Fragment growth-rates of six cultivated coral species: a reference framework for coral transplantation

Virginie VAN DONGEN-VOGELS and Jerôme MALLEFET

Abstract: Coral fragmentation is a natural process of asexual reproduction in many coral species. Fragment size is believed to be an important factor of fragment survival at least in some species. The degradation of coral reefs and its poor recovery in some localities had brought different management plans in coral transplantation. In this study we examined in controlled conditions the variation in fragment growth rates of six different scleractinian species belonging to two different growth forms. We showed that fragment growth rates increased over our 6 month survey and that *Pocillopora damicornis* exhibited the highest growth rate followed in decreasing order by *S. pistillata, Montipora sp.*, *S. caliendrum*, *Echinopora sp.*, and *T. reniformis* which may reflects their life history strategy, but also a difference in their surface-to-volume ratio as well as a difference in their skeletal density. Then, for each species, we determined whether growth rates might be affected by fragment size. We showed that there was a positive significant relationship between growth rate and fragment size, depending, however, on the interval time and the species considered. Difference in physiological resources allocation through a colony lifetime and genetic limitations in colony size may be related to our results. However, as in the wild many other parameters such as predation, can also play a role in fragment survivorship, we suggested that fragment size is an important parameter to take into account to successfully recover local coral population.

Keywords: Coral Growth, Coral Fragmentation, Controled Cultures, Hermatypic Corals

1. Introduction

Many studies have investigated coral fragmentation (LOYA, 1976b : HIGHSMITH, 1982 : WALLACE, 1985 : SEEBAUER, 2001), a natural process used by many coral species to increase their local population density, and thus increase their probability of survival after e.g. physical disturbances (HIGHSMITH, 1982). Previous studies have reported a correlation between fragment size and survivorship in corals (LOYA, 1976b : HIGHSMITH et al. 1980 : HUGHES and JACKSON, 1985 : CHADWICK-FURMAN et al., 2000 : ANTHONY et al., 2002 : SOONG and CHEN, 2003 : GOFFREDO et al., 2004 : ORTIZ PROSPER, 2005), whereas others have not (KINZIE and SARMIENTO, 1986 : BRUNO, 1998 : LIRMAN, 2000). Fragment size is one of the main characteristic of life history in many clonal organisms such as corals (KARLSON, 1988), which are known to have an indeterminate growth and hence unlimited colonial size (HUGHES and JACKSON, 1985 : SEBENS, 1987). While fragment survival may be species-dependent (HALL, 1997), it is still difficult to assess as many coral species have yet to be investigated.

regenerate local coral communities (Bowden-Kerry, 2003). Many studies have focused on in situ fragment survival (e.g. Yap and Gomez, 1985; Soong and Chen, 2003; Lindhal, 2003). The study of fragment growth in controlled conditions (stable physical parameters, no predation) would, however, facilitate the assessment of species-specific fragment growth rate, and hence survival rates. A fragment with higher growth rate would then sustain higher survival rates in the wild as it can extend faster. In particular, the comparison of growth and survival rates in the field and in controlled conditions allow for a direct assessment of species-specific response to predation, macroalgae over growth and flow field (Yap and Molina, 2003). Monitoring coral growth under controlled conditions may then be considered as an absolute prerequisite to provide baseline information for future studies involving coral growth in the field, including bleaching or recovery studies. A better knowledge in the potential relationship between growth rate and size might also provide further insights into the understanding of population dynamics in species of scleractinian corals.

In this context, the objectives of this work were to investigate the growth rate of fragments from six different cultivated species to provide baseline information on the growth of coral fragments after fragmentation under cultivated conditions. More specifically, a specific attention is given to (i) the inter-species variation of growth rate, (ii) the variation in growth rate between two growth forms (foliaceous vs branches), and (iii) the inter-fragments variability in growth rate for a given species.

2. Material and methods

2.1. Coral species

Six different coral species were considered here: three branched species (Stylophora pistillata, Seriatopora caliendrum, and Pocillopora damicornis) and three foliaceous colonial species (Echinopora sp., Montipora sp., and Turbinaria reniformis). All species are hermatypic corals harbouring the symbiotic algae zooxanthellae, which greatly accelerate the process of calcification, thus enabling their host corals to rapidly establish fragments in coral reefs (Sorokin, 1995; Sprung, 2000; Veron, 2000).

2.2. Fragmentation and coral cultures

Cuttings were performed with a pair of pliers on a few mother heads colonies of each coral species, providing a large number of fragments. During the growing period, fragments were placed on plastic plates in 800 l aquaria equipped with a circulating pump (Eheim 1060, 1200 l h⁻¹), allowing sufficient water flow to support coral growth. Illumination was provided with two m et al halide lamps (HQL) located one meter above each aquarium, allowing 100 μE cm⁻² s⁻¹ to 500 μE cm⁻² s⁻¹, from the surface of fragments growing near the glass of the aquarium to the surface of those growing in the centre of the aquarium respectively. Fragments of the same species were clustered to avoid any influence from other coral species and were reorganised every month in the aquaria to minimize the possible effects of water flow and light irradiance. The aquaria seawater temperature was maintained at 26.5–27.5 °C during the whole study. Two aquaria were used in this study. In addition to the studied species, the aquaria contained herbivorous organisms (e.g. fish or invertebrates). The presence of those organisms as well as a weekly cleaning were necessary to prevent excessive algal growth in the aquaria.

In order to measure the growth of fragments, they were taken out of the aquariums and put on a tray for five minutes before weighing them to allow excess water drain away (Delahaye, 2003). Fragments were then weighed one by one. All fragments of the six species were weighed within a day. The weight of each fragment was measured at the beginning of the study in November 2004 (just after fragmentation) and after 8 weeks of recovery, one weight measurement was performed each month from January to May 2005 (n=6 species ×30 to 46 fragments).

2.3. Statistical analysis

A two way analyse of variance was used to test the variation in growth rate with time and between species (factors: species, time, and the
interaction species $\times$ time). Parametric test (Levene's test, $>0.05$) of a one-way analysis of variance was then used in order to compare the increase in growth-rates between coral species with a Scheffe's multiple comparison test, and a $t$-test was done to compare those of the two growth forms (branches vs. foliaceous). Linear regressions were performed in order to test the relationship between the initial weight of the fragments of a given species and their growth rate.

3. Results
All fragments from each of the species investigated showed a similar exponential growth patterns over the 6-month survey. The related growth rates significantly ($p<0.0001$) increased linearly over time (Fig.1). The increasing gradients in growth rates over time were estimated as 0.0095 g week$^{-1}$ ($N=30$) for *Turbinaria reniformis*, 0.0127 g week$^{-2}$ ($N=43$) for *Echinopora* sp., 0.0197 g week$^{-2}$ ($N=46$) for *Montipora* sp., and 0.0164 g week$^{-2}$ ($N=30$) for *Seriatopora caliendrum*, 0.0210 g week$^{-2}$ ($N=37$) for *Stylophora pistillata*, 0.0322 g week$^{-2}$ ($N=39$) for *Pocillopora damicornis*. This results in significantly higher gradients in branched species than in foliaceous ones ($t$-test, $p<0.0001$). However, while *P. damicornis* increased its growth significantly faster than *S. pistillata* and *S. caliendrum* (Multiple comparison Sheffe's test, $p<0.05$), *Montipora* sp. was found to growth significantly faster than the two other foliaceous species ($p<0.05$).

The relationship between fragment weights ($g$) and their related growth rates ($g$ week$^{-1}$) has been investigated for five time intervals over the course of our survey. Our results indicate first that for most species, bigger fragments had significantly higher growth rates for the different time intervals considered. In other words, the length of time it took a fragment to double its weight decrease steadily with larger fragment size. Figure 2 shows for each studied species, the mean growth rates of the fragments as a function of their mean initial weight obtained at the beginning of each interval times. However, the strength of the correlation between initial weight and growth rate varied between species, and showed for most species a general increase of the significant effect of fragment sizes on growth rates through the different time intervals (Table 1). Fragments of *Echinopora* sp. did not show any
size-dependent growth during the first 8 weeks of this study, but well for the following months. In contrast, the decrease of the significant correlation from the $t_{12}$-$t_{16}$ interval time obtained for *P. damicornis* results in that, 20 weeks after fragmentation, the smallest fragment growth as fast as the largest one, and coral growth did not slow down or stop as fragments grew bigger ($p > 0.05$). Although fragments of *S. caliendrum* had the smallest range of initial weight at the beginning of this study, the significant correlation between fragment sizes and growth rates was observed to be stronger than that of the other species (higher correlation coefficient).
Table 1. Growth rate and correlation between initial weight and growth rate for different time intervals over our 6-month survey. Pearson correlation coefficient: * : 5% significance levels, ** : 1% significance levels, and ns : non-significant relationship

<table>
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<tr>
<th>Species</th>
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<td>T. reniformis</td>
<td>30</td>
<td>Pearson corr. (r)</td>
<td>0.60**</td>
<td>0.013 to 0.263</td>
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<td>Echinopora sp.</td>
<td>43</td>
<td>Pearson corr. (r)</td>
<td>0.23ns</td>
<td>0.05 to 0.255</td>
<td>0.05 to 0.675</td>
<td>0.01 to 0.875</td>
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<td>Montipora sp.</td>
<td>46</td>
<td>Pearson corr. (r)</td>
<td>0.50**</td>
<td>0.025 to 0.363</td>
<td>0.025 to 0.875</td>
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<td>S. caliendrum</td>
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<td>Pearson corr. (r)</td>
<td>0.80**</td>
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<td>S. pistillata</td>
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<td>Pearson corr. (r)</td>
<td>0.62**</td>
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<td>0.10 to 1.2</td>
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<td>P. damicornis</td>
<td>39</td>
<td>Pearson corr. (r)</td>
<td>0.34*</td>
<td>1.4 to 6.9</td>
<td>2.1 to 9.4</td>
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4. Discussion
4.1. Growth rate variation between species and growth forms

An early exponential growth in colonial organisms such as corals reflects the ability of each polyp (clone) to produce new polyps (Sebens, 1987). The subsequent linear increases observed in growth rate over time (Fig. 1) may reflect the absence of predation or competition for space as the species considered in this study have grown under optimal conditions.

The differences in the growth rate gradients observed between the studied species might reflect the difference in their life history traits. *P. damicornis*, *S. pistillata*, and *Montipora* sp. are opportunistic species (strategy *) with rapid growth rates and a great capacity to colonise new environment (Loya, 1976a; b: Sorokin, 1995; Connell et al. 1997; Sprung, 2000; Veron, 2000). In contrast, *S. caliendrum*, *Echinopora* sp., and *T. reniformis* use an intermediate strategy and can therefore show characteristics that are more related to a strategy *κ* (Sorokin, 1995). Moreover, our results indicate that branched species have a higher ability in regeneration than foliaceous species. This is consistent with previous observations (Loya, 1976b; Hall, 1997). This difference in growth rate gradients might also be explained by (i) the greater surface-to-volume ration of branched species, and (ii) the difference in skeleton density between species in the fact that it may incur a large drain of resources (Hall, 1997), hence slowing down the growth of dense skeleton fragments. For example, while the branched coral *Acropora* shows a much dense skeleton at the base than at the tip resulting in a fast addition of a fine porous layer of tissue and skeleton at the growing end of its branches, the massive coral *A. palmata*, which has a slower rate of regeneration compared to the branched species *Acropora*, do not show such axial gradient in skeletal density and have a dense column from base to tip (Hall, 1997). However, this is still debated in the literature as Bosscher (1993) showed an inverse relationship in the extension rate and
the skeletal density of colonies of Montastrea annularis, while Anthony et al. (2002) suggest that skeletal density may have only a minor effect on energetic investment during the linear extension of a colony. In this study, the thickness of the skeleton was observed to vary as follow: T. reniformis > Montipora sp. > Echinopora sp. for the foliaceous species, and S. pistillata > P. damicornis > S. caliendrum for the branches species.

4.2. Growth rate variation between fragment size

We identified a size-dependence in growth rates at different time intervals for most of the species investigated, i.e. larger fragments show higher growth rates. However, fragments of Echinopora sp. and especially P. damicornis did not show the same trends as the other species studied here. The non significant relationship between growth rates and initial weight of fragments of Echinopora sp. found at the interval t0-t8 may be due to the fact that all fragments were too small to show any differences in growth rates, or that they may need a longer time interval for recovering from fragmentation. In contrast, we showed that 16 weeks after fragmentation, and therefore after reaching a weight ranging from 5.8 to 20.8 g, all fragments of P. damicornis grew well and fast whatever their size. Kinzie and Sarmiento (1986) found similar results in P. damicornis analysing the skeletal extension rate of branches of colonies from 1.9 to 19 cm in diameter. Moreover, Rodgers et al. (2003) found that after fragmentation, the survival rates of the fragments were size- and species-dependent. In their study, they found that, 11 months after fragmentation induced by experimental trampling in situ, only 5 % of the small fragments of Montipora capitata survived compared to 77 % of larger ones. However, the difference in survival rates for fragments of Pocillopora meandrinae was not highly related to the size of the fragment since 70 to 78 % of fragment survivorship was found for the small size class (<5 cm) to the larger one (>5 cm), respectively. The fact that fragments of S. pistillata, S. caliendrum, Montipora sp., Echinopora sp. (after 8 weeks) and T. reniformis showed growth rates dependent on their initial weight over time might reflect a variability in their growth rate throughout their lifetime, with growth accelerating with fragment size (Loya, 1976b). Moreover, the fact that this relationship between growth rate and size was positive may also reflect a genetic limitation on maximum size which may allow to these species an adaptation to breakage (Hughes and Jackson, 1985). Although this is hard to tell yet here as this study cover only a 6 month period growth under cultivated conditions, S. pistillata is a well known studied species and was found to asexually reproduce by fragmentation in the Gulf of Eilat (Red Sea) (Loya, 1976b).

For some species, the weak correlations observed between growth rates and fragment size at some interval times suggests that factors other than initial size might have influenced the growth rates of the fragments. As this study was performed under fully controlled conditions, these factors might then include differences in e.g. shape and/or genetic composition. Colony or fragment size, as well as the shape of a colony, are critical parameters likely to impact the physiology and ecology of a coral species (Sebens, 1987; Kim and Lasker, 1998).

The energetic investment between tissue and skeletal vary according to the colony size, with for example, colonies with small radius branches showing a greater allocation to tissue formation than to skeletal formation, and inversely for colonies with thicker branches (Anthony et al., 2002). The allocation of resource to skeleton extension may not be the same in every parts of the colony at the same time (Martin and Le Tissier, 1988). A modelling approach of a branching colony showed that small-scale resource translocation in a coral colony has potential effects on the morphology of the colony and this may be regulated by the so-called ‘polymp competition hypothesis’ (Merks et al., 2004). This phenomenon might also be related to species-specific architectural constraints and be genetically regulated. Finally, as abiotic mechanisms is important in the explanation of the morphological patterns in corals (Merks et al., 2003, 2004), small colonies may be more
affected by disturbances than larger colonies. For instance, a massive coral species will be less affected by strong wave action than a thin branched coral species (Riegl and Riegl, 1996: Rodgers et al., 2003: Cros and McClanahan, 2003).

