Effects of larval ontogeny, turbulence, and prey density on survival in red sea bream *Pagrus major* larvae

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Abstract — The effect of turbulence on red sea bream larvae survival was tested at two prey densities and four turbulence levels in the laboratory for red sea bream. The effect of ontogenic stage on feeding behavior parameters was examined. The range of turbulence at which red sea bream larvae could survive and ingest prey increased with larval growth. Therefore, turbulence is an important condition impacting survival of small larvae during the initial period of feeding. At low prey density, larvae fed at the highest feeding rate and had a high RNA : DNA ratio at a medium turbulence level on the order of $10^{-6.5} \, \mathrm{m^2 \, s^{-3}}$. Thus, an optimum turbulence level induces faster growth, and it can be concluded that turbulence plays an important role in larval growth and survival. For interspecific comparison, a feeding success index calculated by numerical modeling in sea bream was compared to that of Pacific bluefin tuna using data reported by Kato et al. (2008). There were large differences in the index. The equivalent curve for red sea bream showed a linear relationship, while that for Pacific bluefin tuna showed a dome-shaped relationship. These results suggest that open-ocean-dwelling Pacific bluefin tuna likely prefer prey that is moving and under conditions of moderate turbulence. Further, tuna requires a greater degree of turbulence during initial feeding periods than does red sea bream.

Key words: red sea bream, oceanic turbulence, energy dissipation rate, RNA/DNA ratio, Pacific bluefin tuna

Introduction

The success of fish larvae feeding in the surface layer of the ocean is dependent on many environmental effects. Flow and UV radiation have been reported to physically affect red sea bream larvae (Kinoshita and Tanaka 1990; Fukunishi et al. 2006). Oceanic turbulence has been raised as one of the environmental factors that controls initial survival rate, as it affects the encounter rate between planktonic predators and their prey, and it has recently been well discussed (Mackenzie and Kiøboe 1995). The relationship between plankton feeding rate and turbulence is dome-shaped, meaning that there is an optimum turbulence level (Rothschild and Osborn 1988). The associated concept of "optimum environmental window" describes the relationship between upwelling strength and recruitment (Cury and Roy 1989). The effect of wind- and tide-induced turbulence on encounter rates between larval fish and their zooplankton prey has been quantified in models and confirmed through laboratory experiments conducted in rearing tanks (Mackenzie and Leggett 1991;

Mackenzie et al. 1994; Mackenzie and Kiøboe 1995; Sundby 1996; Sundby 1997; Stiansen and Sundby 2001). The effect of wind mixing on contact rate for cod larvae and their prey was identified as an important regulatory mechanism in the formation of year class strength of cod (Sundby and Fossum 1990). In an investigation of the effects of ontogenic stage, light, turbidity, and turbulence on the prey attack rate and swimming activity of herring larvae (total length, 15 to 28 mm), turbulence was found to have an effect on prey attack rate (Utne-Palm and Stiansen 2002; Utne-Palm 2004).

Nevertheless, little is known about the effect of turbulence on the feeding rates of fish larvae during the initial feeding period when swimming ability is limited. In particular, the dependence of feeding success on turbulence and subsequent effects on survival and growth remain to be resolved. Elucidation of these relationships is necessary not only for our basic knowledge but also for the development of fish culture techniques. Unsuccessful ingestion of the available diet after yolk absorption is suspected of causing abnormal behavior and morphological development in chinook salmon, *Oncorhynchus tshawytscha* (Heming et al. 1982). A

study of yellowfin tuna, *Thunnus albacares*, indicated that the surface mixed layer of equatorial oceans has an optimum turbulence level that enhances the survival of larvae of this species (Kimura et al. 2004). Results of such studies on the initial survival of fish species that are commercially important suggest that oceanic turbulence should be considered as a physical factor that controls prey ingestion rates by larvae. Previously, Kato et al. (2008) determined that the Pacific bluefin tuna, *Thunnus orientalis*, has an optimum turbulence level similar to that of yellowfin tuna. Turbulent energy dissipation rates on the order of $10^{-7}\,\mathrm{m^2\,s^{-3}}$ were concluded to produce the best feeding and survival rates in fish of the genus *Thunnus* spawning in the open ocean.

Red sea bream, *Pagrus major*, which is one of the most important demersal fish in the Japanese coastal fishery, spawns near the surface layer (Matsuura et al. 1981). Post-hatch larvae have an average daytime depth of 20 m, and the depth range increases to 40 m when the larvae have grown to total length of 7 mm (Tanaka et al. 1983). During the initial feeding period, the larvae, therefore, inhabit the surface layer, which is characterized by weak turbulence. During the juvenile period individuals move to the bottom, where stronger turbulence is generated by bottom friction and tidal flow. Thus, this species shifts its habitat with ontogenic stage. This characteristic makes larvae of red sea bream a good choice for this ontogenic experiment and for comparison to Pacific bluefin tuna of the open ocean. This species is cultured continually in Japan, making it was very easy to obtain fertilized eggs for our experiments.

