

Seasonal variation in the diel spawning time of the coral reef fish *Oxymonacanthus longirostris* (Monacanthidae): parental control of progeny development

Tomoyuki Kokita*, Akinobu Nakazono

Department of Fisheries, Faculty of Agriculture, Kyushu University, 6-10-1 Hakozaki, Higashi-ku, Fukuoka 812-8581, Japan

ABSTRACT: In the tropics, the longnose filefish *Oxymonacanthus longirostris* spawns shortly before sunset. In subtropical Okinawa Island, Japan, however, diel spawning time changed seasonally depending on seasonal changes in water temperature. At that site, spawning occurred in the morning during the early and late breeding seasons, when water temperatures were low. In the middle breeding season, when water temperatures were high, spawning occurred shortly before sunset. Hatching time of embryos was fixed, however, as embryos hatched just after sunset on the second day after spawning throughout the breeding season. Thus, the incubation period from fertilization of eggs to hatching of embryos changed seasonally and was negatively correlated with water temperature. The cumulative temperature from fertilization to hatching was almost constant throughout the breeding season, contributing to the control of larval development rather than the timing of hatching. Consequently, the developmental stage of newly hatched larvae was similar throughout the breeding season. In a rearing experiment that manipulated water temperatures, larvae which hatched at lower than natural ranges of cumulative temperatures were at an extremely immature developmental stage compared to larvae in natural temperature conditions. When water temperatures are low in the breeding season, *O. longirostris* parents shift their spawning time to the morning to ensure their embryos hatch as well-developed larvae. In conclusion, seasonal variation in the diel spawning time of subtropical *O. longirostris* assemblages will be a local adaptation to the strong seasonal changes of water temperature in their environment.

KEY WORDS: Diel spawning pattern · Local adaptation · Fish larvae · Subtropical waters · Developmental stage · Reproduction

INTRODUCTION

Diel patterns of spawning have been studied for many tropical and temperate reef fishes (Thresher 1984). Although the timing of spawning differs for each species, many species spawn at the twilight periods of dawn (e.g. Kohda 1988, Kuwamura 1997) and dusk (e.g. Lobel 1978, Moyer 1979). Tidal cycles also influence time of spawning in some pelagic egg spawners (Robertson & Hoffman 1977, Kuwamura 1981, Robertson 1983). Hypotheses about the ultimate factors influencing the timing of spawning of these fishes have

focused on the larval or adult biology of each species (reviewed by Robertson 1991). Dawn spawning may ensure the food resources in the female's territory from heterospecific competitors because potential diurnal food competitors are fewer or inactive at dawn (Kohda 1988). Dusk spawning may be related to avoidance of egg predation because egg predators are inactive at dusk (Robertson & Hoffman 1977, Johannes 1978, Helfman 1993). Also, spawning shortly after high tide, when the outgoing current is at its peak, may disperse eggs effectively offshore, where predators are lower in density (Johannes 1978). These hypotheses suggest that the adaptive significance of diel patterns of spawning varies greatly from species to species. Some

*E-mail: kokita@agr.kyushu-u.ac.jp

authors have reported that diel spawning time changed in different habitats, regions and seasons with species of labroid fishes (Kuwamura 1981, Moyer & Yogo 1982, Tribble 1982, Colin & Bell 1991). The reasons for such intraspecific variations, however, are not well understood for any species.

The longnose filefish *Oxymonacanthus longirostris*, a small monacanthid (maximum 9 cm in standard length), is a common inhabitant of shallow coral reefs in the Indo-West Pacific (Matsuura 1984). During the breeding season females spawn demersal and adhesive eggs into a tuft of filamentous algae once a day almost every day and parents do not provide egg care (Barlow 1987, Kokita & Nakazono 1998). In the tropics, spawning occurs shortly before sunset, and embryos hatch simultaneously just after sunset on the second day after spawning (Barlow 1987, 1988, pers. comm.). In subtropical Okinawa Island, Japan, however, spawning time changes seasonally (Kokita & Nakazono 1998), providing an opportunity to clarify the reasons for seasonal variations in the timing of diel spawning.