4.3. Fragment size and coral transplantation

Colony size in corals has been often associated with survivorship, growth, and reproduction (e.g. Highsmith, 1982: Loya, 1976b: Babcock, 1991) and many scleractinian corals with size-dependent growth/or survivorship/-or mortality has been already investigated (e.g. Acropora pulchra (Soong and Chen, 2003), S. pistillata (Loya, 1976b: Vago et al., 1997), Fungia granulose (Chadwick-Furman et al., 2000), Balanophyllia europaea (Goffredo et al., 2004), Agaricia agaricite, A. lamareiki, Leptoseris cucullata, Montastrea annularis, Porites astreoides (Hughes and Jackson, 1985)). In the wild, larger colonies have showed a better capacity to resist invasion and damage (Loya, 1976b), as well as to have higher fecundity and lower mortality than smaller colonies (Babcock, 1991), i.e. the probability for a small colony to be completely kill is greater than that for a larger one (Hughes and Jackson, 1985: Babcock, 1991). Soong and Chen (2003) showed that very small fragment (e.g. 1 cm) of Acropora were too small to use for coral transplantation, but that fragment of intermediate size (e.g. 4 cm) was bigger enough to generate high growth rates and therefore had better potential of survivorship. In Edwards & Clark (1998), by comparing many studies involving size-dependent survivorship, they argue that it is hard and dangerous to make a general frame for coral transplantation. Moreover, it was showed that growth rates of fragments highly vary from site and species (Cruz-Pinon et al., 2003: Dizon and Yap, 2006). Moreover, transplanted colonies was found to show lower growth rate than undisturbed colonies (Yap and Gomez, 1985) at least in the short term (0.5 to 1 year after fragmentation) (Edwards & Clark, 1998) and therefore it may suggest considering a longer time of recover, such as in tanks or in shallow water (mariculture), before transplantation. It is clear from our results that, in general, bigger colonies should be used in coral transplantation. However, although the success of transplanted fragments in the wild are depending on many other factors (e.g. type of substrate, wave action (Riegl and Riegl, 1996), predation (Cros and McClanahan, 2003)), we believe, as suggested by Lirman (2000), that size may still affect the long term survivorship of fragments.

5. Conclusions

Although growth rates was showed to vary between the six studied species with general lower growth rates obtained for foliaceous species, the optimal conditions investigated in this study results in that for all species growth rates increased through time. Branched species such as S. pistillata and P. damicornis, or those belonging to the genera Acropora showing high growth rates and recruiting well, have therefore often been used in many transplantation studies (see Edwards and Clark, 1998). This is, in our knowledge, not the case for foliaceous species such as Montipora sp., Echinopora sp., and T. reniformis. However, if we want to enhance coral biodiversity in areas where transplantation is justify, all species have to be considered. This may need previous knowledge on the abiotic and biotic parameters of the transplantation area, as well as the life history traits (Seeauer, 2001) of potential species justified to be transplanted. Only one recent study on transplantation did involve different species of various growth form (Dizon and Yap, 2006). However, in the case where donor colonies may be hard to be supply culturing fragments in optimal conditions may be an option to supply transplants (Edwards and Clark, 1998) of size big enough to minimize the risk of mortality after transplantation. Many (ornamental) coral species have been to grow well in some Aquarium (pers. observations). Those Aquarium Centres have often yet well established materials for growing fragments, so a solution may be to find a certain agreement (or trade-off) between a short term lucrative coral trade and a long term sustainable coral management.
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Seasonal changes in growth and photosynthesis-light curves of *Sargassum horneri* (Fucales, Phaeophyta) in Oura Bay on the Pacific coast of central Honshu, Japan

Atsuko MIKAMI¹, Teruhisa KOMATSU¹, Masakazu AOKI², and Yasutsugu YOKOHAMA³

**Abstract:** We investigated seasonal changes in the growth, photosynthesis-light curves, and chlorophyll content of *Sargassum horneri* (Turner) C. Agardh in Oura Bay on the Pacific coast of central Honshu, Japan, and also characterized the physical environment, including PAR and water temperature. During monthly scuba dives, we tracked the growth of main stems and observed the growth stage of eight to ten individual *S. horneri* that had been marked when their main stems were >10 cm until they disappeared from the substratum after maturity. In addition, we measured the rates of net photosynthesis and dark respiration in upper and lower leaves of four individual *S. horneri* collected monthly with a differential gas volumeter at the monthly mean water temperature, also measuring the weight and chlorophyll content of the leaves. The seasonal changes in the photosynthetic activity of upper leaves based on wet weight and chlorophyll content had different peaks: the former was positively correlated with the length and growth rate of the main stems, and the latter was negatively correlated with plant age. Moreover, the pattern of seasonal changes in photosynthetic activity based on weight was synchronized with changes in the nutrient content of the seawater.

**Keywords:** *Sargassum horneri* (Turner) C. Agardh, photosynthesis-light curve, growth, seasonal change.

*Sargassum horneri* (Turner) C. Agardh, an annual species, is distributed on rocky coasts throughout the Japanese archipelago, except the eastern part of Hokkaido and Okinawa, the Korean Peninsula, and China, and is one of the most common species in Japan (ÜMEZAKI, 1984a; YOSHIDA, 1998). It grows on rocks at water depths of 1 to 5 m (rarely 10 m). Its length can reach several meters, extending to the sea surface in the luxury growth season. Typically, *S. horneri* forms a mixed species forest with other *Sargassum* species, and *Sargassum* forests occupy about 30% of the surface area (85,682 ha) of all seagrass and seaweed beds in Japan (Environment Agency of Japan, 1994). These forests play important roles as both primary producers and habitat in coastal ecosystems due to their great biomass. Around maturation, when the main stem of *S. horneri* attains its maximum length, the plant detaches from the substratum, and the next generation emerges and grows (ÜMEZAKI, 1984b). Therefore, the biomass of *S. horneri* varies seasonally according to the annual life cycle. Recently, *S. horneri* has become commercially exploited as a food resource because it contains biologically active agents, and elucidating its ecology is of major importance.

The seasonal change in the photosynthetic activity of *Sargassum* species may be related to their growth, physiology, and physical condition (PRINCE, 1980; DAWES, 1987; HONDA and OKUDA, 1989; 1990; GAO, 1990b), although...
this has not been evaluated in detail. For example, Gao (1990a) found seasonal changes in the photosynthetic rate of *S. horneri* measured monthly at 20° C and 600 μE m⁻² s⁻¹ for one year, excluding September, and concluded that temperature, growth stage, and nutrient conditions in the sea accounted for the seasonal photosynthetic variability. Prince (1980) reported that a significant decline in the photosynthetic rate of *Sargassum pteropleuron* Grunow was synchronous with leaf senescence and decreased water temperatures in winter. Honda and Okuda (1989, 1990) demonstrated that the maximum photosynthesis rates of vernal and autumnal *S. horneri* and *Sargassum micranaganum* (Kützing) Endlicher differed depending on their stage of maturity.

Several studies in different areas have reported seasonal changes in the growth of *S. horneri* in terms of its biomass and length (Umezaki, 1984b; Taniguchi and Yamada, 1988; Yokoyama et al. 1999), but few studies have examined the seasonal changes in both photosynthetic activity and growth, except a study conducted in Wakasa Bay on the coast of the Sea of Japan (Gao, 1990b). Investigating the seasonal change in photosynthetic activity, which is the basis of growth, helps to understand the relationship between growth and the external environment or internal condition of the plants. In addition, investigations of the same species in a variety of areas that have different physical environments would help to understand these relationships more clearly.

Here we describe the ecological influences on photosynthesis in *S. horneri* under monthly mean water temperature conditions in situ. We measured the photosynthesis-light curves based on both weight and chlorophyll a (chl.a) content of leaves monthly. Growth was assessed from measures of main stem length made while scuba diving to observe the growth stage. We investigated the relationships among seasonal changes in the photosynthetic activity, growth, physiological condition, and abiotic environment of the species. Moreover, based on comparisons with the results from another area (Gao, 1990), we examined the factors causing the seasonal changes in photosynthetic activity and growth.

![Map showing the study site in Shidagaura Cove, Oura Bay, located near the tip of the Izu Peninsula on the Pacific coast of central Honshu, Japan, and the Shimoda Marine Research Center (SMRC), University of Tsukuba. In the lower panel, A and B indicate the measurement locations for water temperature and PAR, respectively.](image)

**Fig.1.** Map showing the study site in Shidagaura Cove, Oura Bay, located near the tip of the Izu Peninsula on the Pacific coast of central Honshu, Japan, and the Shimoda Marine Research Center (SMRC), University of Tsukuba. In the lower panel, A and B indicate the measurement locations for water temperature and PAR, respectively.

**2. Materials and Methods**

### 2.1. Study site

*Sargassum horneri* was collected from Shidagaura Cove in Oura Bay, located near the tip of the Izu Peninsula on the Pacific coast of central Honshu, Japan (Fig. 1). A *Sargassum* forest exists in the subtidal zone consisting of rocks and rock plates at depths of 1 to 5 m with horizontal dimensions of about 100 × 100 m; *S. horneri* was a dominant species at the study site.

### 2.2. Measurement of in situ PAR and water temperature

The photosynthetically active radiation (PAR) in Shidagaura Cove was measured at 10-min intervals from December 2001 to December 2002 with light intensity sensors (MDS...
Mark 5/L; Alec Electronics, Japan) fixed on the sea floor at depths of 1, 2, and 3 m. Surface water temperatures in Oura Bay (Fig. 1) were measured daily by personnel from the Shimoda Marine Research Center of the University of Tsukuba at 10:00 h. The monthly mean surface water temperature was then determined and used for the experiment.

2.3. Measurement of growth

*Sargassum horneri* has one main stem that grows from the holdfast and lateral branches that grow from the main stem (Fig. 2). The length of the main stem serves as an index of individual plant growth. Therefore, ten individuals of *S. horneri* at depths of 2 to 3 m in Shidagaura Cove were selected randomly and marked with tags fixed to the base of the main stem in December 2001. Scuba divers measured the main stem lengths of the marked individuals each month from December 2001 to December 2002, from the time the main stem length exceeded 10 cm until the individual detached from the substratum after maturity. When a marked individual detached, the divers marked a new individual and continued their measurements. The main stem typically grows the longest, although when it is cut off due to wave action or other factors, a lateral branch can grow longer than the main stem. In cases where the lateral branch was longer than the main stem, the lateral branch length was measured. Sprouting and maturity were also examined in situ during the underwater measurements of the main stems. In addition, approximately four individuals were collected for measuring photosynthesis and respiration.

2.4. Measurement of net photosynthesis and dark respiration

Between December 2001 and December 2002, the net photosynthetic and dark respiratory rates of *S. horneri* were measured from October to April when the main stem length exceeded 10 cm. During the experiment, the water temperature was set at the monthly mean from Oura Bay in the previous year. Leaves were measured because they are the primary organ for net primary production of the plant (*Gao* and **Umezaki**, 1989a; *Gao*, 1991). Since the photosynthetic rate of leaves depends on their position, namely the upper or lower portion of the plant (*Gao* and **Umezaki**, 1988, 1989a; *Gao*, 1991; Murase et al. 2000), eight cuttings of leaves (about 5 cm² per cutting) were selected randomly from each portion of the plant for the four individuals collected monthly from Shidagaura Cove. The net photosynthetic and dark respiratory rates for a total of 16 cuttings were measured using the following method.

We used a differential gas volumeter (DGV; Productmeter; Nikko-Kagaku, Japan), which measured the increase or decrease in the rate of oxygen (μ) produced or consumed by the cuttings placed in a small flask (Yokohama and Ichimura, 1969; Yokohama et al., 1986). The DGV has often been used to measure the net photosynthetic and respiratory rates of macroalgae (Yokohama, 1973; *Gao* and **Umezaki**, 1988; Sakanishi et al., 1989; *Gao* and Nakahara, 1990; *Gao*, 1991; Serisawa et al., 2001b). Cuttings were identified by cubicle (mesh case) and kept in an aquarium (5000 ml) with filtered running seawater for about 24 h in the laboratory before measuring the net photosynthetic and dark respiratory rates to avoid effects associated with the trauma of
cutting (SAKANISHI et al., 1988). The net photosynthetic and dark respiratory rates of Sargassum species exhibited apparent day-night rhythms independent of daytime exposures to various intensities of solar radiation (GAO and UMEZAKI, 1989b; GAO, 1990a). Based on this pattern, a series of experiments was started at 13:00 h, and the flasks were shaken by motor for 1 h at a constant light intensity of 400 μE m⁻² s⁻¹ just before the experiment. A 30ml conical reaction flask with a cutting and 10 ml of filtered seawater, and a compensation flask with 10 ml of filtered seawater only were attached to the DVG. The flasks were put in a water bath (30 °C) at a thermostat-regulated temperature matching the monthly mean water temperature measured the previous year. The flasks were irradiated by a lamp (KP-10S 100V-300W ; Philips, Japan) and the light reflected from mirrors placed under the water bath. Seven light intensities (800, 400, 200, 100, 50, 25, 0 μE m⁻² s⁻¹) were applied using neutral density glass filters (TND-50, 25, 12.5 ; Toshiba, Japan). The PAR of the various light intensities was measured with a quantum photon meter (LI-189 ; LI-COR, USA). Oxygen evolution or consumption in the reaction flask was monitored every 3 min for about 20 min per light intensity with continual shaking (amplitude about 2.5 cm, frequency about 130 lap m⁻¹ intervals) in the water bath.

The net photosynthetic and dark respiratory rates under the seven light intensities were fitted to the following approximation of photosynthesis-light curves proposed by Eilers and Peeters (1988):

\[ P = \frac{I}{(aF + bI + c) - R_d} - R_d, \]  
\[ P_m = \frac{I}{(b + 2\sqrt{ac})}, \]  
\[ s = \frac{I}{c}, \]

where \( P \), \( I \), and \( R_d \) are the photosynthetic rate, light intensity, and dark respiratory rate, respectively; \( a, b, \) and \( c \) are constants; \( P_m \) is the maximum net photosynthetic rate; and \( s \) is the initial slope.

After the experiment, the wet weights of the cuttings were measured with an electronic balance (EB-330S ; Shimadzu, Japan). To quantify photosynthetic pigments, the cutting was placed in 10 ml of N,N-dimethyl-formamide (DMF) solution at −25 °C for at least 1 day. The absorbances of the extract at 663.8 nm and 750 nm were measured with a spectrophotometer (UV−3000 ; Shimadzu), and the chl.a levels were calculated using the formula proposed by PORRA et al. (1989).

3. Results
3.1. Water temperature and daily PAR

Figure 3 (a) shows the monthly mean of water temperature and mean daily PAR averaged per month measured at a depth of 1 m in the survey area from December 2001 to December 2002. The monthly mean water temperature increased from February to August and decreased from September to February. A
minimum temperature of 13°C was attained in February and a maximum of 26°C was reached in August and September. The mean daily PAR depended on day length; it was high from May to August and low from November to February. The minimum and maximum values of the mean daily PAR were 7.8 E m⁻² day⁻¹ in January and 26.1 E m⁻² day⁻¹ in May, respectively.