Material and Methods

Effect of turbulence on larvae of different stages

Naturally spawned and fertilized eggs of red sea bream were provided by Kyoto Prefectural Sea-Farming Center on 13 May 2005 and transferred to the Maizuru Fisheries Research Station of Kyoto University. Larvae were hatched in two 500-L tanks and reared by feeding with S type rotifer *Brachionus calyciflorus* (Müller) maintained at a density of 5 individuals mL^{-1}.

For the turbulence experiments, three 200-L were prepared for each turbulence level (water discharge at 0, 10, 30 and 40 L min^{-1}), and 2000 larvae were introduced at 3 days after hatching (Day 3) for Round 1 and Day 7 for Round 2 of the experiment. Mean total length was 2.91 ± 0.38 mm at Day 3 and 3.54 ± 0.37 mm at Day 7. Water temperature was controlled by water heaters to $19\pm1°C$ during the experiments. S-type rotifers *B. calyciflorus* were supplied at 5 individuals mL^{-1} and measured twice daily at five points in each tank. Prey densities were measured twice a day at five points in each tank. 20 of the larvae in each tank were collected and anesthetized with MS222 (meta-aminobenzoic acid ethyl-

ester methanesulfonate, Sankyo, Tokyo, Japan) at 1300 h. Larvae were immediately pressed between a slide and cover slip in order to count the number of rotifers in the digestive tract under a microscope on Day 3 in Round 1 and Day 9 in Round 2. At the end of each Round, the number of surviving larvae in each tank was counted (Round 1, Day 5; Round 2, Day 9).

Four levels of turbulence were produced by changing the flow rates of water pumped through pipes set on the bottom of the tanks (Fig. 1a). The turbulence levels were set at water discharge rates of 0 (only bubbles of air at 0.1 L min^{-1}), 10, 30 and 40 L min^{-1}.

To compare these rates with those in the ocean, the turbulent energy dissipation rate ε (m^2 s^{-3}) in each rearing tank was calculated as follows (Stiansen and Sundby 2001):

$$\varepsilon = \left(\frac{10^b}{Bu_{rms}^{2/3}} \right)^{3/2} \tag{1}$$
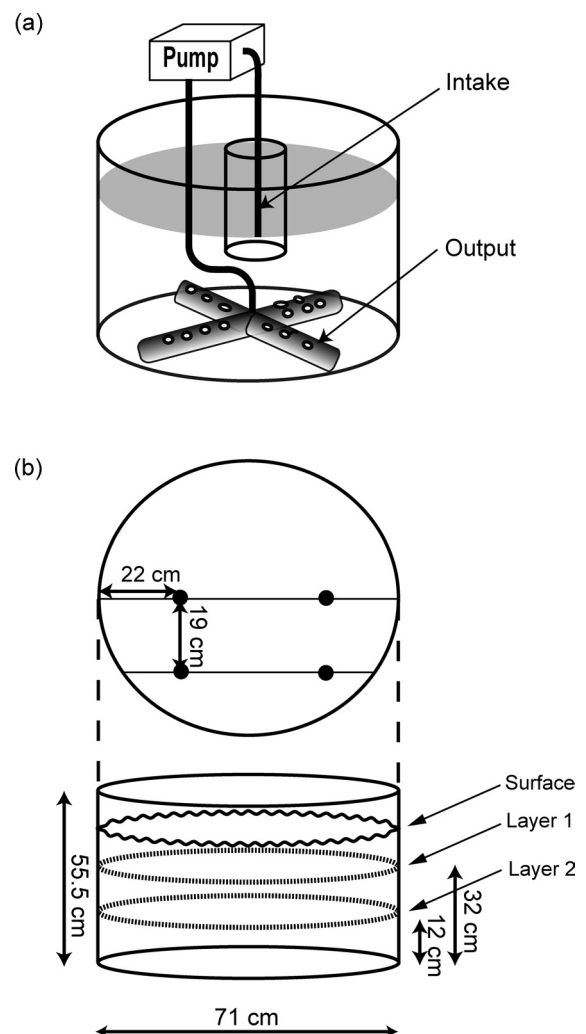