The present study examines the environmental factors influencing seasonal variation in spawning time of *Oxymonacanthus longirostris* and the effects of the variable spawning time on progeny development. We discuss the adaptive significance of this seasonal variability as a local adaptation to subtropical environments for an essentially tropical reef fish.

MATERIALS AND METHODS

Study site and field observations. We conducted the field research using snorkel and SCUBA on the fringing reef of Bise, Okinawa Island, southern Japan (26° 42' N, 127° 42' E) from March 1997 to September 1998. This locality is subtropical, with water temperatures over 30°C in summer and below 20°C in winter (T.K. unpubl. data). Throughout the breeding season (May to September-October), we observed reproductive behavior of tagged *Oxymonacanthus longirostris* in the field and measured water temperature near the bottom almost daily (except for 11 days in 1997 and 23 days in 1998). The details of the study site and the fish tagging method have been reported elsewhere (Kokita & Nakazono 1998). In this species, the male and female released gametes within 2 to 3 s (Barlow 1987). Thus, spawning, egg deposition and fertilization were regarded to occur at the same time. During the breeding season at Okinawa Island, the sun rose between 05:36 and 06:25 h (06:12 h in 1998) and set between 18:10 (18:42 in 1998) and 19:26 h.

Timing of hatching. The timing of hatching of embryos was examined every month of the 1997 breeding season. One egg mass was collected with a tuft of fila-

mentous algae just after spawning and transferred to well-aerated seawater in an aquarium, where it was kept under natural light conditions at a similar temperature to the study site during the same period (range = 25 to 30°C).

In July 1997 and May 1998, we investigated whether hatching would occur synchronously. All newly hatched larvae were removed from the aquarium 30 min after hatching commenced, and we checked the aquarium for additional embryos 1 h later, early the following morning and 30 min after sunset the next day.

Developmental stage of newly hatched larvae. To determine the developmental stage of newly hatched larvae, 3 egg masses collected once a month during the 1998 breeding season were put into perforated plastic bottles, which were then attached to the sea bottom. On the evening (17:00 to 18:00 h) of the second day after spawning (immediately before hatching), these bottles were transferred to the laboratory and maintained in well-aerated seawater under natural light conditions. Soon after hatching, larvae were anesthetized with 100 ppm seawater solution of tricaine methanesulfonate (MS222) and examined for deposition of pigments (10 larvae from each egg mass). Also, total length (TL mm; 10 larvae from 1 egg mass) was measured with a binocular microscope. In addition, we collected another 3 egg masses every month to examine seasonal variation in egg size. Ten eggs from each egg mass were preserved in 10% formalin-seawater solution. As eggs of *Oxymonacanthus longirostris* are nearly spherical (Barlow 1987), we measured diameter only.

Manipulative experiments. To examine the effect of light on the timing of hatching, we altered light conditions around the time of hatching. Two egg masses, which were collected in May 1998, were incubated *in situ* using perforated plastic bottles and were transferred to the laboratory at about 16:00 h on the second day after spawning. Each egg mass was divided into 3 pieces with the algae and placed in separate aquaria. One aquarium was kept under natural light conditions, and the other two were kept in rooms with artificial lighting. The light was switched off 2 h before sunset in one room and 2 h after sunset in the other room. We recorded the timing of hatching of embryos in each aquarium.

As spawning time was influenced by water temperature (see 'Results'), we tested whether the timing of hatching of embryos and the developmental stage of newly hatched larvae would change if eggs spawned in 2 different seasons were incubated in the water temperature of the other season. In May 1998, 1 egg mass was transferred to the laboratory just after spawning, where it was separated into 2 pieces and kept in 2