3.2. Seasonal change in growth

Figure 3 (b) and Table 1 show the monthly mean length and monthly mean growth rate (cm month⁻¹) of main stems standardized using a month of 30 days. The monthly mean length of the main stems reached a maximum of 358 cm in March, and then decreased in April. Field observation revealed that *S. horneri* matured from mid-March to April (Fig. 3 (b)). Entire plants of *S. horneri* detached from the substrata, without residual parts, from April to May (Fig. 3 (b)). Sprouts of new plants were observed on rocks from the beginning of October until the end of November. The monthly mean growth rate of the main stems ranged from 64.8 to 151.3 cm month⁻¹ from December to March. Growth was highest (151.3 cm month⁻¹) from February to March and lowest (12.7 cm month⁻¹) from October to November.

3.3. Chlorophyll a content by wet weight

The chl.a content in the upper leaves ranged from 0.69 to 1.32 mg chl.a g wet wt.⁻¹ (Fig. 3 (c)), and increased with main stem growth (Fig. 3 (b)). However, the values for the lower leaves remained constant between 1.09 and 1.34 mg chl.a g wet wt.⁻¹ throughout the experiment. The chl.a content of the lower leaves was greater than that of the upper leaves from October to December (*t*-test, *P* ≤ 0.05). The chl.a content of the upper leaves approached that of the lower leaves as the plants grew and matured.

3.4. Seasonal change in the photosynthesis-light curves

3.4.1. Maximum net photosynthetic rate

Figure 4 shows the photosynthesis-light curves based on wet weight. The maximum net photosynthetic rate of upper leaves based on wet weight reached a maximum of 3.9 μl O₂ mg wet wt⁻¹ h⁻¹ in March and a minimum of 2.3 μl O₂ mg wet wt⁻¹ h⁻¹ in December (Fig. 5 (a)). The maximum net photosynthetic rate of upper leaves based on the chl.a content reached a maximum of 3.6 μl O₂ μg chl. a⁻¹ h⁻¹ in October and a minimum of 2.0 μl O₂ μg chl. a⁻¹ h⁻¹ in February (Fig. 5 (b)). The net photosynthetic rate of the upper leaves exceeded that of the lower leaves, except in March and April (*t*-test, *P* ≤ 0.05; cf. GAO, 1990b). The differences in the maximum net photosynthetic rates between the upper and lower leaves were substantial during the young stage of growth (October-December), but decreased as the plants grew. At maturation, from March to April, the maximum net photosynthetic rates were similar between the upper and lower leaves.

The maximum net photosynthetic rates of the upper leaves based on wet weight at the mature stage were greater than in the young stage. By contrast, the rates based on the chl.a content at the young stage exceeded those at the mature stage. The chl.a content of leaves increased as the individuals grew, although the photosynthetic activity of the chl.a in leaves decreased as the individuals became older.

3.4.2. Dark respiratory rate

The monthly dark respiratory rates (*Rd*) of the upper and lower leaves of *S. horneri* based on wet weight are given in Fig. 5 (c). The dark respiratory rate of the upper and lower leaves
Fig. 4  Photosynthesis - light curves of the upper and lower leaves of *S. horneri* from December 2001 to December 2002. Open and solid circles indicate results for the upper and lower leaves, respectively. The bars represent the standard deviation (± S.D.) of samples. Temperatures in the panel represent *in situ* water temperatures during measurement of net photosynthetic and dark respiratory rates.

![Diagrams showing photosynthesis-light curves for *S. horneri*](image)

Fig. 5  Seasonal changes in the maximum net photosynthetic rates of *S. horneri* based on the wet weight (a) and chlorophyll *a* content (b). Seasonal changes in dark respiratory rates of *S. horneri* on a wet weight basis (c). Open and solid circles represent the upper and lower leaves, respectively.

![Seasonal changes in photosynthetic rates](image)

Fig. 6  Seasonal changes in the initial slopes on a wet weight (a) and chlorophyll *a* basis (b). Open and solid circles represent the upper and lower leaves, respectively.

![Initial slopes](image)

The rates ranged from 0.05–0.08 and 0.04–0.07 μl O₂ mg wet wt.⁻¹ h⁻¹, respectively, and the maximum dark respiratory rate of upper leaves based on wet weight reached a maximum in January and November and a minimum in April (Fig. 5 (c)). In addition, there was no significant difference in respiratory rates between the upper and lower leaves (*t*-test, *P* > 0.05), except in December, and the difference decreased during the maturation stage (February-April; cf. GAO, 1990b).
3.4.3. Initial slope

The initial slopes of the photosynthesis-light curves based on wet weight and the chl.a content of upper leaves of showed seasonal variation similar to that of the maximum net photosynthetic rate, \( P_{\text{n}} \). Depending on the \( P_{\text{n}} \) in this study, the initial slopes from October to December were higher than those from January to April (Fig. 6 (a, b)). There was little difference in the initial slopes between the upper and lower leaves, except for values based on the chl.a content from October to December.

Smith et al. (1983) reported that the initial slopes of young and mature disks of Macrocystis integrifolia were similar on an area basis, whereas the initial slopes of young disks on a pigment basis were generally higher than those of mature disks. This was also true in our study, suggesting that the chl.a of young leaves adapts to low light intensities.

4. Discussion

The growth rate and maturation of S. horneri in the Shidagaura Cove study differed from those in other areas. Umekazi (1984b) examined the growth in S. horneri off sheltered shores in Obama Bay, a branch bay of Wakasa Bay, in the Sea of Japan, and reported a maximum mean main stem length of 161.0 cm in May and a daily rate of increase in length ranging from 0.054 to 1.96 cm day\(^{-1}\) (1.6 to 58.8 cm month\(^{-1}\)) from September to May. The mean length and growth rate of S. horneri main stems in Shidagaura Cove were more than twice those in Wakasa Bay. The maturation period took place from late March to April in Shidagaura Cove, while it occurred from April to May (Umekazi, 1984b) or May to June (Gao and Umezaki, 1990; Gao and Hua, 1997) in Wakasa Bay. The winter water temperature in Wakasa Bay (10° C in February; Umekazi, 1984b; Gao, 1990b) was lower than that in Shidagaura Cove (13° C in February; Shimoda Marine Research Center; SMRC). Sargassum horneri in Shidagaura Cove, which faces the Pacific Ocean, grew faster, attained larger sizes, and matured earlier than those in Wakasa Bay since water temperature had a positive effect on the growth rate and maturation of plants (De Wree, 1976; Prince and O’Neal, 1979; Ogawa, 1982, 1983). The duration of monthly total sunlight in Maizuru (66.1–96.8 h from December to February) near Obama Bay in winter was less than that in Irouzaki (161.5–189.3 h from December to February) near Shidagaura Cove (Japan Meteorological Agency, 2002). Presumably, the daily total PAR also had a positive effect on growth through photosynthetic activity (Luning, 1993; Uchida, 1993). Therefore, in Shidagaura Cove, the warmer water temperature in winter and the greater solar radiation promoted relatively rapid growth and early maturation of S. horneri.

Younger leaves of Laminaria and Fucus species contain less pigment than those of older leaves (Kuppers and Kremer, 1978; Henley and Dunton, 1995). The chl.a content of the lower leaves of Sargassum species was higher than that of upper leaves (Gao and Umezaki, 1988; Gao, 1990b, 1991). This study also showed that the chl.a content of the lower (older) leaves of S. horneri was greater than in the upper (younger) leaves. However, the chl.a content was similar between these leaf types from January to April, which occurred because the condition of the upper leaves approached that of the lower leaves as they aged. The main stem of S. horneri grows not only at the apical part, but also throughout as growth progresses (Umekazi, 1984b); therefore, the average properties of the upper and lower leaves converge. Accordingly, the differences in the photosynthetic rate, respiratory rate, and initial slope between upper and lower leaves diminished as the plants grew. The chl.a content decreased in April, which is the maturation period (cf. Wheeler, 1980; Gao, 1990b). Degradation of chl.a was responsible for this phenomenon because the plants began to senesce after maturation.

The maximum photosynthetic rates based on wet weight were positively correlated with the increases in main stem length. Gao (1990b) studied the photosynthetic ability of S. horneri leaves in Wakasa Bay and reported that their net photosynthetic rates based on dry weight exhibited two peaks annually: one in November and another in March. Umezaki (1984b) stated that these peaks in photosynthetic
activity roughly corresponded to peaks in the growth rate. In general, annual seaweeds utilize energy produced during a single growing season. It may not be possible for such seaweeds to grow rapidly without high photosynthetic rates.

The estimated photosynthetic rates of upper leaves of *S. horneri* at the monthly mean water temperature and 600 μE m⁻² s⁻¹ in Wakasa Bay (Gao, 1990b) varied from 2–20 ml O₂ g dry wt.⁻¹ h⁻¹ (average 10 ml O₂ g dry wt.⁻¹ h⁻¹) and reached a peak in November, while the maximum photosynthetic rates of upper leaves in this study varied from 13–22 ml O₂ g dry wt.⁻¹ h⁻¹ (average 16 ml O₂ g dry wt.⁻¹ h⁻¹) and reached a peak in March. The mean photosynthetic rates in our study area was 1.6 times greater than in Wakasa Bay, reflecting the larger plant size and high growth speed in our study area. The difference in the peak times of the seasonal changes in the photosynthetic rates at the two localities was probably influenced by changes in nutrient conditions. Seasonal changes in nutrient conditions influence photosynthetic variability and growth in some macroalgae (Chapman and Craigie, 1977; Chapman et al., 1978; Gao, 1990b; Serisawa et al., 2001a). According to Gao (1990b), the highest photosynthetic rate of *S. horneri* in Wakasa Bay occurred during months with high nitrate and phosphate concentrations, ranging from 0.6 to 7.0 μM and from 0.15 to 0.4 μM, respectively. At our study site (Oura Bay), NO₃-N and PO₄-P were high from February to April (8.0 and 0.6 μM, respectively) and low from May to November (2.0 and 0.3 μM, respectively; Serisawa et al., 2001a). Therefore, high nutrient levels in spring may elevate the photosynthetic rate in March. When light and temperature are not limiting factors, nutrient conditions, especially nitrate, constitute a limiting factor for the photosynthetic rate of seagrass and seaweed (Kirk, 1994). Thus, regarding the seasonal changes in the photosynthetic rate based on wet weight observed in this study, the limiting factor may not be light and temperature, but nutrient conditions.

High growth rates and productivity of several *Sargassum* species during periods of low water temperature have been noted (Carpenter and Cox, 1974; De Wreede, 1976). This was also true for *S. horneri* in Shidagaura Cove. It has been reported that the optimum temperature for photosynthetic activity of several macroalgae acclimated to the environmental temperature during a year (Yokohama, 1973; Lee and Brinkhuis, 1988; Gao, 1990b). Although the photosynthesis-temperature curves obtained in short-term experiments (<1 day) indicated a strong influence of temperature (Yokohama, 1973; Gao, 1990b), the results of our study suggest that photosynthetic activity is not strongly influenced by environmental temperature over the long term (>1 month).

The maximum net photosynthetic rates of the upper leaves based on the chl.a content in this study (2.0 and 3.6 μl O₂ μg chl.a⁻¹ h⁻¹) were comparable to those of *Sargassum* patens (2.5 μl O₂ μg chl.a⁻¹ h⁻¹) measured by Gao and Umezaki (1988) and *S. horneri* (1.8–3.5 μl O₂ μg chl.a⁻¹ h⁻¹) by Gao and Umezaki (1988) and Gao (1991). The rates for *Sargassum* species were much higher than those of Ecklonia cava Kjellman (Laminariales, Phaeophyta) (1.0–1.9 μl O₂ μg chl.a⁻¹ h⁻¹, Serisawa et al., 2001b). The maximum net photosynthetic rates based on the chl.a content should be synchronous with the age of the plant.

Temperature, nutrients, and light intensity are factors that affect the growth rate of plants. The seasonal change in the net photosynthetic rates based on wet weight was synchronous with the length and growth rate of the plant, whereas the change based on chl.a content was synchronous with its age. This suggests that photosynthetic rates determined from wet weight measurements reflect external controls. Contrasting estimates of the photosynthetic rate from chl.a measurements may reflect the internal condition (age) of plants.

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Larval and juvenile fish assemblages in surface and subsurface layers of central Sagami Bay, Japan

Masaharu INO1, Masato moteki2, Riou NAGAIWA1, Tadashi MIYAZAKI2, Yoshihiro kurita2 and Hiroshi KONO1

Abstract: Larval and juvenile fish were sampled with a ring net from surface (0–1.5 m) and subsurface (2–5 m) layers of central Sagami Bay, Japan, from November 2002 to October 2003. In all, 15,458 fishes from 100 species and 54 families were collected. The surface layer yielded 2,167 fishes from 58 species, and the subsurface layer produced 13,291 fishes from 67 species. The most abundant species in both layers was Engraulis japonicus, which comprised 57.0% and 85.6% of individuals from the surface and subsurface layers, respectively. A cluster analysis based on fish assemblage similarities revealed that the sampling months were seasonally divided into winter (November to January), spring (March and April), and summer/autumn (June to October). The subsurface in summer/autumn yielded the greatest species diversity (51 species), with neritic-demersal, pelagic, and mesopelagic species being dominant. Of the 15 dominant species occurring in both layers, the distribution of eight appeared to change between surface and subsurface layers as they grew. Based on this and previous studies at other Sagami Bay locations, larval and juvenile fish assemblages appear to vary within the bay, with the surface and subsurface layers of central Sagami Bay dominated by mesopelagic species.

Keywords: Larval and juvenile fish assemblages, Sagami Bay, vertical distribution, seasonal occurrence
これらの研究では、沿岸浅海域では10 mから数十mの間隔で、沖合や外洋では数十mから100 m程度の間隔で採集深度が設定されている。これまで、表層とそのわずかに下の層（表層層）に着目した稚魚群集の比較を行った研究は、内湾やサゴ礁域といった浅海域や河口などで行われている（Leis, 1991；甲原・河野, 1999；鎌ら, 2003）。これらの研究から、数mの深度の差によっても、種や発育段階により鉛直分布様式が異なることが明らかにされ、内湾への浸透様式や稚魚の分散様式に影響を与えることなどが示唆されている。一方で、沖合や外洋域では表層深m程度の鉛直分布様式について明らかにした研究は少ない。本研究では、相模湾中央部の表層域における稚魚絞りとその季節変化について明らかにするとともに、表層層（0～5 m）における稚魚絞りの鉛直的な出現様式を明らかにすることを目的として、表層（0～1.5 m）と亜表層（2～5 m）に限った年間の採集を行った。

Fig. 1. Map showing the study site (★) in Sagami Bay, Japan, where surface and subsurface fish were sampled.