Fig. 1. (a) Schematic view of experimental tanks and the turbulence-generating apparatus. (b) Points for measurement of current velocity, and layers of measurement in the rearing experiments.
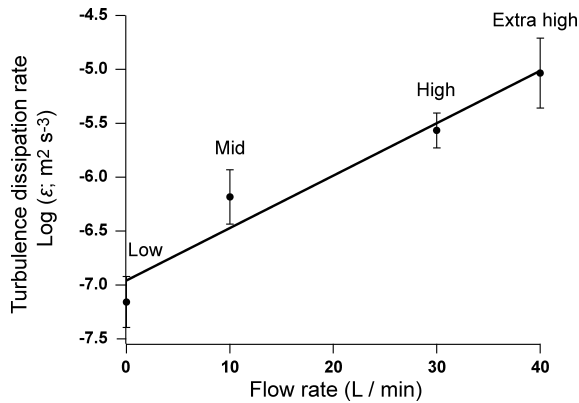
Fig. 2. Relationship between turbulent energy dissipation rate and flow rate in the experimental apparatus. Error bars show standard deviations.

where b is the intercept on the linear regression assuming a slope of −5/3, B is a constant, and u_{rms} is the root mean square of the turbulent velocity; u_{rms} was measured by an acoustic Doppler velocity meter at eight points (four points for each layer) in the tank (Fig. 1b). B is a non-dimensional universal undetermined constant assumed to be of order one (Tennekes and Lumley 1974), and therefore the chosen value of B was 1.

We examined the relationship between flow rate and the log transformed turbulent energy dissipation rate (Fig. 2). The turbulent energy dissipation rate ranged from $10^{-7.0}$ to $10^{-5.0}\,\mathrm{m^2\,s^{-3}}$ and fit to a linear regression with Pearson's correlation, $r=0.974$ ($P<0.05$). Accordingly, four turbulence levels (termed Low, Mid, High, and Extra high) were established for the turbulent energy dissipation rates.

Effect of turbulence on prey density

In the following year (2006), rearing experiments were conducted in the same way as in 2005, except that the effect of turbulence on prey density was examined. Eggs were obtained on 30 May 2006, and the rearing period was set at Day 3 to 5. Mean total length was $3.11\pm0.22\,\mathrm{mm}$ and developmental stage of the larvae was the post flexion stage at the beginning of the experiment. S-type rotifers were supplied to the tanks at 5 individuals $\mathrm{mL^{-1}}$ (high prey density) or 0.1 individuals $\mathrm{mL^{-1}}$ (low prey density). Because low prey density was particularly difficult to maintain, prey densities were measured five times daily at five points in each tank and additional rotifers were supplied as needed to maintain the target density. The mean population density of zooplankton in Yuya Bay, Yamaguchi Prefecture—a spawning nursery ground of red sea bream that opens out into the Sea of Japan—is 0.0326 to 0.0659 individuals $\mathrm{mL^{-1}}$ (Hamasaki et al. 1980). Therefore, the low prey density used in this experiment was on the supposition of natural conditions.

Turbulence levels were set at 10 and 30 L min^{-1}. In general, tanks were prepared in triplicate for each level, but due

to problems at our facility, only two tanks were prepared for each turbulence level and prey density in this experiment. As in the 2005 experiments, the log-transformed turbulent energy dissipation rates were estimated to be on the order of $10^{-7.0}$ to $10^{-5.0}\,\mathrm{m^2\,s^{-3}}$. Accordingly, the three turbulence levels were termed Low, Mid, and High. On Day 5, the number of rotifers in the digestive tract was counted under a microscope, and number of surviving larvae in each tank was counted.

Ten larvae from each turbulence level were frozen in individually in labeled 1.5-mL Eppendorf tubes and then stored in a freezer at −80°C until nucleic acid analyses. RNA and DNA in the whole body were determined by the method of Caldarone et al. (2001). Briefly, nucleic acids were quantified fluorometrically using ethidium bromide as the fluorophor on a microplate fluorescence reader (Biolumin 960, Molecular Dynamics Inc., CA, USA) with excitation and emission wavelengths of 520 and 630 nm, respectively, to determine the total nucleic acid concentration. Then, the RNA was enzymatically digested by the addition of RNase (Ribonuclease A from bovine pancreas; Sigma R6513) and the quantity of RNA was determined by subtracting the second reading from the first. Standard calibration curves for RNA were constructed using serially diluted preparations of 18S- and 28S-RNA (from calf liver, Sigma R0889). Standard calibration curves for DNA were constructed using serially diluted preparations of DNA (from calf thymus, Sigma D4764). From these readings, we calculated the RNA : DNA ratio.

