for adaptation and learning effects of turbidity by predators, trials were conducted either by increasing or decreasing the level of turbidity one after another. After each set of trials was completed, jack mackerel were anesthetized using 2-phenoxyethanol and SLs were measured. The bell diameters of moon jellyfish were also measured after each set of trials. Water temperature was 19.0–20.0°C in ayu trials and 21.2–24.9°C in red sea bream trials. Light intensity was 338–440 lux for ayu and 400–510 lux for red sea bream larvae during the experiments.

Statistical analysis

The bell contraction rate of moon jellyfish was compared among different turbidities using ANOVA. Survival rate of larvae was arcsine-transformed prior to analysis to improve the homogeneity of variance and was compared using ANOVA followed by Tukey's multiple-comparison test. Student's *t* test was applied to compare the survival rate of the larvae between different predator species in each prey species and turbidity. For these comparisons, survival rate data were pooled for all the size groups of red sea bream larvae because of the shortage of replications. Student's *t* test was also used to compare survival rate between ayu yolk-sac and ayu post-larvae.

The survival rate of red sea bream against moon jellyfish had a relatively wide range and so was fitted to a logistic model to examine the ontogenetically critical size for predator avoidance as follows:

$$S = 1/(1 + \exp(-g(L - L_{50}))),$$

where S is the survival rate, g is the gradient of S, L is the SL of fish larvae, and L_{50} is the SL when $S = 0.5$. The value of g and L_{50} were obtained by the least-squares method using Microsoft Excel's solver.

Results

Activity of predators and predation process

There was no discernible difference in activity of jack mackerel between 0 and 50 ppm. Some individuals swam hyperactively at 300 ppm for the first 1 min or so, but they calmed down during acclimatization. The mean number of bell contractions of moon jellyfish per 30 s was 17.9 ± 4.5 (mean ± SD) at 0 ppm, 17.5 ± 3.7 at 50 ppm, and 19.4 ± 3.3 at 300 ppm turbidity concentrations; there were no significant differences among the turbidity treatments (ANOVA, $P = 0.16$).

When larvae encountered a jack mackerel at 0 ppm, larvae of both species were captured immediately after being introduced to the experimental tank. A small number of larvae survived at 50 ppm for 1 min or so after exposure to predators. Predation of larvae occurred much later at 300 ppm.

When larvae encountered a moon jellyfish, larvae of both species were captured by tentacles after being drawn into the water current generated by the jellyfish, then they were gradually transferred to the gastric pouch. Almost all small larvae were preyed upon once they were touched, presumably due to the effects of jellyfish neurotoxin. Larger larvae often escaped from a jellyfish once, but then their swimming speed gradually reduced, and some of them were eventually preyed upon (Fig. 1).

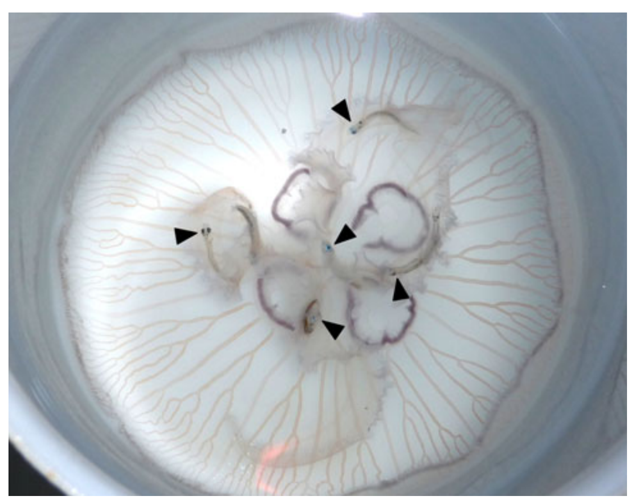

Fig. 1 Ayu post-larvae (23.3 mm average standard length) preyed upon by a moon jellyfish (133 mm bell diameter). *Arrowheads* represent ayu larvae captured by a jellyfish