aquaria with well-aerated seawater under natural light conditions. In one aquarium the seawater temperature was higher than ambient (30°C: treatment unit) and in the other aquarium the seawater was ambient (25°C: control unit). This procedure was repeated in July 1998, when the ambient seawater was higher. In one aquarium the seawater temperature was ambient (30°C: control unit) and the seawater in the other aquarium was lower than ambient (25°C: treatment unit). Control seawater temperatures in aquaria did not differ from natural conditions by more than 0.4°C. Ten newly hatched larvae from each egg piece were anesthetized and photomicrographed. Deposition of pigments and 5 morphometric variables, i.e., TL, body depth (BD mm; maximum), head depth (HD mm; through the eye), eye diameter (ED mm; maximum) and yolk-sac area (YA mm²) of each larva were measured from the photomicrograph. TL, BD and HD were used as an indicator of larval size, ED as an indicator of ocular development and YA as a measure of the yolk reserves (see Kerrigan 1997). As this experiment was unreplicated in design, a further experiment needs to be carried out.

Data analyses. As water temperature and day length are considered to influence seasonal variations in the spawning time of fishes (Kuwamura 1981, Tribble 1982, Kashiwagi et al. 1987), we examined relationships between spawning time and these 2 environmental factors. We calculated the incubation period (h) and cumulative temperature (°C · h) from fertilization of eggs to hatching of embryos for each spawning observed, and partitioned these data into half-month periods. On the basis of our results (see below), we defined the incubation period as the period from fertilization to sunset on the second day after spawning (i.e., hatching time). The cumulative temperature was calculated by multiplying the daily water temperature on the day of spawning by the incubation period for each spawning.

All data were analyzed statistically using non-parametric tests, including Kendall's rank correlation test and Kruskal-Wallis test. Fisher's exact probability test and Mann-Whitney *U*-test were used to detect differences in larval development between controls and treatments in the experiment manipulating temperatures.

RESULTS

Seasonal variation in diel spawning time

Spawning occurred from 20 May to 7 October in 1997 and from 9 May to 8 September in 1998. Seawater temperature during the breeding season ranged from 24.2 to 31.0°C in 1997 and 24.2 to 33.0°C in 1998. Spawning time ranged from 10:04 to 19:10 h in 1997 and from 09:55 to 18:59 h in 1998. In both years, spawning occurred in the morning during the early breeding season and gradually became later until the middle breeding season, when it occurred shortly before sunset (Fig. 1a). During the late breeding season, spawning time gradually returned to the morning in 1997, but this was not seen in 1998 because fish stopped reproducing in September.

The pattern of change in spawning time throughout the breeding season correlated strongly with water temperature (Fig. 1b; Kendall's rank correlation test, $\tau = 0.75$, $p < 0.001$, $n = 202$ in 1997; $\tau = 0.59$, $p < 0.001$, $n = 169$ in 1998). Spawning occurred in the morning