Calculation of feeding success index

For interspecies comparison, feeding success rates for red sea bream was calculated based on the following theory established by Rothschild and Osborn (1988). The *velocity V* (cm s^{-1}) of the fish larvae relative to that of a rotifer is determined by the following equation (Lough and Mountain 1996):

$$V = \frac{u^2 + 3v^2 + 4w^2}{3(u^2 + w^2)^{0.5}} \quad (2)$$

where u is the swimming speed of the rotifer (cm s^{-1}), v is the swimming *speed* of the larval fish (cm s^{-1}), and w is the turbulent velocity (cm s^{-1}). We took u and v to be 0.005 cm s^{-1}. Larvae swimming speed was dependent by body length (Müller 2008). Skiftesvik and Huse (1987) estimated cod larvae swimming speed at 0.25 (*body length*) s^{-1} in rearing experiments. In our study, we calculated the swimming speed for larvae to be 0.4 cm of body length. Therefore, we took v to be 0.1 cm s^{-1}. The turbulent velocity term w was calculated by Eq. (3) (Mackenzie and Leggett 1991):

$$w^2 = 3.615(\varepsilon r)^{2/3} \quad (3)$$

where ε is the turbulent energy dissipation rate (W m^{-3}) and

r is the distance (m) between the larval fish and the rotifer. r is determined by $N^{-0.333}$ where N is the number of rotifers per m³. The rate of contact with the rotifer, C (*number of rotifers* s⁻¹) is determined by the relative *velocity* (V) times the density of rotifers D (*number of rotifers* m⁻¹), as follows.

$$C = VD \tag{4}$$

where $D = \pi R^2 N$. Here, the reaction distance, R (cm), of the larvae was taken to be 0.038 (Laurence 1985).

The feeding success index, S, was determined by the following equation:

$$S = \frac{F}{C} \tag{5}$$

Where the feeding rate F (individuals/larvae*)* was determined from the rearing experiments.

The survival rate was calculated by following the equation.

Survival rate (%)=(the number of larvae at the end of the Round)/(the number of larvae at the beginning of the Round)×100

$$\tag{6}$$

Results

Changes in effects of turbulence with ontogenic development

The results at different turbulence levels are shown in Figure 3a. In Round 1, the highest survival rate of 71.1±0.02% (mean±SD) was observed at the "Mid" turbulence, although there was no significant difference in survival rate between "Low" and "Mid" turbulence ($P>0.05$, Tukey-Kramer test). Larvae could not survive at the higher turbulence conditions, "High" and "Extra high". There was a significant difference in survival rate between "Low" and "Mid" and "High" and "Extra High" ($P<0.05$, *t*-test). In Round 2, the highest survival rate was observed at "Mid" (67.9±0.03%). Although the survival rate at "Low" was slightly lower than that at "Mid", there was no significant difference between the two levels ($P>0.05$, Tukey-Kramer test).

The number of rotifers in the digestive tract of larvae on Day 3 in Round 1 and Day 9 in Round 2 are shown in Figure 3b. The number of rotifers in the digestive tract for "Low" and "Mid" turbulence levels was significantly higher than that at "High" and "Extra High" levels in Round 1 ($P<0.05$, Tukey-Kramer test). There were no significant differences between survival rates at any of the turbulence levels on Day 9 in Round 2 ($P>0.05$, Tukey-Kramer test).

Effect of turbulence on prey density

Survival rates with different prey densities during the initial feeding period are shown in Figure 4a. The survival
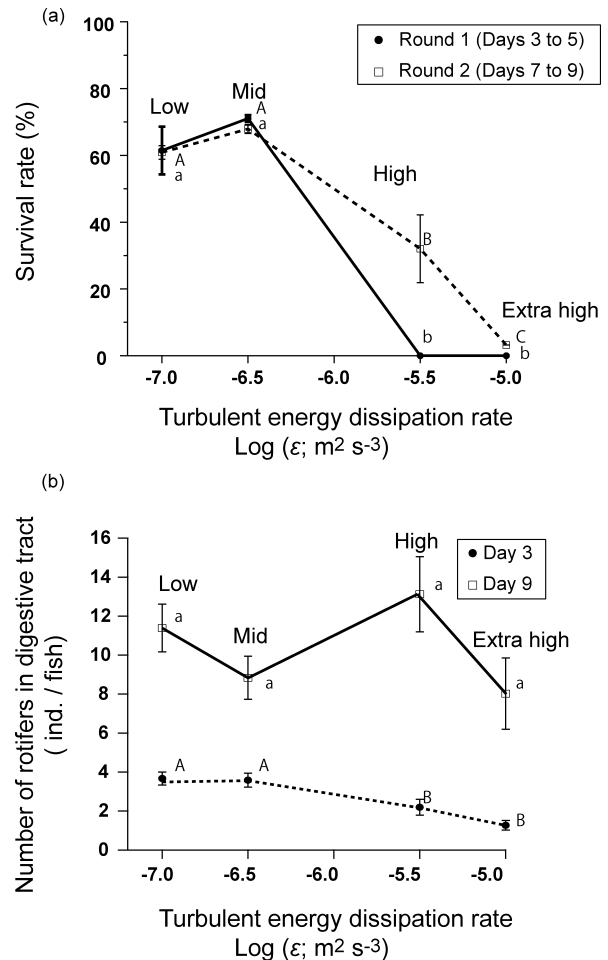