Survival rates

For red sea bream larvae, mean survival rate was significantly higher at 300 ppm compared with the other turbidity treatments when they were exposed to jack mackerel [ANOVA followed by Tukey's honestly significant difference (HSD) test, $P < 0.05$; Fig. 2a]. When they were exposed to moon jellyfish, however, there was no significant difference in survival rate among turbidity treatments. Survival rates of larvae exposed to moon jellyfish for the 0 and 50 ppm treatments were significantly higher than those exposed to jack mackerel (Student's t test, $P < 0.05$). Older and thus larger red sea bream larvae tended to have better survival against predation by moon jellyfish (Table 1). The logistic model of the survival rate of red sea bream against moon jellyfish was as follows (Fig. 3):

$$0\,\text{ppm: } S = 1/(1 + \exp(-5.53(L - 8.63))),$$
$$50\,\text{ppm: } S = 1/(1 + \exp(-4.46(L - 7.60))),$$
$$300\,\text{ppm: } S = 1/(1 + \exp(-3.33(L - 8.49))).$$

These models show that the survival rate of red sea bream against moon jellyfish has an inflection point at about 8 mm SL regardless of turbidity.

For ayu yolk-sac larvae, with jack mackerel as predators, mean survival rate was higher at 300 ppm compared with other turbidity treatments (ANOVA followed by Tukey's HSD test, $P < 0.05$; Fig. 2b). In contrast, when moon jellyfish were the predators, there was no difference in survival rate among the turbidity treatments. Survival rate when exposed to jack mackerel at 300 ppm treatment was significantly higher than when exposed to moon jellyfish (Student's t test, $P < 0.05$).

When ayu post-larvae were exposed to jack mackerel, survival rate was 0% at both 0 and 50 ppm, but 60% at 300 ppm (Fig. 2c). When moon jellyfish were predators, survival rate was 38% (0 ppm), 59% (50 ppm), and 68% (300 ppm), and survival rate at 300 ppm was significantly higher than that at 0 ppm (ANOVA followed by Tukey's HSD test, $P < 0.05$). Survival rates when exposed to moon jellyfish at 0 and 50 ppm treatments were significantly higher than when exposed to jack mackerel (Student's t test, $P < 0.05$), but there was no interpredator difference at 300 ppm.

Comparing survival rates of yolk-sac larvae and post-larvae of ayu when exposed to jack mackerel, the survival rate of the latter was significantly lower than the former at 0 and 50 ppm turbidity (Student's t test, $P < 0.05$; Fig. 2b, c), but there was no difference at 300 ppm. In contrast, the survival rate when exposed to moon jellyfish for ayu post-larvae was significantly higher than for yolk-sac larvae under all the turbidity conditions (Student's t test, $P < 0.05$; Fig. 2b, c).