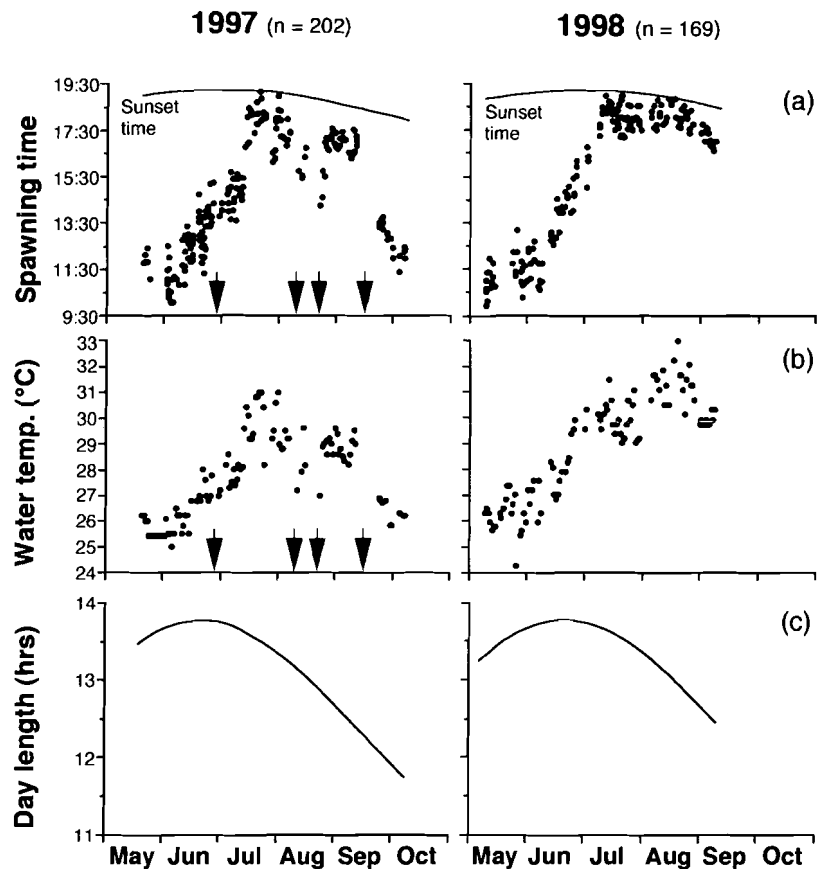


Fig. 1. *Oxymonacanthus longirostris*. Monthly changes in (a) spawning time, (b) water temperature and (c) day length throughout the breeding season in 1997 and 1998. Arrows indicate the days when typhoons hit in or near the study site

when water temperatures were relatively low and shortly before sunset when water temperatures were relatively high. Importantly, spawning time changed depending on short-term fluctuations in water temperature, such as a lowering of water temperatures caused by typhoons near the study site. Although the correlation between day length and spawning time was significant (Fig. 1c; Kendall's rank correlation test, $\tau = 0.23$, $p < 0.001$, $n = 202$ in 1997; $\tau = 0.15$, $p < 0.005$, $n = 169$ in 1998), correlation coefficients were extremely low. These results indicate that water temperature is more important than day length in influencing seasonal variation of spawning time in *Oxymonacanthus longirostris*.

Timing of hatching

Throughout the breeding season, hatching occurred simultaneously within a 30 min period after sunset on the second day after spawning. In experimentally manipulated light conditions, embryos hatched when the light was switched off, regardless of the hatching time of the embryos under natural light conditions.

The incubation period from fertilization to hatching (defined earlier) differed significantly among half-month periods (Kruskal-Wallis test, $H = 174.2$, $df = 9$, $p < 0.001$ in 1997; $H = 134.5$, $df = 8$, $p < 0.001$ in 1998; Fig. 2a), and was negatively correlated with water temperature (Kendall's rank correlation test, $\tau = -0.71$,

$p < 0.001$, $n = 202$ in 1997; $\tau = -0.62$, $p < 0.001$, $n = 169$ in 1998). Consequently, the cumulative temperature from fertilization to hatching fell within a very narrow range throughout the breeding season (Fig. 2b; 1405 to 1478°C · h in 1997 and 1453 to 1536°C · h in 1998). Ranges of cumulative temperatures were within 6% of the total value in both years. The cumulative temperature among half-month periods, however, varied significantly (Kruskal-Wallis test, $H = 87.0$, $df = 9$, $p < 0.001$ in 1997; $H = 59.8$, $df = 8$, $p < 0.001$ in 1998).

In the temperature-manipulated experiment, all embryos hatched shortly after sunset on the second day after spawning, regardless of the temperature of the water and the time of spawning. Therefore, cumulative temperatures from fertilization to hatching in treatments were higher (May: morning spawning, higher temperature rearing) or lower (July: late-afternoon spawning, lower temperature rearing) than those in the control (Table 1).