Fig. 3. (a) Relationship between survival rate of red sea bream larvae and turbulent energy dissipation rate. Error bars show standard errors (n=3). (b) Relationship between number of rotifers in the digestive tract of red sea bream larvae and turbulent energy dissipation rate. Error bars show standard errors (n=3). Significant differences (Tukey's test $p<0.05$) between turbulence levels are indicated by different letters.

rate at "Low" turbulence under low prey density was lower than that under high prey density. At "Mid" and "High" turbulence levels, there was almost no difference in survival rate between low and high prey densities. At low prey density, the survival rate showed an optimum at the turbulence level at "Mid", as occurs in tuna species.

We examined the number of rotifers in the digestive tract of larvae on Day 5 at each turbulence level and prey density (Fig. 4b). The maximum number of rotifers was observed at "Low" turbulence under high prey density and at "Mid" turbulence under low prey density. At "Mid" turbulence, there were more rotifers in the digestive tracts of larvae in tanks with high prey density than with low prey density.

The relationship between RNA : DNA ratios and turbulent energy dissipation rate at each prey density is shown in Figure 5. The ratio is a useful indicator of nutritional condi-
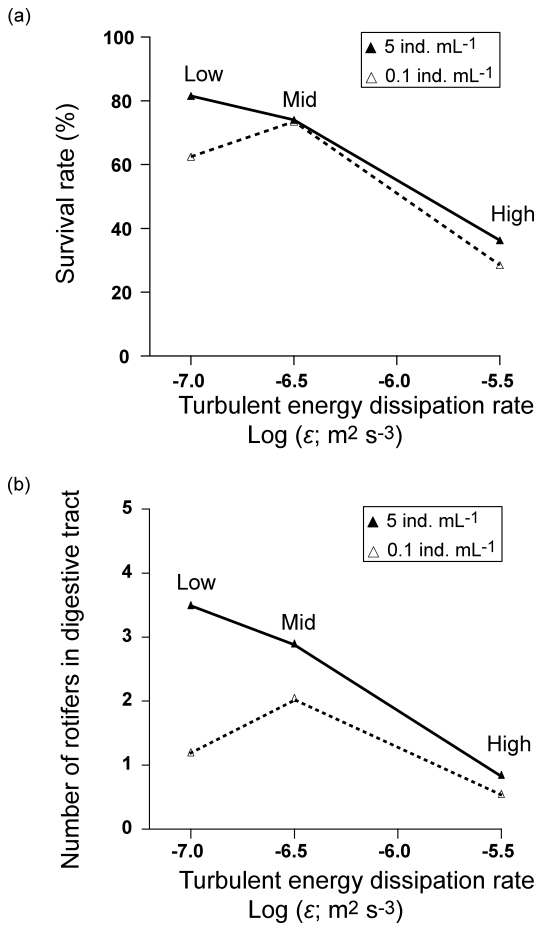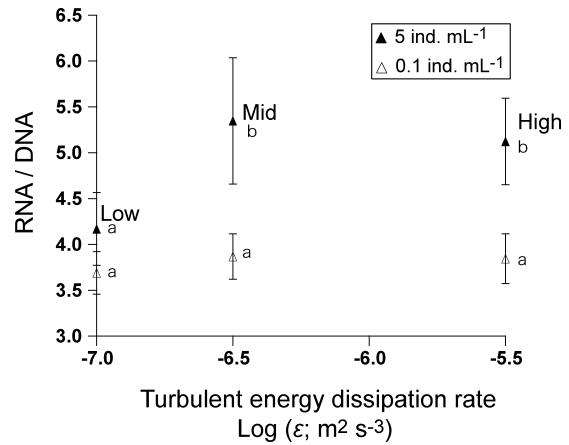
Fig. 5. Relationship between RNA : DNA and turbulent energy dissipation rate for high and low prey density. Error bars are standard error (n=20–40). Significant differences (Tukey's test $p<0.05$) between turbulence levels are indicated by different letters.