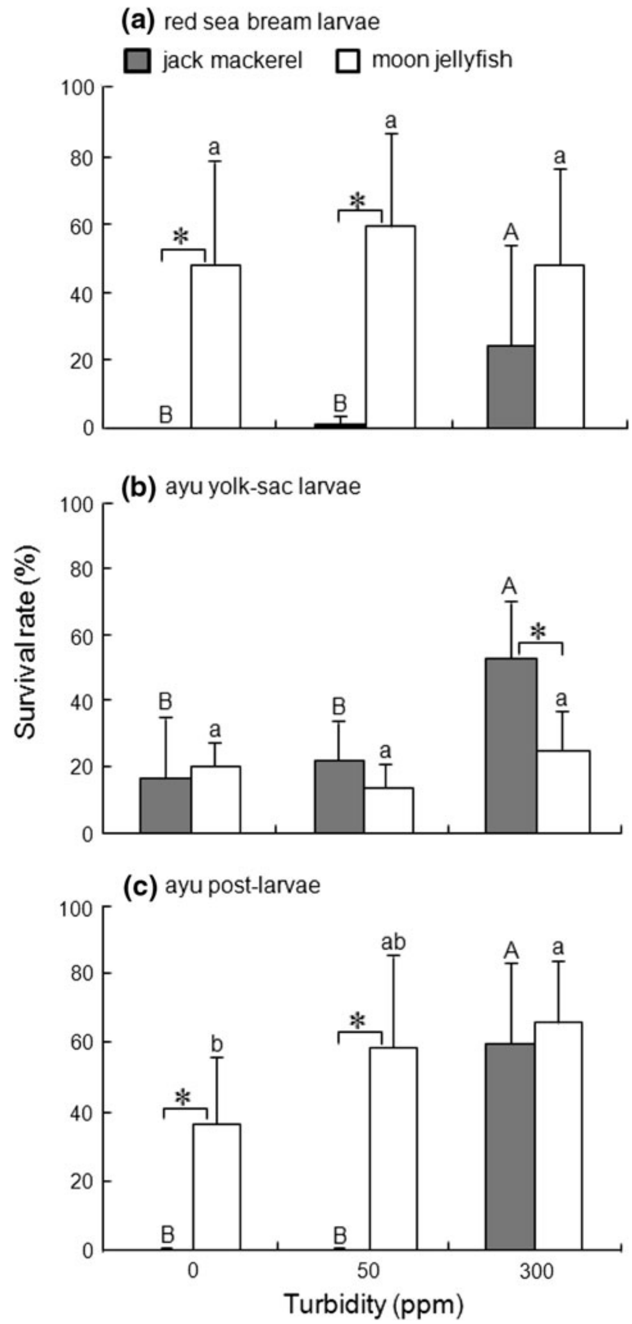

Fig. 2 Survival rates of **a** red sea bream, **b** ayu yolk-sac larvae, and **c** ayu post-larvae by jack mackerel and moon jellyfish at 0, 50, and 300 ppm kaolin turbidity. *Different letters* indicate significant differences of survival rate among turbidity conditions (Tukey's HSD test, $P < 0.05$). *Asterisk* indicates significant difference of survival rate between jack mackerel and moon jellyfish (Student's t test, $P < 0.05$). *Vertical bars* indicate standard deviations

Clearance rate, defined as the number of larvae preyed upon by moon jellyfish per 1 h [10], was calculated for each size of larvae in each turbidity (Table 2). The clearance rate decreased with SL in each species, and rates for ayu larvae were generally higher than rates for red sea bream larvae.

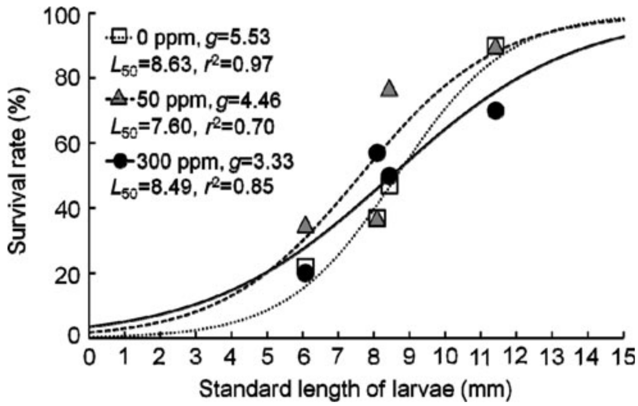

Fig. 3 Relationship between standard length (*L*) and survival rate (*S*) against moon jellyfish in each turbidity condition in red sea bream larvae. *Squares* 0 ppm, *triangles* 50 ppm, *circles* 300 ppm. Logistic models, $S = 1/(1 + \exp(-g(L - L_{50})))$, are fitted for each turbidity. *g* gradient of *S*, L_{50} *L* when $S = 50$

Table 2 Clearance rates of moon jellyfish (number of larvae preyed upon/number of moon jellyfish individuals/hour) on red sea bream and ayu larvae under the three different turbidity conditions

Prey species	SL ± SD (*n*) (mm)	Clearance rate		
		0 ppm	50 ppm	300 ppm
Red sea bream	6.1 ± 0.3 (20)	50.5	35.0	53.6
	8.2 ± 0.9 (20)	33.6	33.6	19.0
	8.4 ± 1.1 (20)	25.5	8.7	23.1
	11.4 ± 2.1 (20)	3.5	3.5	11.9
Ayu				
Yolk-sac larvae	6.6 ± 0.3 (100)	160.0	196.0	127.3
Post-larvae	24.4 ± 1.8 (40)	98.1	53.2	39.3