2. 材料と方法

採集は、東京海洋大学研究練習船“鯨龍丸”により、相模湾中央部の定点（Fig. 1: 35°00′ N, 139°20′ E, 深約 1,500 m）において、2002年11月から2003年10月の期間中、月に1回（2002年11月11日, 12月15日, 2003年1月16日, 3月10日, 4月16日, 5月21日, 6月15日, 7月8日, 8月6日, 9月8日, 10月4日）、稚魚ネット（直径1.3 m, 目合330 μm）とORIネット（直径1.6 m, 目合330 μm）による曳網をほぼ同時に行行った。曳網は日中に、船速2ノットで、表層（深度 0～1.5 m）では稚魚ネットを用い、亜表層（2～5 m, 亜表層）はORIネットを用い、船尾で、それぞれ水平曳網を行った。表層での曳網は、ネットが水面から出ないよう行った。亜表層での曳網深度はワイヤー長とワイヤーの傾斜から算出した。ORIネットには閉閉装置を用いていないが、投揚網はできるだけ速やかに行行った。曳網時間は10～15分で、網口に相当水計を取り付け、ろ水量を算出した（平均±標準偏差: 表層765±256 m³, 亜表層88±350 m³）。曳網開始の直前にCTD(Falmouth Scientific, Inc., ICTD)により水温と塩分の観測を行った。ただし、2003年2月はCTD観測のため、採集は行われていない。採集された稚魚絞りは、採集直後に5％海水ホルマリンで固定し、選別、同定の後、70％エチアルコールで保存した。同定は主に沖山（編）（1988）に従い、和名、学名および分類体系は中坊（編）（2000）に従った。体長の計測には、15 mm以上の個体はノギスを用い、それ以下の個体は接眼ミクロメーターを用いた。

稚魚絨毛ホルマリン固定やネット採集時に与えられる刺激により収縮することを広く知られている（Theilacker, 1980; Fox, 1996; Porter et al., 2001）。本研究では、採集からサンプル固定・処理までの過程をできるだけ速やかに行い、収縮の軽減を図った。また、測定は、収縮の進行が十分に停止していると考えられる少なくとも6ヶ月経過したのちに行った（Theilacker, 1980; Fox, 1996）。

3. 結 果

3.1 水温と塩分

水温は2月に最低値（表層13.0℃, 亜表層14.8℃）を、8月に最高値（25.1℃, 24.2℃）を記録した（Fig. 2）。塩分については、亜表層では8月にやや下がるもの（33.3）が、それ以外の月では33.9（6月）から34.7（12月）の間を推移した（Fig. 2）。一方、表層の塩分は大きく変動し、2月、6月および8月で低い値を示した（それぞれ32.3, 33.4, 30.2）。

3.2 出現魚種の概要

採集された稚魚絨毛は、17品54科10種以上15,458個体であった（Table 1）。最も多く採集された種は、カタク
チワシ Engraulis japonicus で、全個体数の72.3%を占めた。次いで多かったのが、マアジ Trachurus japonicus (2.8%)、テングクダイ属Apogon spp. (2.4%)、カサゴ Sebastes marmoratus (1.8%)、テングクダイ Labracoglossa argenticentris (1.2%)であった。

表層で採集された仔稚魚は、43科58種以上2,167個体（未同定種263個体を含む）であった（Table 1）。個体数で最も多かった種はカタクチイワシで、1,235個体（37.0%）が採集された。次いで、カタクチイワシ Lampadena luminosa (2.6%)、テングクダイ属 (2.5%) などが多かった。一方、中層層では、5科37種以上13,291個体（未同定種1,674個体を含む）が採集された。カタクチイワシが最も多く9,942個体が採集され、85.6%を占めた。他にマアジ (3.1%)、テングクダイ属 (2.4%)、カサゴ (1.3%)、スズメダイ Chromis notata notata (0.9%)、ハオホゼ Hypodytes rubripinnis (0.8%) などが多かった。

3.3 種類と個体数の経時変化

種類についてみると、11月から翌年6月まではよく似た経時変化を示したが、8月では、表層層で最大の28種を示したのに対し、表層に出現したのはわずか3種であった（Fig. 3）。個体数では、11月から1月まで表層と亜表層で同様に推移したが、3月から8月までは表層層で多く、表層層では3月に18.5個体の最小値を、8月にも19.7個体を記録した。

3.4 月間の群集組成の類似度に基づくクラスター解析

クラスター解析の結果、類似度0.10で11～1月（冬季）と3～10月の2つのクラスターに分かれた（Fig. 4）。さらに、後者のクラスターは、類似度0.15で3～4月（春季）と6～10月（夏・秋季）に分かれて、それぞれ類似度0.40と0.27でクラスターを形成した。

3.5 成魚の生息場所タイプ別出現状況

成魚の生息場所タイプ別に観ると、表層と亜表層で中深層タイプが多く採集された（Table 2: 2種 vs. 15種）。また、その他のタイプは両層で0～4種の違いしかなかった。

クラスター解析の結果に基づき、1年間を冬、春季および夏・秋季の3季に分けて、生息場所タイプ別出現状況をFig. 5にまとめた。総出現種数は夏・秋季の亜表層層が最も多く、すべてのタイプを合わせて51種が出現した。同じ時期の表層はそれに次いで44種だった。最も少なかったのは春季の表層で、わずか5種が出現した。また春の表層層も8種と少なかった。冬季は表層と亜表層でほぼ同じだった（それぞれ18種と19種）。浅海底生タイプはすべての季節／層で優占した。表層ではいずれの季節も過半数を越えがいた（55.6～80.0%）、亜表層では冬季に過半数を超えたもの（63.2%）、春季と夏・秋季にはやや少なく過半数に達しなかった（それぞれ50%と49%）。中深層タイプは、夏・秋季の亜表層で大きな割合を占めた（29.4%）が、他の季節／層では0～21.1%だった。表層タイプは、表層、亜表層でそれぞれ20.5%（9種）と21.6%（11種）を占めたが、他の季節／層では1～4種ののみ出現した。大規模タイプはいずれの季節／層でも少なく、出現種数は0～2種であった。

3.6 主要種の構成

各季節で個体数が10%以上を占めた種を主要種として、個体数を対象変数log_{10}(x + 1)）としたのち、その組合成をFig. 6に示した。冬季はカサゴ、カタクチイワシ、サギフエMacroramphous scolopax、タカノハダイGoniaspis zonatusなど12種が主要種となっ
た。一方、春季はカタクチイワシとメバルSebastes inermisのみがあり、夏・秋季は、カタクチイワシ、テングクダイ属、マアジ、スズメダイなど9種が主要種となった。

3.7 種ごとの層別出現比と全長構成

1,000 m³当たりの個体数の和が10以上だった31種について、種ごとの層別出現比を検討した（Fig. 7）。表層のみに出現したのは3種（9.7%）、表層と亜表層の両層に出現したのは20種（64.5%）、亜表層のみに出現したのは8種（25.8%）だった。

さらに、両層に出現した20種のうち、30個体以上出現した種については全長群別を検討した（Fig. 8）。全長のモードが亜表層より表層で大きい種は、カタクチイワシ
Table 1. Larval and juvenile fishes collected from central Sagami Bay, Japan, from November 2002 to October 2003.

<table>
<thead>
<tr>
<th>Family/Order</th>
<th>Species</th>
<th>Number of individuals</th>
<th>Month</th>
<th>Size range (TL, mm)</th>
<th>Adult habitat type</th>
<th>Species code</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Surface</td>
<td>Subsurface</td>
<td>Total</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anguilliformes</td>
<td>Anguilliformes sp.</td>
<td>1</td>
<td>3</td>
<td>3</td>
<td>Aug</td>
<td>4.1-4.6</td>
</tr>
<tr>
<td>Engraulidae</td>
<td>Engraulis japonicus</td>
<td>1235</td>
<td>9942</td>
<td>11177</td>
<td>Dec-Oct</td>
<td>2.7-27.7</td>
</tr>
<tr>
<td>Gonorynchidae</td>
<td>Gonorynchus abbreviatus</td>
<td>76</td>
<td>76</td>
<td>76</td>
<td>Oct</td>
<td>7.1-20.9</td>
</tr>
</tbody>
</table>
| Gonostomatidae | Cyclopterus ab 
sp.                        | 2         | 2          | 2     | Oct                | 6.1-7.4           | M             |
|                | Cyclopterus pseudopalid 
alla                     | 1         | 1          | 1     | Jan                | 21.1              |              |
|                | Cyclopterus sp.1                              | 31        | 33         | 64    | Dec,Jun-Oct        | 3.1-13.0          | M             |
|                | Cyclopterus sp.2                              | 1         | 1          | 1     | Dec                | 5.3               | M Cy         |
| Stomidae       | Stomias affinis                              | 1         | 1          | 1     | Aug                | 3.9               | M             |
| Astronesthesida| Astronesthes sp.                             | 1         | 1          | 1     | Nov                | 7.8               | M             |
| Synodontidae   | Synodontida sp.                              | 31        | 31         | 62    | Aug                | 2.1-5.9           | N Sa          |
| Myctophidae    | Diaphus sp.                                  | 3         | 3          | 3     | Aug                | 5.2-9.8           | M             |
|                | Hygophum proximum                           | 6         | 6          | 12    | Aug                | 4.2-5.8           | M             |
|                | Lampadula luminosa                           | 57        | 57         | 114   | Oct                | 2.8-4.9           | M             |
|                | Lampadula sp.1                               | 7         | 7          | 14    | Jun                | 9.1               | M             |
|                | Lampadula sp.2                               | 1         | 1          | 1     | Oct                | 3.2-4.9           | M             |
|                | Nannobrachium sp.1                           | 1         | 1          | 1     | Dec                | 2.7-3.6           | M             |
|                | Nannobrachium sp.2                           | 7         | 7          | 14    | Dec                | 3.8-4.3           | M Na          |
|                | Nannobrachium sp.3                           | 6         | 6          | 12    | Aug                | 7                 | M             |
| Triphoturis microchir |                           | 1         | 1          | 1     | Oct                | 6.3               | M             |
|                | Myctophidae sp.                              | 1         | 1          | 1     | Oct                | 6.3               | P             |
| Trachipteridae | Desmodema sp.                                | 1         | 1          | 1     | Oct                | 6.3               | P             |
| Ophididae      | Stremno imberbis                             | 1         | 1          | 1     | Oct                | 6                 | N             |
| Gigantactinida | Gigantactinida sp.                           | 2         | 1          | 3     | Jun,Oct            | 3.0-3.3           | M             |
| Holocentridae  | Myripristis sp.                              | 2         | 2          | 4     | Oct                | 3.2-4.4           | N             |
| Macroramphosida| Macroramphosida sp.                          | 25        | 6          | 31    | Nov,Mar            | 4.2-7.7           | C Ma          |
| Syngnathidae   | Syngnathus schlegeli                         | 1         | 1          | 1     | Mar                | 9.2               | N             |
| Mugilidae      | Mugil cephalus cephalus                      | 2         | 2          | 4     | Nov                | 5.6-6.0           | N             |
| Exocoetidae    | Parellicthys brachypterus                    | 1         | 1          | 1     | Jun                | 6.1               | P             |
|                | Cololabroscia coarct 
ata                    | 9         | 1          | 10    | Dec-Jan            | 5.4-9.1           | P Co          |
| Scombresocida  | Helicolenus hilgendorfis                     | 1         | 1          | 1     | Dec                | 3.2               | N             |
| Scorpaenidae   | Sebastus marmoratus                          | 94        | 178        | 272   | Dec-Jan            | 2.2-8.2           | N Sm          |
|                | Sebastus hubsi                               | 1         | 1          | 1     | Dec                | 4.4-6.6           | N             |
|                | Sebastus inermis                             | 12        | 20         | 32    | Jan-Mar            | 4.2-6.9           | N Si          |
|                | Sebastus vulpes                              | 5         | 5          | 10    | Mar                | 3.1-3.5           | N             |
|                | Scorpaenidae sp.1                            | 1         | 1          | 1     | Dec                | 1.8               |              |
|                | Scorpaenidae sp.2                            | 1         | 1          | 1     | Jan                | 4.8               |              |
|                | Scorpaenidae sp.3                            | 1         | 1          | 1     | Aug                | 3.3               |              |
|                | Scorpaenidae sp.4                            | 1         | 1          | 1     | Oct                | 8.6               |              |
|                | Scorpaeniformes sp.                          | 1         | 1          | 1     | Aug                | 3.7               |              |
| Scorpaeniformes| Hypodytes rubripinnis                        | 4         | 105        | 109   | Apr-Aug            | 1.7-4.2           | N             |
| Tetarogidae    | Lepidotrigla sp.                             | 14        | 14         | 28    | Aug                | 1.5-3.2           | N             |
| Triglidae      | Platyepterus sp.                             | 45        | 45         | 90    | Jun-Aug            | 1.7-5.6           | N             |
| Platyepterus   | Leptotremus awae                             | 3         | 3          | 6     | Oct                | 7.7-12.1          | N             |
| Cyclopteridae  | Liparis tanakai                              | 1         | 1          | 1     | Jan                | 13                | C             |
| Liparidae      | Lateolabrax sp.                              | 3         | 12         | 15    | Dec-Mar            | 2.2-6.1           | N Lat         |
| Moronidae      | Sarcaea maragatae                            | 1         | 1          | 1     | Dec                | 4.6               | N             |
| Serranidae     | Agononida sp.                                | 54        | 313        | 367   | Aug-Oct            | 2.1-10.5          | N Ap          |
| Agononidae     | Scombrops boops                              | 1         | 1          | 1     | Jan                | 5.4               | N             |
| Scombropidae   | Coryphaena hippurus                          | 1         | 1          | 1     | Oct                | 13.4              | P             |
| Coryphaenidae  | Decapterus sp.1                              | 1         | 1          | 1     | Jan                | 11                | P             |
| Carangidae     | Decapterus sp.2                              | 1         | 1          | 1     | Jun                | 8.2               | P             |
|                | Seriola lalandi                              | 1         | 1          | 1     | Nov                | 3.9               | P             |
|                | Seriola quinquergad 
ata                    | 5         | 24         | 29    | Apr-Aug            | 2.3-50.3          | P              |
|                | Seriola rivoliana                            | 1         | 1          | 1     | Oct                | 7.5               | P             |
|                | Trachurus japonicus                          | 13        | 418        | 431   | Jun-Oct            | 2.8-6.1           | P Tr          |
|                | Carangidae sp.1                              | 1         | 1          | 1     | Aug                | 3.7               | P             |
|                | Carangidae sp.2                              | 1         | 1          | 1     | Oct                | 8.2               | P             |
|                | Carangidae sp.3                              | 1         | 1          | 1     | Oct                | 5.5               | P             |
|                | Emmelichthys struhsaheri                     | 1         | 1          | 1     | Aug                | 3.7               | P             |
| Emmelichthidae| Parapristipoma trifineatus                   | 1         | 1          | 1     | Jun                | 3                 | N             |
| Haemulidae     | Stilgo japonica                              | 1         | 1          | 1     | Oct                | 7.1-10.0          | N             |
| Sillaginidae   | Upenes japonicus                             | 19        | 19         | 38    | Aug-Oct            | 6.5-14.3          | N             |
| Mullidae       | Chaetodontolus septentrionalis               | 1         | 1          | 1     | Oct                | 8.5               | N             |
| Pomacentridae  | Gonistius zonatus                            | 29        | 10         | 39    | Nov-Jan            | 2.1-7.5           | N Gz          |
| Cheilodactylida| Abudesfufy vaigenis                          | 4         | 4          | 8     | Oct                | 9.1-14.9          | N             |
| Pomacentridae  | Chromis notata notata                       | 4         | 117        | 121   | Aug-Oct            | 2.6-11.8          | N Ch          |
相模湾中央部の表層・亜表層の仔稚魚相

Tabla 2. Number of species of larval and juvenile fishes from surface and subsurface layers in central Sagami Bay, Japan, by each adult habitat type

| Adult habitat type    | Number of species |  |
|-----------------------|-------------------|
|                       | Surface | Subsurface |
| Neritic-demersal      | 37      | 33         |
| Continental slope     | 2       | 1          |
| Pelagic               | 12      | 12         |
| Mesopelagic           | 6       | 15         |

Fig. 3. Monthly changes in numbers of species and individuals of larval and juvenile fishes collected from surface (open circles and squares) and subsurface (solid circles and squares) layers in central Sagami Bay, Japan, from November 2002 to October 2003.