Fig. 4. (a) Relationship between survival rate of red sea bream larvae and turbulent energy dissipation rate at two prey densities (n=2). (b) Relationship between number of rotifers in the digestive tract of red sea bream larvae and turbulent energy dissipation rate at two prey densities (n=2).

tions, as has been shown previously in several larval fish studies (Clemmesen 1989; 1994). At low prey density, the differences between ratios at each turbulence level were not significantly different ($P>0.05$, t-test). However, under high prey density, RNA : DNA ratios at turbulence level "Low" and "Mid" and between turbulence levels "Low" and "High" were significantly different ($P<0.05$, Tukey-Kramer test). Therefore, larvae at "Mid" turbulence under high prey density could be expected to have the optimum nutritional condition. Under turbulence level "Low", there was no significant difference in RNA : DNA ratios between the high and low prey densities ($P>0.05$, t-test).

Contact rate between prey and predator and feeding success index

The contact rate, from Eq. (4), which increases with increasing turbulence level, depends on the turbulent energy dissipation rate. The contact rate at "Extra High" turbulence (0.93 rotifers s^{-1}) was four times that at "Low" turbulence (0.21 rotifers s^{-1}).

Discussion

Observations at different ontogenic stages show that the range of turbulence at which red sea bream larvae can survive and ingest food became wider as the larvae grew. Dower et al. (1997) modeled the size-dependent effects of turbulence on larval feeding. In our experiments, larger red sea bream larvae were able to ingest food under stronger turbulence than could smaller ones. During the juvenile period, they move lower in the water column, where stronger turbulence is generated by bottom friction and tidal flows. Therefore, the findings in this experiment are strongly related to vertical migration; species with larger larvae derive slightly greater benefits from exploiting turbulent conditions.

Utne-Palm (2004) found that a decrease in turbulence from 1×10^{-6} to $8\times10^{-8}\,W\,kg^{-1}$ had a generally negative effect on the prey attack rates of small- and medium-sized Atlantic herring. Larvae under low turbulence conditions are less able to use their energy. On the other hand, larvae under the greater, optimum turbulence condition are more likely to be in good nutritional condition and show faster growth rates. The RNA : DNA ratios of larvae were the highest under "Mid" turbulence conditions in our experiments. Under optimum turbulence conditions, larvae can probably expend smaller amounts of energy on feeding and transfer larger amounts of energy to growth.

For interspecific comparison, a feeding success index was calculated through numerical modeling for red sea bream and Pacific bluefin tuna using data from Kato et al. (2008) and compared. Tables 1 compiles feeding rate and contact rate parameters for a range of turbulences for bluefin tuna from Kato et al. (2008). There were no significant differences in prey contact rates for red sea bream and Pacific

Table 1. Feeding rate (ind./larvae) of Pacific bluefin tuna[1].

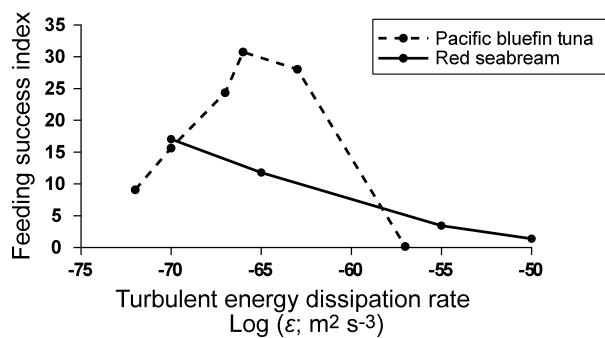| Turbulence dissipation rate Log(ε; m^2 s^{-3})	Feeding rate (individuals/ larvae) F	The rate of contact with the rotifer (individuals/s) C
−7.2	1.8	0.20
−7.0	3.5	0.22
−6.7	6.6	0.27
−6.6	8.9	0.29
−6.3	10	0.36
−5.7	0.09	0.55

[1] Adopted from Kato et al. (2008).

Fig. 6. Relationship between feeding success index and turbulent energy dissipation rate, as calculated from a predator–prey model.

bluefin tuna. However, these results did not match the data for number of rotifers in the larval digestive tracts in the rearing experiments with the two species. The relationship between turbulent energy dissipation rate and feeding success index in red sea bream and Pacific bluefin tuna (Fig. 6) shows that for Pacific bluefin tuna, the curve is dome-shaped, but in red sea bream, the feeding success index decreases with increasing turbulence. Numerical modeling and rearing experiments of Pacific bluefin tuna reveal that the feeding success index versus turbulence curve is dome-shaped, with a peak at the same turbulence level that was optimal for survival; in red sea bream the curve shows a linear trend.