Morphological characteristics of newly hatched larvae

Egg size differed significantly among months (Kruskal-Wallis test, $H = 81.9$, $df = 4$, $p < 0.001$), and was largest in May and smallest in August (Fig. 3a). Egg size was negatively correlated with water temperature (Kendall's rank correlation test, $\tau = -0.62$, $p < 0.001$, $n = 150$). Furthermore, body length of newly

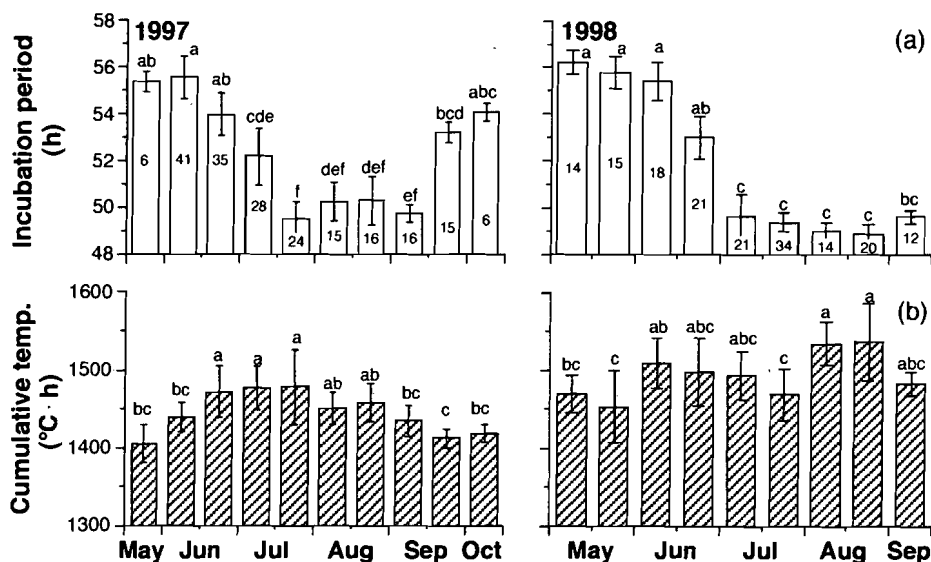


Fig. 2. *Oxymonacanthus longirostris*. Monthly mean (\pm SD) of (a) the incubation period from fertilization of eggs to hatching of embryos and (b) the cumulative temperature from fertilization to hatching throughout the breeding season in 1997 and 1998. Sample sizes and results of Dunn's multiple comparison test are given. Bars with the same letters are not significantly different (at $p < 0.05$)

Table 1. *Oxymonacanthus longirostris*. Comparisons of morphometric measurements between the control and treatment larvae in the experiment manipulating water temperatures. Values denote mean \pm SD. Differences were tested by Mann-Whitney *U*-test and Fisher's exact probability test (*)

Characteristic	Control larvae (n = 10)	Treatment larvae (n = 10)	Difference	
			<i>U</i>	<i>p</i>
Higher temperature rearing (May)				
Cumulative temp. ($^{\circ}\text{C} \cdot \text{h}$)	1418	1701		
% of pigmented larvae	100.0 (10/10)	100.0 (10/10)		= 1.0*
Total length (mm)	2.88 \pm 0.14	2.98 \pm 0.17	28.5	>0.1
Body depth (mm)	0.22 \pm 0.02	0.26 \pm 0.02	7.5	<0.002
Head depth (mm)	0.33 \pm 0.03	0.37 \pm 0.03	14.5	<0.007
Eye diameter (mm)	0.23 \pm 0.01	0.24 \pm 0.01	41.0	>0.4
Yolk area (mm ²)	0.26 \pm 0.02	0.24 \pm 0.04	30.0	>0.1
Lower temperature rearing (July)				
Cumulative temp. ($^{\circ}\text{C} \cdot \text{h}$)	1459	1216		
% of pigmented larvae	90.0 (9/10)	10.0 (1/10)		<0.001*
Total length (mm)	2.78 \pm 0.18	2.43 \pm 0.12	6.5	<0.001
Body depth (mm)	0.20 \pm 0.02	0.17 \pm 0.01	7.0	<0.001
Head depth (mm)	0.32 \pm 0.03	0.28 \pm 0.02	21.0	<0.03
Eye diameter (mm)	0.19 \pm 0.01	0.17 \pm 0.01	13.0	<0.004
Yolk area (mm ²)	0.18 \pm 0.01	0.20 \pm 0.05	46.0	>0.8