4. 考察
4.1 相模湾中央部の仔稚魚組成の特徴
本研究の結果を基に、三浦半島の西部沿岸において稚魚ネット
Fig. 4. Dendrogram of sampling months, based on the Bray-Curtis similarity coefficient, for larval and juvenile fish assemblages in central Sagami Bay. Data from surface and subsurface layers were combined for the analysis.

Fig. 5. Fish species numbers by adult habitat type in each season (Winter, November to January; Spring, March and April; Summer/Autumn, June to October). C, continental slope; M, mesopelagic; N, neritic-demersal; P, pelagic.
相模湾中央部の表層・亜表層の仔稚魚相

Fig. 6. Seasonal species assemblages (Winter, November to January; Spring, March and April; Summer/Autumn, June to October) in central Sagami Bay, Japan. Surface and subsurface layer data are combined. Species comprising >0.5% of the total number of individuals are shown. Percentages are based on the number of individuals per 1,000m³. See Table 1 for species codes.

(服部，1964; 松田, 1969; 千田, 1962a) は、本研究でも個人数で主種となっている。一方で、内湾や沿岸の主要種であるアミメハギ、メバル、カサゴ、サメヌメイ、スズキ属 Lateolabrax spp.（森, 1995; 加納ら, 2002）なども多く採集されていることから、相模湾中央部の仔稚魚相は、外洋的な要素と内湾/沿岸的な要素を併せ持っているものと考えられる。

本研究では、8月の標層を除くと、個体数・種数の経月変化は、冬と夏で個体数が少ないものの両側で比較的類似した様式を示した。両層は水温や塩分においては概ね均質な環境にあるが、2月と8月の表層で塩分が低い（2月は採集が行われていない）。したがって8月の表層において個体数・種数が極端に少ないのは、表層での一時的な塩分の低下による影響を受けるものと考えられる。採集を行った海域は、特に黒潮系沖合水の影響を受ける場所と考えられる（古岡, 2004）が、相模湾湾部に相模川や酒呑川といった大きな河川があり、集中的な降雨による河川水の流入が、表層に分布する仔稚魚へ与える影響は広範囲に及ぶことが示唆される。

4.2 中深層性魚類仔稚魚の出現

本研究と同じ地点において、MTDネットを用いて仔稚魚の鉛直分布の研究を行った Sassa and Kawaguchi (2006) では、昼夜ともに表層（0 m）では中深層性魚類の仔稚魚はほとんど採集されていない。この研究では、表層の次に深い採集深度は25mとなっているため、水平曳きを行うMTDネットによる採集では、理論的にはネットとネットの間となる1〜24 m層に分布する仔稚魚は採集されない。本研究で得られた中深層性魚類の仔稚魚は、カガミワシを除いてSassa and Kawaguchi (2006) では得られていないが、少なくとも0〜5 m付近、特に中種の中深層性魚類の仔稚魚が出現する2〜5 m層は、一部の中深層性の種にとっては重要な生息場所となっている可能性がある。外洋域（北太平洋）において鉛直分布の研究を行ったKoizumi (1980) では、出現した中深層性魚類24種のうち14種が0〜25 m層で採集され、そのうちオニハダカ属Cyclothone sp.など3種については、全個体数の65〜82%が0〜25 m層から採集されている。また、Sassa et al. (2002) は黒潮を横断する海域で研究を行い、ハダカワシ科魚類のうちトンガリハダカ亜科 Lampaniinaeの仔稚魚は0〜30 m層に多く出現し、ハダカワシ亜科Myctophinaeでは50〜150 m層に出現することが示している。本研究では、ハダカワシ亜科のツマリドリグリハダカ Hygophum proximumが6個体採集されているものの、696個体はトンガリハダカ亜科に含まれ、これはSassa et al. (2002) の結果とは一致する。

4.3 表層と亜表層の仔稚魚組成の比較

表層と亜表層では、亜表層の方が種数も個体数も多い出現している。また、表層より亜表層のみに出現する種の方が多く、さらに、各層の出現比が80%以上を占めた種は、表層と亜表層でそれぞれ5種（16.1%）と10種（51.6%）であった（Fig. 7）。また、季節ごとに出現種数で見たときには、表層と亜表層では仔稚魚にとっての重要性はあまり変わらないが、夏・秋季の亜表層では、中深層タイプの種が表層よりも多く出現している（Fig. 5）。

これまで国内沿岸で行われた鉛直分布についての研究では、表層より深層は10 mに設定されているが（山本, 1963; IDA, 1972; 中田・今井, 1981; 今本ら, 1997), この10mを本研究の亜表層とみなした場合、それらの研究でも亜表層に個体数が多い。ただし、大阪湾の6定点で鉛直分布を調査した研究（今本ら, 1997）によると、浅い水域（水深20 m以下）では、亜表層より表層で個体数が多いことが指摘されている。このことは東京湾の湾奥浅海帯で行われた研究でも示されており、表層（0〜1.5 m）の方が亜表層（5〜10 m）より個体数も種数も多く出現している（甲原・河野, 1999）。

4.4 成長に伴う生息深度の変化

両層に多く出現した15種のうち8種において、成長に伴う生息深度の変化が認められた。このような現象はいくつかの種ではよく知られているが（IDA, 1972; 中田・今井, 1981; 桑原・鈴木, 1984; Grönkjer and Wieland, 1997; Nagasawa et al., 2000）わずか数mの深度でも生息層を変化させる種が比較的多いことを示している。
いくつかの主要種について、以下に既往の文献との比較を行った。

カサゴ 若狭湾での研究（桑原・鈴木, 1983）では、カサゴ仔魚は表層（0 m）付近に多くものので、25 m付近まで分布することが明らかにされている。しかし本研究では、表層と亜表層とを比較するとほぼ同程度の密度で分布しており、0 ～ 5 m程度の範囲で密度はあまり変わらないことが示唆される。また、表層と25 m層に出現する個体の体長組成を比較したところ差異は認められておらず（桑原・鈴木, 1983）、この点については今後研究と一致している。

メバル メバルでは表層に小型の個体が多く、着底に伴い深い海面に移動することが知られているが（体長約10 mm以下）（NAGASAWA et al., 2000）、本研究で得られた小さいサイズ（全長4.2～6.9 mm）では生息層を変化させないと考えられる。

サバ属 本州中部の太平洋側で研究を行ったIDA（1972）によると、サバ属は、表層と深層10 mで比較した場合小型の仔魚（全長モード3.0～4.5 mm）が10 m付近に多く、やや大きな個体（3.5～5.0 mm）が表層で多く採集されている。一方本研究では、サバ属は表層ではあまり採集されず亜表層（2 ～ 5 m）で多く採集されており、相模湾中央部におけるサバ属の生息深度の変化は深度0 ～ 5 mでは不明瞭となっている。また東京湾の表層では、サバ属は湾内で多く採集されているが湾口部近傍ではあまり採集されていない（長原ら, 2005）。これらのことから、水域によって鉛直分布の様式が異なる可能性も示唆される。

アカカマス 本種は、本研究では表層と亜表層で同程度の密度で分布していたが、若狭湾（桑原・鈴木, 1982）では表層（0 m）付近でのみ採集され、25 mでは全く採集されていない。本種は、少なくとも深度0 mから5 m付近まで分布し、その層の間に成長を伴い表層から亜表層へ分布の中心を変えるものと考えられる。

スズメダイとアミメハギ 成長に伴い生息層を変化させる種の中には、両層に出現するサイズの幅が大きい種も多いが、スズメダイとアミメハギでは、まったくサイズレンジが重ならない。この2種では、表層で採集されているのはやや大きな個体で個体数も少ない。この2種はある時期に流れ漂に付随して生活することが知られ（広崎, 1963：井田, 1966）、本研究で採取された大型の個体は何らかの漂流物に付随していたものか採取されたものと考えられる。

5. 結 論

相模湾中央部の仔稚魚の種組成から判断すると河川の効果と内湾／沿岸的な要因を塩分して考えられる。また、中深層性魚種の仔稚魚の出現において、周辺水域の仔稚魚相と比較して特徴的であり、特に亜表層は、中深層性魚種の一部の種にとっては重要な

Fig. 7. Distribution ratio of larval and juvenile fish species per 1,000 m$^2$ of surface and sub-surface layers in central Sagami Bay, Japan. Species with >10 individuals sampled are shown.
生息場所となっている可能性がある。相模湾では、表層
～亜表層（深度 0 ～5 m）に中深層魚類の仔稚魚が比
較的多く出現することは、これまであまり知られていな
かった。

種ごとの出現比や出現種数では、表層の方が表層より
よりも様々な仔稚魚の生息場所としての重要性が高いと考え
られるが、一方で、わずかな深度の違いでも、成長に
伴い生息場を変化させる種が比較的多いことも明らかと
なった。このような表層と亜表層における出現様式の違
いや移動が、どのような要因によってもたらされるのかは
明らかではないが、餌生物の分布や密度などの関連を
検討する必要があると思われる（Blaber and
Blaber, 1980; Sherman et al., 1984; Boerhelt
and Morgan, 1985; 中田・岡崎, 1999）。

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Fishery biology of *Loligo edulis* in Moroiso Bay, Kanagawa Prefecture, Japan

Natinee Sukramongkol, Kotaro Tsuchiya, Tadashi Tokai, and Susumu Segawa

**Abstract:** The swordtip squid, *Loligo edulis* Hoyle, 1885 was collected from set-net fishery in Moroiso Bay, Miura Peninsular, Kanagawa Prefecture, Japan, during April 2002 and September 2003. A total of 2,127 individuals (1,146 males and 981 females) from the mantle length between 33 and 213 mm were examined. The maturation, reproductive cycles and spawning period were determined for both sexes. Age and growth were analyzed from statolith increments and hatching date was estimated by the back calculation. Statoliths of 350 males (35–187 mm mantle length) and 232 females (39–213 mm mantle length) were examined. The estimated age ranged from 79 to 298 days for male and 83 to 277 days for female. The hatching dates were estimated to be from May 2002 to April 2003. The spawning season occurred throughout the year and the main spawning period took place between June and August. Exponential growth model was used to describe the relationship of mantle length and the estimated age of hatching month group.

**Keywords:** *Loligo edulis*, fishery biology, age, hatching dates, maturation

1. Introduction

*Loligo edulis* (Hoyle, 1885) is a neritic loliginid squid distributed over the Indo-West Pacific region from central Japan to South China Sea, and northern Australia (Roper et al., 1984; Carpenter and Niem, 1998). In the southern parts of Japan Sea, the landing of *L. edulis*, caught mainly by jigging, set-net and bottom trawls, fluctuated throughout the year (Natsukari and Tashiro, 1991).

Studies on fishery biology of *L. edulis* were conducted under two major research projects in the western Japanese waters (Seikai Reg. Fish. Res. Lab. et al., 1978; Yamaguchi Pref. Open Sea Fish. Exp. St. et al., 1983 and 1986). The life cycle of *L. edulis* was estimated to be one year based on the validated statolith increments and the spawning season extended throughout the year from the information of the degree of maturity and the size of this species (Tashiro, 1977; Natsukari et al., 1988). Wide variation in growth rates and existence of seasonal forms were reported on *L. edulis* in the western coast of Japanese waters (Ogawa et al., 1983; Yamada et al., 1986; Natsukari et al., 1988).

In Tokyo Bay and Sagami Bay, monthly change of the catches of the commercially important squids was reported based on the data of the landings for six years from 1984 to 1990 (Kuboshima, 1992). Landing of *L. edulis* from set-net fisheries in the east coast of Sagami Bay is throughout the year and the monthly catches had a peak between January and February (Kuboshima, 1992). Although *L. edulis* is an important species for the fisheries in Miura Peninsula, Kanagawa Prefecture, there have been little information about the aspects of fisheries biology in this area, such as growth, maturation and reproduction. In the present paper, study of the fishery biology on maturity, age and growth of *L. edulis* were carried out based on the monthly specimens through a year collected from the set-net.
fishery in Moroiso Bay located at the tip of Miura Peninsula.

2. Materials and methods

Specimens of *L. edulis* used in the present study were collected once a month from April 2002 to September 2003 from set-net in Moroiso Bay. After removal of statoliths for age determination, specimens were initially fixed with 10% formalin and preserved in 40% isopropyl alcohol (*Roper* and *Sweeney*, 1983). Specimens were dissected to determine sex and maturity stages. Dorsal mantle length (ML in mm), nidamental gland length (NGL in mm), and testis length (TL in mm) were measured with a digital caliper to the nearest 0.1 mm. The total body weight (BW in g) was measured to the nearest 0.1 g with a digital balance. A total number of 2,127 individuals of *L. edulis* with mantle length ranged from 33 to 187 mm (n=1,146) and 36 to 213 mm (n=981) for male and female, respectively, were examined.

Sex ratio (F/M) was analyzed monthly and significant differences between the calculation ratio and the expected ratio 1:1 (female: male) were tested using the Chi-Square test.

Since the sexual maturity stages were determined based on the definition of stages I to VI of *Lipinski* and *Underhill* (1995), in the present study stages I and II were defined as immature stage, stage III as maturing stage, stages IV and V as mature stage, and stage VI as spent.

Testis length index for males and nidamental gland length index for females were expressed as follows:

Testis length index (TLI) = (Testis length/Mantle length) × 100,

Nidamental gland length index (NGLI) = (Nidamental gland length/Mantle length) × 100.

Monthly mean value of maturity index (TLI and NGLI) was used for an index to determine the size of maturity and seasonal change of the size in maturity.

The relationship between the mantle length (ML in mm) and total body weight (BW in g) was expressed as $BW = aML^{b}$, where $a$ and $b$ are constants, which was fitted by the least-squares linear regression of log transformed variables. The effect of sex on exponent $b$ of the ML-BW relationships was investigated using a test for homogeneity of slopes (ANCOVA).

For age determination specimens were randomly selected from the samples collected between October 2002 and September 2003 and if the specimens of any sampling months were less than 30 individuals, all the specimens were used. Statoliths from a total of 350 males (ML ranged from 35 to 187 mm) and 232 females (ML ranges from 39 to 213 mm) were readable and used for the age estimation.