Differences in the development of mechanoreceptors among different species may explain the difference in this relationship. Neuromasts play an important role in the detection of zooplankton (Jones and Janssen 1992; Mukai 2006). Pacific bluefin tuna yolk-sac larvae have well-developed mechanoreceptors: a pair of large, free neuromasts behind the eyes, seven pairs of neuromasts on the head, and seven pairs on the trunk (Masuma 2006). In contrast, the red sea bream larvae have only one pair of neuromasts on the head (Ishida 1987). Therefore, Pacific bluefin tuna larvae depend on the mechanoreceptors more strongly than do red sea bream larvae. In other words, they are more suited to capturing rotifers which show fine movements and their feeding rate under the optimum turbulence level for feeding is higher

than under the low turbulence level. However, as the organs were very sensitive, it is very easy for these to become damaged. Blaxter and Fuiman (1989) indicated that turbulence due to aeration damaged the cupulae of herring, flounder, plaice, cod and halibut larvae in culture conditions. Therefore, Pacific bluefin tuna could not ingest prey under turbulence in excess of the optimal range. This suggests that feeding rates for the red sea bream larvae decrease with increasing turbulence. Vision is also used for prey detection and capture (Blaxter 1968, Blaxter 1969). Therefore, the possibilities that differences in vision caused differences in feeding success cannot be ruled out. These considerations require further study.

Comparison of the survival rates of red sea bream to those of Pacific bluefin tuna (Kato et al. 2008) showed large differences. Red sea bream can survive and feed under calm conditions. In contrast, Pacific bluefin tuna larvae need higher, but within the optimal range, turbulence for survival and feeding. The optimum turbulent energy dissipation rate is around 5×10^{-7} m^2 s^{-3} (Kato et al. 2008). On the other hand, the optimum turbulent energy dissipation for red sea bream was 1×10^{-7} to 3×10^{-7} m^2 s^{-3}. These results suggest that the presence of a moderate amount of turbulence is more important for the initial survival of Pacific bluefin tuna larvae than for red sea bream larvae.

References

Blaxter, J. H. S. 1968. Light intensity, vision, and feeding in young plaice. J. Exp. Mar. Bio. Ecol. 2: 293–307.

Blaxter, J. H. S. 1969. Visula thresholds and spectral sensitivity of flatfish larvae. J. Exp. Biol. 51: 221–230.

Blaxter J. H. S. and Fuiman, L. A. 1989. Function of the free neuromasts of marine teleost larvae. *In*: Coombs, S., Gorner, P. and Munz H. (Eds.), The Mechanosensory lateral line: Neurobiology and evolution. pp. 481–499. Springer, New York.

Caldarone, E. M., Wagner, M., St. Onge-Burns, J. and Buckley, L. J. 2001. Protocol and guide for estimating nucleic acids in larval fish using a fluorescence microplate reader. Northeast Fisheries Science Center Reference Documents: 1–22.

Clemmesen, C. 1989. RNA/DNA ratios of laboratory-reared and wild herring larvae determined with a highly sensitive fluorescence method. J. Fish Biol. 35: 331–333.

Clemmesen, C. 1994. The effect of food availability, age or size on the RNA/DNA ratio of individually measured herring larvae—laboratory calibration. Mar. Biol. 118: 377–382.

Cury, P. and Roy, C. 1989. Optimum environmental window and pelagic fish recruitment success in upwelling areas. Can. J.

Fish. Aqua. Sci. 46: 670–680.

Dower, J. F., Miller, T. J. and Leggett, W. C. 1997. The role of microscale turbulence in the feeding ecology of larval fish. Adv. Mar. Biol. 31: 169–220.

Fukunishi, Y., Masuda, R. and Yamashita, Y. 2006. Ontogeny of tolerance to and avoidance of ultraviolet radiation in red sea bream *Pagrus major* and black sea bream *Acanthopagrus schlegeli*. Fish. Sci. 72: 356–363.

Hamasaki, S., Ōuchi, A. and Tsuruta, A. 1980. Distribution and abundance of zooplankton in Yuya Bay. Bull. Seikai Reg. Fish. Res. Labo. 54: 45–57 (in Japanese with English abstract).

Heming, T. A., McInerney, J. E. and Alderdice D. F. 1982. Effect of temperature on initial feeding in alevins of chinook salmon (*Oncorhynchus tshawytscha*). Can. J. Fish. Aquat. Sci. 39: 1554–1562.

Ishida, K. 1987. Studies on the development of sense organs and behavior in marine fish larvae and juveniles. PhD Thesis, University of Tokyo, Tokyo.

Jones, W. R. and Janssen, J. 1992. Lateral line development and feeding behavior in the mottled sculpin, *Cottus bairdi* (Scorpaeniformes: Cottidae). Copeia. 2: 485–492.

Kato, Y., Takebe, T., Masuma, S., Kitagawa, T. and Kimura, S. 2008. Turbulence effect on the survival rate and ingestion rate of bluefin tuna, *Thunnus orientalis*, larvae on the basis of a rearing experiment. Fish. Sci. 74: 48–53.