SL standard length, *SD* standard deviation

Discussion

Predator-specific effect of turbidity on survival of fish larvae during ontogeny

Turbidity increased survival when the predator was jack mackerel for both prey species of fish larvae, whereas for moon jellyfish predation turbidity did not have a major effect. Sørnes and Aksnes [37] reported that two-spotted goby *Gobiusculus flavescens* ate prey more efficiently than lobed comb jellyfish *Bolinopsis infundibulum* in high-light-intensity conditions, and vice versa in the opposite conditions. Therefore, in general, visually limited environments work as a refuge for fish larvae against visual predators but not against tactile predators, suggesting that blooms of jellyfish in turbid waters can substantially reduce fisheries resources of a coastal region in which larvae live.

The survival rate of ayu larvae when exposed to moon jellyfish was generally lower than that of red sea bream larvae in all turbidity treatments. When all size ranges and turbidity levels were combined, the mean survival rate with jellyfish was 37% for ayu and 53% for red sea bream larvae. Ayu larvae were thus more vulnerable to predation by moon jellyfish than red sea bream larvae when compared within the present larval size ranges (note, however, that they differ between species), even though the latter were exposed to moon jellyfish for three times longer than the former during the experiment. Analysis of clearance rates supported this general trend of the present study (Table 2). Titelman and Hansson [17] calculated clearance rates of fish larvae by moon jellyfish based on their research and data from the literature and found that clearance rates could range from 1.2 to 195 larvae preyed upon by an individual moon jellyfish in 1 h depending on jellyfish diameter and prey fish species. Among three fish species exposed to relatively large (5–16 cm bell diameter) moon jellyfish, larvae of herring and capelin suffered higher clearance rates than those of cod *Gadus morhua* [17]. As the former two species have a *shirasu* larval period, our findings are consistent with their report. Furthermore, Masuda [38] reported that chub mackerel *Scomber japonicus* and jack mackerel were able to escape from moon jellyfish when they attained 6 mm SL, whereas anchovy larvae were preyed upon even when they attained 23 mm SL. The high vulnerability of *shirasu* larvae is attributable either to their fragile skin surface or to their inferior locomotive capability. The former point would be supported by Hunter et al. [39], who reported that mortality rates and damage level to the brain and eye of northern anchovy *Engraulis mordax* were higher than those of chub mackerel when exposed to ultraviolet radiation, implying relative weakness of the skin surface of the anchovy.

Post-larvae of ayu were eaten more easily by jack mackerel than yolk-sac larvae under the 0 and 50 ppm turbidity conditions, but there was no such difference under the 300 ppm condition. This is probably because jack mackerel can find larger larvae more easily due to the increased conspicuousness with body size. Reid et al. [40] also reported that the survival rates of larger-sized fathead minnows *Pimephales promelas* were lower than smaller larvae in turbid conditions when exposed to largemouth bass *Micropterus salmoides*. The absence of an intersize difference in survival at 300 ppm may imply that high turbidity worked as a refuge for post-larvae despite the large body size due to their transparent body. In contrast, when ayu larvae were exposed to moon jellyfish, mean survival rate of post-larvae was significantly higher than that of yolk-sac larvae at all the turbidity levels. This may be because of improvements of swimming speed [41], visual ability [42], and sensory organs [43] with which escape ability from moon jellyfish increased. Therefore, in *shirasu* larvae such as ayu, inconspicuousness is suggested to be an important factor to avoid visual predators, whereas swimming ability is likely to be a key factor to avoid tactile predators.