Paired statoliths were dissected from fresh specimens following the method of *Dawe* and *Natsukari* (1991). The right statolith was used for counting increments and the left one was kept in reserve. Statoliths were mounted on microscopic slides in Eukitt™ mounting reagent (*Sigma-Aldrich Inc.* ) and allowed to dry for 1 week. Ground and polished statoliths were made with abrasive waterproof paper and 3M rubbing film. Statolith increments were observed under an optical microscope (×400) and images were taken for increment analyses. Counting the increments was made from the natal ring (*Natsukari et al.*, 1988) to the edge of the rostrum (Fig.1). To estimate the degree of counting error (t-test) the increments on the same statolith were counted twice for 20 statoliths and no significant difference ($p>0.05$) was detected between the first and the second count for the same statolith.

Since the daily deposition of statolith increments has been validated in a number of loliginid species (*Jackson*, 1990; *Rodhouse* and *Hatfield*, 1990; *Jackson*, 1994; *Lipinski et al.*, 1998) including *L. edulis* (*Natsukari et al.*, 1988), age in the present study was estimated relying on the assumption that the increments of *L. edulis* formed daily. Date of hatching was estimated by the back-calculation departing from the date of the capture. Spawning time was estimated to be one month before hatching based on the embryonic studies of *Natsukari* and *Tashiro* (1991).

Since the asymptotic growth models has been demonstrated not relevant to describe cephalopod growth (*Alford* and *Jackson*, 1993; *Jackson et al.*, 2000) and the recent extensive studies of myopsid squid growth of the family.
Loliginidae using statolith ageing techniques have been revealed a short lifespan less than and/or about 1 year (*Loligo chinensis*, Jackson and Choat, 1992; *L. vulgaris*, Natukari and Komine, 1992; *L. pealei*, Brodzia and Macy, 1996). The non-asymptotic growth models, included linear, exponential and power curves have been applied in many studies (*L. vulgaris*, Rocha and Guerra, 1999; *L. gahi*, Hatfield, 2000; *L. plei*, Jackson and Forsythe, 2002; *L. forbesi*, Challier et al., 2006). In the present study the exponential curve was chosen to describe the growth of *L. edulis* because the exponential functions can describe growth over the life cycle including the embryonic phase of loliginid squids (Forsythe and Hanlon, 1989; Hanlon et al., 1989) not because of the fitting growth models give a better correlation coefficients (Challier et al., 2006).

Squid hatched in the same month was grouped together to analyze the hatching season and growth. To calculate the growth curves the value of 2.0 mm in ML was assigned for the size of hatchlings of *L. edulis* (Natukari and Tashiro, 1991). The exponential equation, $ML = 2.0e^a$ was applied to the relationship between the estimated age (t in days) and mantle length (ML in mm); where a is constant.

The statistic analysis for their residual sum of squares and the corresponding mean error using the dummy-variable approach (Quinn and Keough, 2002) on the relationships between estimated age and mantle length in each hatching month group by sex. All statistical analyses were conducted with a 0.05 significant level.

3. Results

3.1 Size composition

The minimum ML was 33 mm for male and 36 mm for female both captured in April 2002 and the maximum was 187 and 213 mm ML for male captured in March and female in June 2003, respectively (Fig.2). Small squid less than 45 mm ML occurred in April-May and September-November. Larger individuals over 130 mm ML were collected during May-June, August 2002 and January, and March to September 2003 (Fig.2). There was a tendency that
the main mode of the length distribution increased from April (45–55 mm ML) to August 2002 (95–105 mm ML), slightly increased (45–75 mm ML) during a period from September 2002 to January 2003, and main mode shifted to relatively larger size (larger than 100 mm ML) from May to August, 2003 (Fig.2).

The equations relating the body weight to mantle length of males and females were expressed as \( BW = 0.00037ML^{1.25} \) (\( r^2 = 0.99 \), \( n = 615 \),...
Table 1 Summary of size range in mantle length and maturity indices of testis length index (TLI) and nidamental gland length index (NGLI) of each stage from I to V for males and females Loligo edulis

<table>
<thead>
<tr>
<th>*Maturity stages</th>
<th>Male</th>
<th></th>
<th>Female</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>Mantle length</td>
<td>Testis length index</td>
<td>n</td>
</tr>
<tr>
<td></td>
<td></td>
<td>min</td>
<td>max</td>
<td>mean</td>
</tr>
<tr>
<td>I</td>
<td>63</td>
<td>35</td>
<td>77</td>
<td>55.9</td>
</tr>
<tr>
<td>II</td>
<td>163</td>
<td>33</td>
<td>120</td>
<td>70.8</td>
</tr>
<tr>
<td>III</td>
<td>79</td>
<td>63</td>
<td>141</td>
<td>104.3</td>
</tr>
<tr>
<td>IV</td>
<td>34</td>
<td>98</td>
<td>181</td>
<td>135.6</td>
</tr>
<tr>
<td>V</td>
<td>12</td>
<td>131</td>
<td>187</td>
<td>155.7</td>
</tr>
</tbody>
</table>

*stage I and II are defined as immature, stage III as maturing and stage IV and V as mature stages, respectively.

33–187 mm in ML) and BW= 0.00036ML\(^{2.54}\) (\(r^2 = 0.98, n = 526, 36–213 mm in ML), respectively. There was no significant difference in the exponent \(b\) between males and females (F=0.41, d.f. 1,1137, p>0.05).

3.2 Sex ratio

Monthly sex ratio (F/M) varied from 0.5 in August (2002) to 1.5 in July (2002) with a mean \(\pm\) SD of 0.9 \(\pm\) 0.3. Although males were more numerous than females over the entire sampling period, seasonal variation of sex ratio was not significantly different from 1.0 (p >0.05) except in August 2002 and February 2003 (p<0.05), with significantly outnumbered male at the ratio of 0.5 and 0.7.

3.3 Maturation stages and size

Immature squid (stage I and II) were predominant in both sexes (Table 1). The maximum size of immature male and female was 120 and 134 mm ML, respectively, both captured in January. The minimum size of maturing (stage III) male was 63 mm ML captured in October and that of female was 85 mm ML captured in June. Length distribution in each maturity stage overlapped each other especially among maturing (stage III) and matured (stage IV) stages (Table 1). The mean size of mature squid (Stage IV and V) ranged from 135.6 to 155.7 and 139.5 to 177.8 for males and females, respectively. The minimum size of mature males (stage IV) was 98 mm ML captured in June and females of 95 mm ML captured in November. Males larger than 141 mm ML and females larger than 177 mm ML were all matured (Table 1).

Testis length index increased with increase in ML and majority of the males larger than about 120 mm ML were matured with the index of 35–44 % (Fig.3). In females nidamental gland length index of stages I, II and III was relatively constant around 10 % regardless the ML of less than about 180 mm ML and that of the matured females larger than about 110 mm ML was increased more than 20% (Fig.3).

Seasonal change in maturation

The seasonal changes of the proportion of the number of each maturity stage indicated that maturing and mature squid increased from May to August in both sexes they often held a highest proportion in August, they abruptly decrease after September 2002 (Fig.4). Although a large proportion of matured males appeared also in March 2003, number of maturing and mature female was very small from September to March (Fig.4).

Seasonal changes in testis length index of males and nidamental gland length index of females showed a main peak in August 2002 in both sexes with a secondary peak only for males in March 2003 (Fig.5). These results indicated that the main maturation period for L. edulis in Miura Peninsula was estimated to be June to August with a secondary maturation peak in March only for males. However, small number of maturing and mature individuals was appeared all through the study period (Fig.5).
Fig. 3. Relationship between mantle length and maturity index for males and females *Loligo edulis* from April 2002 to September 2003.

Fig. 4. Percentage of immature, maturing, and mature individuals of *Loligo edulis* for males and females from April 2002 to May 2003.
3.4 Age and hatching date

Age of *L. edulis* estimated from the number of increments of statoliths ranged from 79 days (42 mm ML) to 298 days (144 mm ML) for males and 83 days (39 mm ML) to 277 days (128 mm ML) for females. Most of the estimated ages of squid collected in October to December 2002 were relatively young within a range from 80 to 170 days (Fig.6). Although most of the squid collected from January to May was older than previous month, there was no clear tendency of the monthly change in age structure (Fig.6). The number of specimens from June to September was small, but the range of the estimated age was wide and older in range from 125 to 298 days. The mean age ±SD in each month ranged from 126.1 ± 16.4 (October 2002) to 255.0 ± 26.1 (August 2003) for male and from 130.4 ± 29.6 (October 2002) to 220.0 ± 52.4 (August 2003) for female.

Based on the back calculation for the hatching dates of specimens from October 2002 to September 2003, the squid were hatched from May 2002 to May 2003 for males and May 2002 to April 2003 for females (Fig.7). For males, mode of the hatching month shifted monthly from May-July hatching (in October sampling month) to December-May hatching (in February sampling month) (Fig.7). That of females also showed the similar tendency with males (Fig.7). The result that the monthly age structure of collected specimens indicated no typical seasonal changes (Fig.6), also confirmed the continuous recruitment of young squid of the similar ages older than 3 months after hatching in the area (Fig.7).

Although the size at estimated age of the squid varied wide, there was a tendency that mantle length increased with increase in age and the relationships between ML and estimated age (t in days) in each hatching month from May 2002 to February 2003 were expressed by exponential curves with growth coefficient ranging from 0.020 to 0.026 (Fig.8). The value of the squid hatched in June 2002 was 0.026 and it decreased to the minimum value of 0.020 in October to November and February 2003 (Fig.9). There was no significant different in the relationship between ML and estimated age between males and female of each hatching month from May 2002 to February 2003 (F=35.4, d.f. 11,538, p=0.967).

3.5 Spawning and recruitment period

Main spawning season of the population in Moroiso area was estimated from June to August based on the results of maturation stages and reproductive organ length indices (Fig.4 and 5). Spawned eggs in the area will hatch after one month from July to September. *L. edulis* hatching at main spawning season in the area will recruit and captured by set-net in Moroiso Bay during a period from November to February from 3 to 6 months after hatching (Fig.7).

Although the proportion of matured
Fig. 6. Monthly estimated age frequency distribution of *Loligo edulis* collected from October 2002 to September 2003.

Fig. 7. Monthly distribution of hatching dates of each sampling month from October 2002 to September 2003 of *Loligo edulis* males and females.
individuals was very small, the secondary spawning season was estimated to be from January to April (Fig.4 and 5) and would be hatched between February and May, which would be recruited to the fishery ground and landed from June to October (Fig.8) even though the amount was very small.

4. Discussion

In Kyushu and southwestern coast of the Japan Sea, *L. edulis* was an important fisheries resource and catches was fluctuate from May to December with two peaks during June-July and October-November (FURUTA, 1978; OKAJIMA et al., 1983). In contrast with the Japan Sea coast, annual catches on the coast of Sagami Bay and Tokyo Bay were reported relatively small with two peaks in January and March, respectively. And a lower peak existed during November-December which was the same period to the east coast of Sagami Bay and Tokyo Bay (KUBOSHIMA, 1992). In the present study, adult and young *L. edulis* occurred throughout the year which was similar to the description of KUBOSHIMA (1992) in the east coast of Sagami Bay.

There was no significant difference in the relationship between mantle length and body weight among sexes of *L. edulis* in Moroiso. The relative growth coefficients from the power equation (exponent b) of the relationship between ML-BW have been reported varies with seasons and locations from the east China Sea to Hyogo Prefecture region over a range of 1.8–2.2 and 1.7–2.4 for males and females, respectively (YAMADA et al., 1983). The exponent of 2.53 for male and 2.54 for female of this study in Pacific coast took a little higher value compare with those at the western Japan Sea.

The minimum size of fully matured specimens in the present study was 98 mm and 95 mm ML for male and female, respectively, which were larger than that of 70–80 mm ML in male and smaller than that of 110–120 mm in female reported in Nagasaki Prefecture (TASHIRO, 1977; SEIKAI Reg. Fish. Res. Lab. et al., 1978). CHOTIYAPUTTA (1994) reported that “*L. edulis* sub sp.” matured at a size of 30 mm ML in the Gulf of Thailand. The degree of maturity and size of squids has a great variation according to season and locality (JACKSON, 1993) especially for tropical loliginid squids such as *L. chinensis* and *L. duvauceli* in Thai waters (CHOTIYAPUTTA, 1994).

In Moroiso Bay, matured individuals occurred throughout the year and the main maturation period was estimated to be June to August with a secondary maturation peak in March only for males based on the maturity index and back calculated hatching date. On the coast of Kyushu the spawning season of the species extends throughout the year (SEIKAI Reg. Fish. Res. Lab. et al., 1978) but in the north or east it tends to become shorter (NATSUKARI and TASHIRO, 1991). In the northern area of Yamaguchi and Hyogo Prefectures, the spawning period of the species was shorter with three main spawning periods in spring, summer and autumn (YAMADA et al., 1983). Because Moroiso is located nearly the northern limit for this species in the Pacific coast (NATSUKARI and TASHIRO, 1991), the main spawning season in the present study was limited in shorter period from June to August and the number of matured squid in other season was very small especially in females.

The estimated hatching dates for *L. edulis* in the present study revealed the seasonal change of the hatching and growth in each hatching month for the monthly collected specimens. The squid caught from April to June hatched mainly from September to February. The seasonal change of the growth coefficient a in present study suggested the difference in growth rates of *L. edulis* in different hatching months or seasons in Moroiso Bay. The environmental conditions such as temperature and food availability were suggested to be the main factors affecting the growth of the seasonal groups of squid (COELHO and O’DOR, 1993). Based on the analysis of seasonal samples of tropical loliginid squid, JACKSON and CHOTA (1992) also pointed out that there was considerable seasonal variation in growth. To analyze the growth of *L. edulis* the further study will be needed in relation with environmental factors and maturity condition of the squids.

The life span of *L. edulis* was reported to be 1 year (TASHIRO, 1977; SEIKAI Reg. Fish. Res. Lab. et al., 1978) and that was supported by...
Fig. 8. Relationships between estimated age from statolith increments (days) and mantle length (mm) of *Loligo edulis* by month of hatching coupled with sea surface temperature (°C) from May 2002 to February 2003.
age analysis of statolith increments (NATSUKARI et al., 1988). In contrast, the maximum age estimated in the present study was less than 9 months for females and 10 months for males which younger than previous study (NATSUKARI et al., 1988). The present study is the only report of the age analysis of L. edulis in the Pacific coast and there will be a possibility that L. edulis in the Pacific coast have a better growth and mature and spawn in shorter period compare with those in the Japan Sea (NATSUKARI et al., 1988).

Acknowledgements
The authors would like to thank Moroiso Fisheries Cooperation, Miura Fisheries Cooperation Kanagawa Prefectural Fisheries Technology Center, and Aquamarine Fukushima for providing the squid specimens in this study. We also appreciate to the Ministry of Education, Culture, Sports, Science, and Technology of Japan for the partially supported as a scholarship grant.

References


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Do the ayu (*Plecoglossus altivelis altivelis*) born in the river with an inlet or large estuary in its mouth perform a homing?