Kimura, S., Nakata, H., Margulies, D., Suter, J. M. and Hunt, S. L. 2004. Effect of oceanic turbulence on the survival of yellowfin tuna larvae. Nippon Suisan Gakkaishi. 70: 175–178 (in Japanese with English abstract).

Kinoshita, I. and Tanaka, M. 1990. Differentiated spatial distribution of larvae and juveniles of the 2 sparids, red and black sea bream, in Shijiki Bay. Nippon Suisan Gakkaishi. 56: 1807–1813 (in Japanese with English abstract).

Laurence, G. C. 1985. A report on the development of stochastic models of food limited growth and survival of cod haddock larvae. *In*: Laurence, G. C. and Lough, R. G. (Eds.), Growth and Survival of Larval Fishes in Relation to the Trophodynamics of Georges Bank Cod and Haddock. pp. 83–150, NOAA Technical Memorandum, Woods Hole.

Lough, R. G. and Mountain, D. G. 1996. Effect of small-scale turbulence on feeding rates of larval cod and haddock in stratified water on Georges-Bank. Deep-Sea Res. II. 43: 1745–1772.

Mackenzie, B. R. and Leggett, W. C. 1991. Quantifying the contribution of small-scale turbulence to the encounter rates between larval fish and their zooplankton prey—effects of wind and tide. Mar. Ecol. Prog. Ser. 73: 149–160.

Mackenzie, B. R., Miller, T. J., Cyr, S. and Leggett, W. C. 1994. Evidence for a dome-shaped relationship between turbulence and larval fish ingestion rates. Limnology and Oceanography. 39: 1790–1799.

Mackenzie, B. R. and Kiøboe, T. 1995. Encounter rates and swimming behavior of pause-travel and cruise larval fish predators in calm and turbulent laboratory environments. Limnology and Oceanography. 40: 1278–1289.

Masuma, S. 2006. Studies on broodstock management and spawning ecology of bluefin and yellowfin tuna in captivity. PhD. Thesis, Kyushu University, Fukuoka (in Japanese).

Matsuura, H., Arizono, M. and Kakuda, N. 1981. Research on transportation and distribution of eggs of cultured red sea bream—II. Distributional pattern of eggs and larvae. Bull. Seikai Reg. Fish. Res. Lab. 56: 89–109.

Mukai, Y. 2006. Role of free neuromasts in larval feeding of willow shiner *Gnathopogon elongatus caerulescens* Teleostei, Cyprinidae. Fish. Sci. 72: 705–709.

Müller, U. K. 2008. Swimming and Muscle. *In*: Finn, R. N. and Kapoor, B. G. (Eds.), Fish larval physiology. pp. 523–549, Science Publishers, New Hampshire.

Rothschild, B. J. and Osborn, T. R. 1988. Small-scale turbulence and plankton contact rates. J. Plankton Res. 10: 465–474.

Skiftesvik, A. B. and Huse, I. 1987. Behavior studies of cod larvae, *Gadus morhua* L. Sarsia. 72: 367–368.

Stiansen, J. E. and Sundby, S. 2001. Improved methods for generating and estimating turbulence in tanks suitable for fish larvae experiments. Sci. Mar. 65: 151–167.

Sundby, S. and Fossum, P. 1990. Feeding conditions of Arcto-Norwegian cod larvae compared with the Rothschild-Osborn theory on small-scale turbulence and plankton contact rates. J. Plankton Res. 12: 1153–1162.

Sundby, S. 1996. Turbulence-induced contact rates in plankton: the issue of scales. Mar. Ecol. Prog. Ser. 139: 305–307.

Sundby, S. 1997. Turbulence and ichthyoplankton: Influence on vertical distributions and encounter rates. Sci. Mar. 61: 159–176.

Tanaka, M., Sugiyama, M., Tamai, K. and Miyaji, K. 1983. The ecological studies of the larvae and juveniles of red sea bream in Shijiki Bay—II. An observation of the vertical distribution of pelagic larvae and juveniles. Bull. Seikai Reg. Fish. Res. Lab. 59: 33–45.

Tennekes, H. and Lumley, J. L. 1974. A First Course in Turbulence. The MIT Press, Cambridge.

Utne-Palm, A. C. and Stiansen, J. E. 2002. Effect of larval ontogeny, turbulence and light on prey attack rate and swimming activity in herring larvae. J. Exp. Mar. Biol. Ecol. 268: 147–170.

Utne-Palm, A. C. 2004. Effects of larvae ontogeny, turbidity, and turbulence on prey attack rate and swimming activity of Atlantic herring larvae. J. Exp. Mar. Biol. Ecol. 310: 147–161.