Costello and Colin [44] examined the mechanism of prey capture by a moon jellyfish under laboratory conditions and suggested that moon jellyfish can capture prey organisms that have a slower escape speed than its induced flow velocity during contraction of its bell margin. The average bell diameter of moon jellyfish used in our experiment was 96.6 mm for red sea bream, 116.8 mm for ayu yolk-sac larvae, and 132.2 mm for ayu post-larvae, and by extrapolating Costello and Colin's [44] data, flow velocity at the bell margin was estimated as ca. 33, 35, and 35 mm/s, respectively. Fukuhara and Kishida [45] reported that the swimming speed of red sea bream larvae was approximately 50 mm/s at 6 mm SL. In the present study, when all turbidity levels were combined, the mean survival rate of red sea bream against jellyfish was 26% at 6.1 mm SL, 43% at 8.2 mm SL, 58% at 8.4 mm SL, and 83% at 11.4 mm SL (Table 1). Swimming velocity of ayu larvae estimated by Tsukamoto and Kajihara [41] increased from approximately 20 mm/s at 6 mm SL to 50 mm/s at 12 mm SL. The present study also revealed that the mean survival rate of ayu against jellyfish was 20% for yolk-sac larvae and 50% for post-larvae when all the turbidity levels were combined (Table 1). Therefore, improved escape performance with growth against jellyfish in the larvae of both fish species can be explained by the development of their swimming capability. The logistic model of the survival of red sea bream larvae when exposed to moon jellyfish had an inflection point at ca. 8 mm SL, suggesting that their size refuge from moon jellyfish is close to this value. Nakayama et al. [27] reported that red sea bream larvae larger than 8 mm SL were not preyed upon by moon jellyfish in their 5-min trials, which was consistent with the present study. Further experiments using a wider size range of prey animals may elucidate a critical size for avoiding predators in each predator–prey combination.

When moon jellyfish were used as predators, the survival rate of ayu post-larvae was higher at 300 ppm than at 0 ppm (Fig. 2c). This may be because turbid environmental conditions caused some change in the behavior of ayu larvae. A decrease in swimming activity induced by turbidity would reduce the jellyfish encounter rate and thus could result in the lower mortality. Engström-Öst and Mattila [46] reported that, in the presence of competitors and the stimuli of a visual predator, turbidity reduced swimming activity in pike *Esox lucius* larvae, whereas activity increased in turbid environmental conditions in herring [47] and walleye *Stizostedion vitreum* [48]. Meager and Batty [49] reported that swimming activity in Atlantic cod *Gadus morhua* juveniles was nonlinearly affected by turbidity. Because turbidity can either increase or decrease activity of fish larvae, we should confirm this on a species-by-species basis. Furthermore, turbidity might have induced school formation in ayu post-larvae with which they detected and escaped from jellyfish more efficiently. Indeed, we observed that ayu larvae tended to form schools more often in turbid water (Ohata R, unpubl. data, 2008). The effect of turbidity on schooling should also be confirmed quantitatively in future study.

Potential impact of anthropogenically increased turbidity concurrent with jellyfish blooms on the survival of fish larvae

Recently, increases of turbidity have been reported in coastal regions worldwide because of anthropogenic eutrophication [3–5]. Our results indicate that turbid water serves as a refuge from visual predators, whereas this tactic does not work against tactile predators. Therefore, increased turbidity is likely to increase the relative importance of tactile predators. Furthermore, jellyfish populations have been globally increasing, and fish nursery grounds in coastal and estuarine areas may not be effective refuges from jellyfish. Indeed in the Black Sea, a clear negative correlation has been shown between water turbidity and fish abundance, in particular for anchovy [50]. Eiane et al. [18] reported that jellyfish dominate a fjord where water transparency and light intensity are low. Therefore, anthropogenic effects may induce both an increase of turbidity and blooms of jellyfish, the combination of which may seriously damage larval fish populations in coastal regions.

Anthropogenically induced turbidity often accompanies low dissolved oxygen conditions because dissolved oxygen is expended when organic matter contained in turbid water is decomposed [51]. Shoji et al. [26] reported that moon jellyfish prey upon red sea bream larvae in low dissolved oxygen concentrations more than in high dissolved oxygen concentrations. They implied that the relative importance of moon jellyfish predation on fish larvae increases when the oxygen concentration declines in coastal waters during summer. Many species of fish larvae utilize coastal areas as nursery grounds, thus fish larvae are threatened by increasing jellyfish populations which are resilient to hypoxic and high-turbidity conditions. If jellyfish dominate in high-turbidity waters [18] and fish larvae have turbiditaxis [9], the predation impact can be even greater; not only ayu and red sea bream but also many other species of fish larvae using coastal areas as nursery grounds may be increasingly threatened by jellyfish predation. Further study to reveal the behavior of fish larvae in high-turbidity conditions is required together with a survey of jellyfish abundance in relation to turbidity.

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