Ebrahim ALJAMALI, Izumi KINOSHITA, Minoru SASHIDA, Takashi HASHIMOTO and Jun-ichi NUNOBE

**Abstract:** The distribution of ayu larvae and juveniles from the Kagami River were investigated around Urado Inlet, into which the river flows, from October 2004 to June 2005. The downstream swept larvae were distributed over the inside of inlet, and were never found outside the inlet. Vertically, they tended to be dispersed from the surface to the bottom, and to be concentrated at the surface when more developed. The larvae (yolk-sac to flexion stages) of 4–10 days old (chiefly 4–6 days old) occurred. In shallow waters around Urado Inlet, the larvae and juveniles continued to occur from November to May, in particular were assembled in the Kagami estuary located in the bottom part of inlet in January and February. Their main stages were postflexion around 20 mm BL. These facts suggest that the ayu larvae born in the Kagami River immigrate to shallow waters of the inner part of inlet, where they are nursed until upstream migration, after pelagic life in the inlet without migration into the open sea. Consequently, it is presumable that they perform a homing.

**Keywords:** Ayu, larvae and juveniles, Kagami River, Urado Inlet

**Introduction**

The ayu *Plecoglossus altivelis altivelis* is amphidromous osmerid fish with an annual life cycle, and spawns in the lower reaches of rivers in autumn. Usually hatched larvae immediately sweep downstream to the sea, where they spend the winter months until ascending rivers as juveniles in spring.

In the 1980s, it was found that abundant ayu larvae were aggregated along surf zones of sandy beaches facing Tosa Bay (SENTA and KINOSHITA, 1986). This discovery played an important role to advance study on the early life history of ayu in subsequent works. Furthermore, it was shown that amounts of ayu larvae and juveniles remain and grow within the Shimanto (Kochi Prefecture) and Kumano (Wakayama Prefecture) estuaries until spring, and their growth rates estimated were higher in the estuary than outside surf zones (TSUKAMOTO et al., 1989; TAKAHASHI et al., 1990). However, it is incompletely corroborated whether the remainders had never experienced pelagic life in the sea, and little is known about its significance in the entire population (TAKAHASHI et al., 1998, 1999, 2000, 2002, 2003).

Recently, we found ayu larvae remaining in the Kagami River, flowing across central Kochi City (the capital of Kochi Prefecture). In this paper, to clarify mechanism of remaining in the river, larval distribution and migration were detailed in the Kagami estuary and Urado Inlet, being interposed between the river and Tosa Bay.

**Materials and methods**

Surveys for collection of the ayu larvae and juveniles, being categorized into two (pelagic and immigration periods), were made monthly from October 2004 to June 2005. For the pelagic larvae, horizontally discrete depth at surface, middle and near the bottom layers and oblique from near the bottom to surface tows with a
larva net (1.3 m mouth diameter, 0.5 mm mesh aperture) were carried out at Stns. L1-L3 (inside the Urado Inlet) and L4 (outside the inlet), respectively (Fig. 1). Of which, at only Stn. L3, a specialized beam trawl (0.25 × 1.5 m-mouth, 1 mm mesh aperture) was used. This net was modified after KUPELS (1975) and designed to keep 5 cm apart the lower beam of the mouth from bottom to collect pelagic larvae distributed near the bottom. Towing depths and filtered water volumes (m³) were checked and calculated using a diver’s watch (Log Memory 1473, Casio) and flow meter (2030R, General Oceanics), respectively. No data was near the bottom of Stns. L1 and L2 in November due to unsuccessful tow.

For the immigrated larvae and juveniles, a seine net (1 × 4 m, 1 mm mesh aperture) (KINOSHITA et al., 1988) was used at Stns. S1-S10 arranged along shallow waters around Urado Inlet (Fig. 1). Two persons kept the net stretched, and waded backward in the waters, from ankle- to neck-depth along the shore-line for a distance of ca. 30 m (2 min.).

All samples were preserved in 10% sea-water formalin, and sorted ayu specimens were transferred to 80% ethanol and subsequently were measured their sizes by developmental stages (KENDALL et al., 1984). Unlabeled lengths are body lengths (notochord length in yolk-sac, preflexion and flexion larvae, and standard length in postflexion larva and juvenile).

A maximum 30 and 50 specimens from collections in the inlet and shallow waters, respectively, for each station of each sampling date were selected randomly for age determination from otolith (sagitta) (TSUKAMOTO and KAJIHARA, 1987).

Water temperatures and salinities were measured at the surface and bottom of each shallow water station (Stns. S1-S10) and at 0.5 m-intervals from the surface to bottom of each inlet station (Stns. L1-L4) with HSCCTS (Model 30, YSI Inc.) and STD (AST500-P, Alec Electronics), respectively.

Results
1. Distribution of pelagic larvae in the inlet
   1) Physical condition

   According to vertical profiles of temperature

Fig. 1. Chart of Urado Inlet showing stations where the ayu larvae and juveniles were collected form October 2004 to June 2005. For the pelagic larvae, sampling were made at Stns. L1-L3 and L4 (double and open circles), and for the immigrated larvae and juveniles, sampling were made Stns. S1-S10 (triangles). Shaded areas indicated eelgrass beds.

   and salinity, temperature decreased monthly from November to February, and stratification and mixed layers in salinity were formed in and outsides of the inlet, respectively (Fig. 2). In January and February, outside water mass being higher salinity tended to influx through
the bottom layer.

2) Distribution of the larvae
A total of 1,476 ayu yolk-sac (3.4–7.3 mm), preflexion (4.3–8.6 mm), flexion (6.2–13.4 mm) and postflexion (12.0–20.4 mm) larvae were collected from November to February, with a peak in November (Fig. 3). Horizontally, most abundance was found at Stn. L1, but none of larvae was appeared at Stn. L4 in any months. Vertically, the larvae tended to be dispersed throughout the layers from the surface to around 5 m-depth in all months, and in November and December, they were somewhat more densely distributed around 5 m-depth.

3) Compositions of size and developmental stages
Most of samples were composed of chiefly the yolk-sac and preflexion larva in with modes at 5.1–5.5 to 6.6–7.0 mm (Fig. 4). The compositions little changed among months, but somewhat varied both horizontally and vertically. In November and December, larger and more developed larvae were distinctively distributed at Stn. L1 than Stn. L3. Furthermore, the flexion larvae over 8 mm tended to be more abundant at the surface except of Stn. L2 in November.

4) Monthly changes in age and hatching period
Ages and hatching dates of the larvae ranged from 3 to 30 days and from 29 October 2004 to 22 January 2005, respectively (Fig. 5). Modal age was 5 days in any months, and some larvae older than one week also occurred in the inlet. Hatching dates were distributed from late October to late January, and their duration of each month sample was largely isolated, i.e. larvae collected. November, December, January and February were born in late October to early November, late November to early December, middle January and late January, respectively.

2. Distribution of immigrated larvae and juveniles along shallow waters
1) Temperature and salinity
Monthly changes in average water temperature and salinity of four sites are shown in Fig.

![Figure 2](image)

Fig. 2. Monthly changes of vertical isotherms and isohalines on the section of Stns. L1-L4 in Urado Inlet from November 2004 to February 2005.
Fig. 3. Monthly changes of vertical distributions of the ayu larvae in Urado Inlet from November 2004 to February 2005. The diameter of each circle is drawn in proportion to the cube root of density (n/1000 m$^3$) of larvae collected, of which the largest and smallest were 681.1 and 1.0 at the middle layer of Stn. L1 in November and the surface layer of Stn. 2 in February, respectively. Crosses represent no ayu larvae.

6. Average temperature was lowest in February in most of sites, and kept higher in Tanesaki beach (Stn. S10) and Kinugashima (Stn. S9) in November to February and March to May, respectively. Salinity was kept to be highest in Tanesaki beach, and to be higher in Tanesaki beach and Kinugashima than in estuarine sites (Stns. S1-S8). Consequently,
Fig. 4. Monthly, horizontal and vertical comparisons of frequencies of size and developmental stages of the ayu larvae collected with a larva net in Urado Inlet from November 2004 to February 2005.
monthly relationship between two physical parameters showed a reciprocal pattern.

2) Distribution of larvae and juveniles

A total of 1,117 larvae and juveniles (6.5–46.0 mm) were collected in the shallow waters around the inlet from November to May with a peak in January. Horizontal distributions were monthly showed in Fig. 7. Between December and February, larvae and juveniles aggregated in the Kagami estuary (chiefly Stn. S4), but almost disappeared from March forward. Conversely, few larvae and juveniles appeared along the coast of Kinugashima (Stn. S9) located in the central inlet, and sporadic occurrences were found along Tanesaki beach (Stn. S10) near the mouth of the inlet.

3) Monthly changes of size and developmental stages

Size and developmental stage compositions of specimens collected from the shallow waters along the inlet were spatially and monthly showed in Fig. 8. Specimens were composed of chiefly the postflexion stage and all juvenile stage in November to Mach and April to May, respectively. In the Kagami estuary (Stns. S1-S6), modal sizes were 12.1–13.0 mm in December, 11.1–12.0 and 14.1–15.0 mm in January, and 12.1–13.0 and 16.1–17.0 mm in February, and increased monthly. In the Kokubu estuary (Stns. S7-S8) and Kinugashima (Stn. S9),
modes were 13.1–14.0 or 14.1–15.0 mm, and little changed monthly. In Tanesaki beach (Stn. 10), chiefly postflexion larvae with a mode at 10.1–11.0 mm appeared in December, thereafter interposing January to March when few collected, and juveniles larger than 30 mm suddenly occurred in April.

4) Comparison of age and hatching date between the estuary and beach

Ages and hatching dates of the larvae and juveniles ranged from 6 to 135 days and from 23 October 2004 to 26 January 2005, respectively (Fig. 9). To examine the duration of residency of the immigrated larva, their age and hatching date distributions were compared for each month between the Kagami estuary (Stns. S1-S6) and Tanesaki beach (Stn. S10), where specimens were more abundant (Fig. 9). In the Kagami estuary, modal age was at 16–20 days in December, subsequently exhibited two peaks at 11–15 and 31–35 days in January, and their range widened toward older with pleural modes in February. Hatching dates were distributed from early November to late January, and distribution overlaps were seen over occurrence period, in particular being distinctive between January and February. In Tanesaki beach, apparently different age groups with modes at 11–20 or 81–85 days were present in December and April, respectively; furthermore, hatching dates were distributed for November in the former and for January in the latter, and never had overlapped between two groups.

Discussion

The ayu pelagic larvae never went outside of the inlet, and were denser in the inner part of the inlet (Fig. 3). On the other hand, CPUE of immigrated larvae and juveniles were considerably greater in the Kagami estuary than in other sites (Fig. 7). Considering overlapped duration of hatching, the swept larvae had led pelagic life for less than one-month in the inlet, and their residence term had been more than two-month until the juvenile stage in the Kagami estuary (Figs. 5, 9). Compared size frequencies between Stn. L1 and Stns. S4-S6, larger and older specimens in the former station overlapped distinctively with smaller and younger ones in the latter stations (Figs. 4, 5, 8, 9). From these facts, it is conceivable that most of ayu born in the Kagami River immigrate and use the shallow waters of the estuary as their nursery ground, immediately after the pelagic life in the inlet, without going out Tosa Bay. Furthermore, their disappearing from the Kagami estuary suggests migrating upstream the river in March. Consequently, it is presumable that the unique migration makes ayu larvae home actively. Abundances of ayu larvae and juveniles along neighboring beaches outside of the Shimanto River mouth compares poorly with those of others (the Shimonokae, Niyodo and Monobe Rivers) flowing into Tosa Bay (SENTA and KINOSHITA, 1986; HAMADA and KINOSHITA, 1988; AZUMA et al., 1989, 2003a, b; KINOSHITA, 1993; FUJITA, 2005). This seems to be attributed to the remaining of ayu larvae in the Shimatno estuary (Takahashi et al., 1990) like the Kagami River of the present study. Hence, it is possible that ayu born in the river with an inlet or large estuary in its mouth stay in the inlet or estuary and can perform the homing, they indeed supporting the stock of
each river.

In the present study, a number of larger pelagic larvae could be frequently collected especially at the surface of the inlet (Fig. 4). This phenomenon was seldom found in coastal waters of Tosa Bay and the other waters.

Fig. 7. Monthly changes of horizontal distributions of the ayu larvae and juveniles around Urado Inlet from November 2004 to May 2005. The diameter of each circle is drawn in proportion to the cube root of CPUE [(n/haul (2 min.)) of larvae and juveniles collected, of which the largest and smallest were 90.2 at Stn. S4 in February and 0.2 at Stn. S9 in April, respectively. Otherwise same as in Fig. 4.
Fig. 8. Monthly and horizontal comparisons of frequencies of size and developmental stages of the ayu larvae and juveniles collected with a seine net in the shallow waters around Urado Inlet from November 2004 to May 2005.
(Senta, 1967; Tsukamoto, 1988; Yagi et al., 2006), but was similar to that in Toyama Bay, the Japan Sea (Tago, 2002). This differentiation could be attributable to consequence of the water column. Inside of Urado Inlet, stratification column in salinity persisted constantly during the present study (Fig. 2). In Toyama Bay, vertical profile of salinity was shown merely at two stations of one survey, and distinctive haloclines were formed at layer shallower than ca. 1 m-depth (Tago, 2002). Conversely, off the mouth of the Takahashi River, the Inland Sea of Seto, mixed column was developed (Senta, 1967). In Tosa Bay, when waters were stratified and mixed vertically, larger larvae were marginally and hardly collected, respectively (Yagi et al., 2006). These information possibly reveal that larger larvae also continue to be distributed at the surface in themselves when stratified water column, but was dispersed vertically and there was little chance for them being collected when mixed water column due to their extremely lower density by a severe mortality. In the Shimanto estuary, distribution near the bottom of larger larvae over 10 mm is likely a special example that larvae after consuming yolk-sac to near the bottom of themselves, because their relative specific gravity had to become higher under a brackish environment (Kitajima et al. 1998).

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References


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The antagonistic bacterium that represses the growth of eel pathogens, *Edwardsiella tarda*

Kohsuke NOGUCHI*1, Kazuo IWATA*2, Masachika MAEDA*1

**Abstract:** *Edwardsiella tarda* shows the serious pathogenicity to many fishes. In particular eel aquaculture industry suffers a big damage with this pathogen. To repress its growth several drugs are using, but there are little effective to prevent this disease, because antibiotic resistance microbes are appeared. And vaccine under development is not yet in practical use. Therefore in this study antagonistic bacterium that represses pathogenic microbes in the process of microbial interactions was used for prevention of eel diseases. As a result, *E. tarda* infection to eel was restrained using bacteria EKZ-2 which was isolated in the coastal environment of Miyazaki City. Also, in eel aquaculture in situ, a difference was observed with the number of death in case of the bacterial dosage, which the survival number of the eel was much higher using EKZ-2 than that without EKZ-2. This results suggest that eel could be protected from the *E. tarda* infection by addition of antagonistic bacteria in situ.