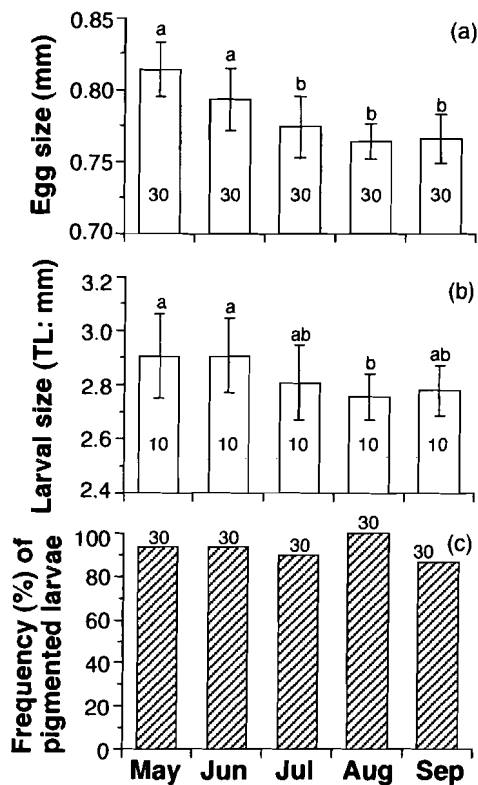


Fig. 3. *Oxymonacanthus longirostris*. Monthly mean (\pm SD) of (a) egg size and (b) total length (TL) of newly hatched larvae and (c) the frequency of newly hatched larvae with pigments throughout the breeding season in 1998. Sample sizes and results of Dunn's multiple comparison test are given. Bars with the same letters are not significantly different (at $p < 0.05$)

hatched larvae significantly differed among months (Kruskal-Wallis test, $H = 9.9$, $df = 4$, $p < 0.05$; Fig. 3b). Such seasonal variation in larval length was most likely influenced by seasonal change in egg size. This was not detected, however, because mean larval length was not significantly correlated with mean egg size, possibly due to the small sample size (Kendall's rank correlation test, $\tau = 0.80$, $p > 0.05$, $n = 5$). Throughout the breeding season, most of the newly hatched larvae had pigments on the upper and lower parts of the myomeres and tail (Fig. 3c, see also Fig. 4). These results indicate that the developmental stage of newly hatched larvae was similar throughout the breeding season, despite seasonal changes in the size of larvae at hatching.

For the manipulative experiment conducted in May, all of both the control and treatment (reared at a higher temperature) larvae had normal pigmentation of newly hatched larvae reared under natural conditions (Fig. 4, Table 1). Furthermore, most morphometric variables of the larvae, except for BD and HD, did not differ significantly between the 2 groups (Table 1), although the treatment larvae appeared more developed than the control larvae (Fig. 4). Conversely, in the July experiment, almost all control larvae were pigmented, but almost all treatment larvae (reared at a lower temperature) were unpigmented (Fig. 4, Table 1). Moreover, TL, BD, HD and ED of treatment larvae were significantly smaller than those of the control larvae (Table 1). Thus, embryos reared in lower than natural water temperatures at that moment hatched at an immature developmental stage.