**Keywords:** aquaculture, Edwardsiella tarda, antagonism, bacteria, eel

*Edwardsiella tarda*は多くの魚類に病原性をもち、特にウナギ、ヒラメ等の重要養殖魚種に大きな被害を及ぼす。また、人魚共通魚病原菌の疑いももたれている（BOCKEMÜHL et al., 1971）。この疾患では、薬剤効果の低い場合が多く、また抗生物質耐性菌の出現等も危惧されている。

このような薬剤効果の低い状況において、薬剤に依存しない養殖方法として、有用微生物を使用して病害微生物を防除する生物防除法（バイオコントロール）が期待されている（前田, 2005）。

本研究では、*E. tarda*の増殖抑制作用を保持する拮抗細菌を探索し、この培養菌体をウナギ（Anguilla japonica）へ経口投与することにより、*E. tarda*感染症の発症が抑制可能であるかを検討した。

大型海藻クロメ（Ecklonia kurome）の遊走子から分離した細菌株EKZ-2株はグラム陰性で、運動性（+）、シトクロームオキシダーゼ試験（+）、ブドウ糖無発酵等の性状を示したため、OKUZUMI et al. (1981)の分類スキームにおいて*Pseudomonas* III/IVに属する考えられた（Table 1）。また、塩分存在下における細菌株の増殖をZoBell2216E培地（ZoBELL, 1943）で3日間培養（温度22℃）して行ったところ、低塩分濃度（2.5g/L NaCl）でも増殖した（Fig. 1）。

次にEKZ-2株の、*E. tarda*に対する増殖抑制活性を検討した。方法としては、ZoBell2216E培地に供試菌と病原菌を同時に同時に行った培養接種し、病原菌の増殖が、病原菌単独接種对照区と比較し、遅滞するか否かによって判定した（前田, 2005）。この結果、EKZ-2株は抗*E. tarda*活性
Table 1. *Edwardsiella*-static activity of the strain EKZ-2 and its tentative identification

<table>
<thead>
<tr>
<th>Bacterial strain</th>
<th><em>Edwardsiella</em>-static activity</th>
<th>Gram-stain</th>
<th>Motility</th>
<th>Cytochrome oxidase test</th>
<th>O-F test</th>
<th>Tentative identification</th>
</tr>
</thead>
<tbody>
<tr>
<td>EKZ-2</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>Genus <em>Pseudomonas</em></td>
</tr>
</tbody>
</table>

Fig. 1. Growth of the EKZ-2 strain in different NaCl concentrations for 3 days at 20°C through the method of plate count.

を保持していることが判明した（Fig. 2）。

*E. tarda*感染防除実験は有用細菌（EKZ-2）投与実験区と無投与区を設定して行った。各区ともウナギ15尾ずつを供試し、有用細菌投与区ではEKZ-2株を50ml/kgの割合で配合飼料に混合し、ウナギ（約30g/尾）に体重の3%相当の餌量として投与した。無投与区では細菌無添加の配合飼料を投与した。各区ともにウナギを2週間30°Cで給餌飼育した。その後、病原菌*E. tarda*を10^6, 10^7, 10^8 CFU/mlの濃度にて用い、ウナギ腹腔内に0.5mlの量にて注射し、ウナギ死亡数を実験区と対照区とで比較した（Table 2）。この結果、*E. tarda*の濃度を10^6 CFU/mlに調整した場合、EKZ-2投与区では全尾が生存し、細菌無投与区では15日で11尾が死亡した（Fig. 3）。この結果は、有用菌投与により、エドワジエラ症感染が防除されることを示唆している。さらに、細菌投与区においては、飼食等の活動の低下が観られてなかったことから、EKZ-2株のウナギへの悪影響はないか、あるいは少ないものと判断した。

続いて、養殖場におけるEKZ-2株投与実験を行った。実験に使用した養殖場ではハウス加温式養殖を行っており、水温は約30°C、1池（150 m²）当たりに約2万尾のウナギを飼育している。3日
Table 2. Survival number of eel after injection of the different concentration of *E. tarda*

<table>
<thead>
<tr>
<th>Concentration of <em>E. tarda</em> (CFU/ml)</th>
<th>With the Strain EKZ-2</th>
<th>Without the Strain EKZ-2</th>
</tr>
</thead>
<tbody>
<tr>
<td>$10^6$</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>$10^5$</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>$10^4$</td>
<td>15</td>
<td>4</td>
</tr>
</tbody>
</table>

Fig. 3. Cumulative mortality of eel with and without oral administration of the *E. tarda*-antagonistic bacterium.

Fig. 4. Cumulative mortality of eel in pond trial after administration of *E. tarda*-antagonistic bacterium.
間培養したEKZ-2株（菌数約10^{7} CFU/ml）を50ml /kgの濃度で混合した配合飼料を約2ヶ月間ウナギへ投与し、生理数を対照生産区（菌無投与区）と比較した。この結果、EKZ-2株と区区では、細菌投与後53日間において約500尾の死亡が見られたのに対して、細菌無投与区では約3500尾が死亡した（Fig. 4）。

以上のように、ウナギ養殖において、細菌投与区と無投与区とにおける死亡数は有意な差が見られなかったが、このような結果は、ウナギ養殖池水への拮抗細菌の添加によりE. tarda感染の防除されることを示唆している。

なお、E. tardaへの増殖阻害作用を保持する拮抗細菌は少なく、Dopazo et al. (1988)の研究でも、E. tarda抑制効果を保持する細菌はみられなかったと報告している。また水産養殖における生物防除製剤の研究総説（Maeda, 2004）においても、E. tardaに対する拮抗細菌の報告例はみられない。

謝辞

クレラ工業、丸山生物製造にはEKZ-2株大量培養のご協力いただき、ここに深謝申し上げます。また、佐土原養殖組合糸崎本組合長からはウナギ養殖施設の提供及び有益な助言をご賜りましたことを深く感謝申し上げます。

文献


2006年12月13日受付
2007年2月1日受理
Virginie VAN DONGEN-VOGELS and Jerôme MALLEFET: Fragment growth-rates of six cultivated coral species: a reference framework for coral transplantation

断片化は、自然な断片化の一過程として多くの種のサンゴにみられる。断片のサイズは、少なくともいくつかの種においては断片の生残にとって重要な要素であると信じられている。ある地域での珊瑚礁の退縮および回復不良は、サンゴの移植における異なった管理計画をもたらしてきた。本研究では、2つの成長型に属する6種の造礁サンゴについて、管理条件下における断片の成長速度を調べた。その結果で我々は、断片の成長速度が6ヶ月の調査の間、増加し続けたこと、また、成長速度がPocillopora damicornisで最大で、次いで、Stylophora pistillata, Montipora sp., Seriatopora caliendrum, Echinopora sp., Turbinaria reniformisの順で大きかったことを示し、さらに、それらの表面積・体積比ならびに骨密度の種による違いについても言及した。続いて、それぞれの種について、成長速度が断片サイズに影響されているか否かを測定し、両者の間には有意な正の相関があることを示した（ただし、測定が実施された期間と実験の対象となった種に限ってのことであるか）。我々の得た結果には、群落の存続期間を通じての生理的物質の割当ての違いおよび群落サイズの遺伝的制限が関与しているのかも知れない。しかし、天然水域においては他の多くの限定要素（例えば餌食）が断片の生残状況に影響を与えることを考え、我々は、断片サイズが、局地的なサンゴ群落をうまく回復させるために考慮すべき制限要素のひとつであるということを示唆した。

（Laboratory of Marine Biology, Catholic University of Louvain (UCL), Batiment Kellner, 3 Place Croix du Sud, 1348 Louvain-La-Neuve, Belgium）

三上温子、小松穣久、青木優和、横浜康裕：本州中部太平洋沿岸大浦湾におけるアカモク（ヒバタマ目、褐藻植物門）の生長と光合成—光曲線の季節変化

本研究では、本州中部太平洋沿岸の大浦湾におけるアカモクの生長、光合成—光曲線、クロロフィルa含量の季節変化を調べるとともに、光合成効率放射や水温を含む物理環境の季節変化についても調べた。高長が10cm以上になっただアカモク8—10個体に印をつけ、成熟後基質から流出するまで毎月スキューバ潜水によりこれらの個体の茎長を計測すると同時に生長段階を観察した。さらに、毎月アカモク4個体を探集し、差動式検測計の一種であるプロドクトメーターにより、毎月の平均水温下におけるアカモク個体の上部と下部の葉部の純光合成速度および暗呼吸速度を計測した。また、これらの葉部のクロロフィルa量と重量も測定した。単位湿重量あたりおよび単位クロロフィルa量当たりの上部葉部における光合成活性のピークは異なった季節であり、前者の季節変化は茎の長さおよび生長速度と正の相関があり、後者の季節変化は個体の年齢と負の相関があった。さらに、単位湿重量あたりの光合成活性の季節変化のパターンは、海水中的栄養塩濃度の変化に同調していることが示唆された。

（東京大学海洋研究所 ☎164-8639 東京都中野区台1-1-5-1 Tel: 03-5351-6515 Fax: 03-5351-6542 E-mail: mikami@nenv.k.u-tokyo.ac.jp）

スッカモンコン オナチニー・土屋光太郎・東海 正・瀬川 進：神奈川県諸磯湾底定置網におけるケンサキイカの漁業生物学的研究

神奈川県三浦半島諸磯定置網において、2002年4月から2003年9月に魚獲されたケンサキイカLoligo edulisを毎月1回採集し、外装長組成、性比、成熟度を調べるとともに、平衡石を採取し平衡石の輪紋数に基づき日齢査定を行い、孵化日の推定を行った。この結果、諸磯定置網には年年にわたりケンサキイカが魚獲され、年にわたって成熟した個体が採集された。主産卵期は6～8月で、産卵期の個体の孵化後の日齢は雌では79日（外装長32mm）～298日（外装長144mm）、雄では82日（外装長32mm）～277日（外装長128mm）であった。日齢から逆算した孵化日は2002年5月から2003年4月で、諸磯定置網では主産孵化後3～6ヶ月の個体が魚獲されていることが明らかにされた。月別の雌雄の個体数や外装長と湿重量の関係、孵化月別の外装長と日齢の関係などには雌雄差があらわれなかった。

（東海海洋大学海洋科学部：☎108-8477 東京都港区港南4-5-7）
Ebrahimm A. Jamali・木下泉・指田穣・橋本隆志・布部淳一：河口に入江もしくは大きな河口域を持つ河川で生れたアユは母川回遊をするか？

土佐湾に面する浦戸湾において、2004年10月－2005年6月の間、浦戸湾に注ぐ錦川産のアユ仔稚魚の分布と回遊について調査した。流下仔魚は、水平的にはほぼ浦ノ内湾全域に拡がるが、湾外には全く出ていなかった。鉛直的には表層から底層まで出現し、より発達した個体は表層で多い傾向を示した。日数をみると、11－1月とも4－6日齢の卵黄囊期と前屈曲期仔魚が中心に出現し、8－10日齢の屈曲期仔魚も比較的多く分布した。しかし、彼らの孵化日を月間で比較すると、どの月の個体も、湾内混合には1ヶ月も滞在していた。一方、浦戸湾周辺の浅水域では、仔稚魚は11－5月の間出現し、その盛期は1－2月であった。水平的には錦川河口域を中心に分布し、特に2月ではほぼそこで出現しなかった。出現した発育段階は、湾奥では体長20 mm前後の後屈曲期仔魚であったが、湾口の砂波帯では30－40 mmの稚魚期のものが多く出現した。孵化日をみると、両水域とも、11月生まれの個体は1ヶ月も滞在しなかったが、12月生まれの個体は湾奥では1－2ヶ月の間滞在する傾向を示した。湾口の砂波帯では、1月生まれの稚魚期の個体が4月に突然出現した。これらのことから、錦川産のアユ仔稚魚は、湾外にはほとんど出ることなく、湾内で通常の海域より長い浮遊生活を送った後、河口域浅水域に集じ、そこで成育場とした後、週水するという、ほぼ母川回帰に近い回遊を行っていることが示唆された。

（連絡先著者：〒781-1164 東京市宇佐町井戸194 高知大学海洋生物研究教育施設）
学 会 記 事

1. 2006年6月4日（土）日伝会館会議室において、平成18年度水産研究発表会が開かれ発表題目と発表者は次の通り。　
平成18年度 水産研究発表会　
期日：平成18年6月4日（日）　
場所：日伝会館会議室（東京都渋谷区恵比寿3-9-25　電話：5421-7641）

プログラマム　
午前（10:00-12:00）　
1. 光の量や質が植物色の発達へ及ぼす影響　　○松本 明・荒川久幸・森永 勁（海洋大）
2. 沿岸海域の呼称に見る環境観の共通性　　一日本海・地中海を対象一　　○矢内秋生（武蔵野大・人間部・環境）
3. 生物ポンプを考慮したCO2海洋移動における濃度予測の検討　　○中村倫明
和田 明・長谷川 一幸（日大・院・環境科学）
4. 東京湾の湾奥部における水中強度に自己増幅した魚類の季節変化　　○酒井一之・茂木正人・河野 博（海洋大）
5. フィリピン、パラワン島のアゾキハタの性転換と成熟、産卵期について　　○三品裕昭・茂木正人・河野 博（海洋大）
6. カワラシノボリの個体間相互作用に関する研究　　一活動パターンと個体間における行動一　　○小島慶一・森川由隆（三重大学人間）

午後（14:00-16:00）　
7. 松島湾で採取したノリ網と海水から検出した微生物群集　　○奥村 裕（石黒看護大）
8. 気仙沼湾における透明度の長期変動について　　○松本 明・荒川久幸
9. すれ違い中の水文水質の影響を考慮した魚類の行動について　　○長谷川直子（滋賀県大・環境科学）
10. 「拓海」仮流流の導出と発散に関する研究　　○長谷川直子・長谷川大介・山崎秀勝（海洋大）
11. 東京湾口部における鉛直変動（現場データと数値実験との比較）　　○栗田準裕・山崎秀勝・長島秀樹（海洋大）・鈴木大二朗（港空技研）　
12. 東京湾口部における海況モニタリング　　○藤井楽平・北出裕二郎・井桁庸介

2. 2006年6月4日（土）日伝会館会議室において第47回（平成18年度）総会が開かれた。
議題は次の通り。
1. 平成18年度事業報告
2. 会員移動状況　

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2）活動状況　
評議員会 1回（17/5/27）
幹事会 2回（17/3/22, 17/5/20）
総会 1回（17/6/4 日伝会館）　
学術研究発表会 1回（17/6/4 日伝会館）　
学会賞授与 石丸 隆（東京海洋大学17/6/4日伝会館）

3）編集関係　
学会誌「La mer」20 (2), 43 (3) 発刊　

2. 平成17年度収支決算報告　
収入の部　
前年度繰越金 51,667
正会員会費 664,000 83名
65歳以上会員 168,000 28名
学生会員会費 24,000 6名（4000×6名）
学習会費 110,000 （7社、11口）
句読点、超過貢献印刷費 1,81,000
雑収入 96,657 （DVD販売、研究発表会、学术著作権使用料他）　
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合計 3,191,370
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原案通り承認された。

5. その他
終了後アトレ恵比寿店ライフにおいて懇親会がひらかれた。

6. 新入会員

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7. 退会（逝去者含む）
柳川三郎 金沢延幸 木 広一 福田雅明 有賀祐勝
桜井仁人 能登谷正浩 中村重久

8. 住所変更
寺崎 誠 〒248-0011 鎌倉市扇ケ谷4-16-22
La mer (Bulletin de la Société franco-japonaise d’océanographie)
Tome 44 (2006)

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