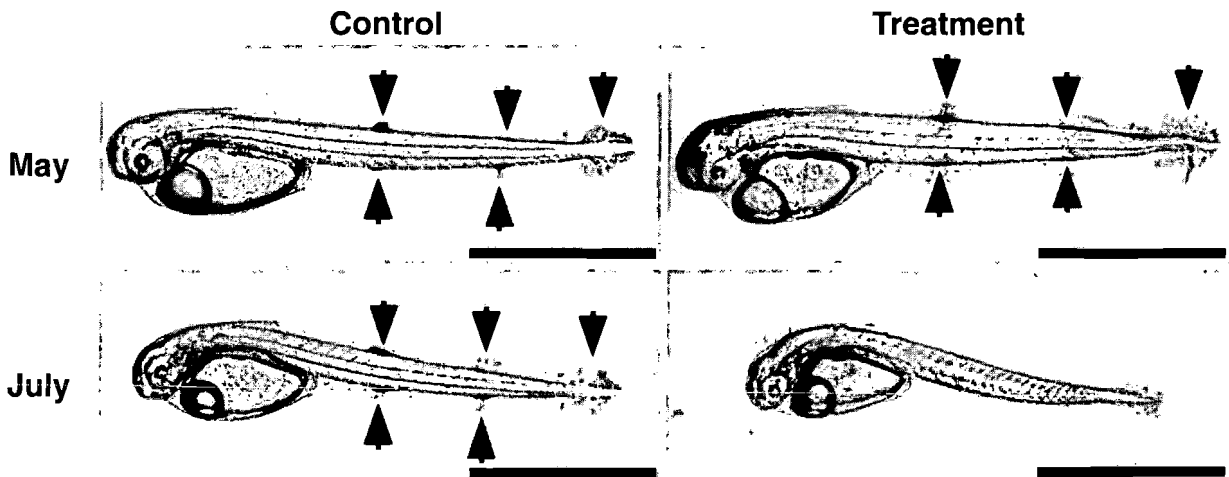


Fig. 4. *Oxymonacanthus longirostris*. Newly hatched larvae in the experiment manipulating water temperatures. Arrows show pigments on the upper and lower parts of the myomeres and tail. Scale bar = 10 mm

DISCUSSION

To our knowledge, the remarkable seasonal variation in the diel spawning time of *Oxymonacanthus longirostris* inhabiting subtropical waters has not been recorded in other fishes. Seasonal variations of water temperature in the subtropics determined this variability. In tropical areas, such as Enewetak Atoll and Guam, where water temperatures are higher and more stable, female *O. longirostris* spawn shortly before sunset (Barlow 1987, 1988, pers. comm.). Similarly, spawning occurred shortly before sunset in the subtropics during the annual maximum water temperatures. These results show that subtropical *O. longirostris* shifts spawning time to the morning in the early and late breeding seasons when water temperatures were lower.

In contrast to the variable spawning time, hatching occurred simultaneously just after sunset on the second day after spawning throughout the breeding season. In tropical and temperate reef fishes, the embryos of many demersal egg spawners hatch just after sunset (e.g. Kohda 1988, Gladstone 1994, Kawase & Nakazono 1995), when most predators of larvae (zooplanktivores) are less active than during the day (Robertson & Hoffman 1977, Johannes 1978, Helfman 1993). Thus, dusk hatching may be advantageous in avoiding such predators. Generally, hatching of fish is a developmental stage-specific phenomenon; however, some triggering stimuli, either extrinsic or intrinsic, have to be received by the appropriately developed embryos to induce the hatching enzyme secretion which causes hatching (Yamagami 1988). Light is an important environmental cue that may influence fish hatching (Kohda 1988, Yamagami 1988). Our laboratory experiment

showed clearly that the timing of hatching in *Oxymonacanthus longirostris* was controlled by levels of light, and sunset was the cue to hatch on the second day after spawning. Importantly, embryos are ready to hatch earlier than sunset on the second day because they hatched 2 h prior to sunset in artificial conditions.

The incubation period from fertilization to hatching varied seasonally due to seasonal variation in the diel spawning time of the parents and the fixed hatching time of the embryos, and was negatively correlated with water temperature. Consequently, the cumulative temperature from fertilization to hatching was similar throughout the breeding season. Thus, parents control the cumulative temperature by changing the diel spawning time throughout the breeding season. When water temperatures were manipulated, hatching of embryos reared in both high and low temperatures occurred at the same time as hatching of embryos reared under natural conditions. Therefore, the constant cumulative temperatures found in naturally reared embryos did not contribute to controlling the time of hatching in embryos. However, they were effective in controlling progeny development. The developmental stage of newly hatched larvae was similar throughout the breeding season, even though larval body length changed seasonally, corresponding to the seasonal variation in egg size. In contrast, the developmental stage of larvae that hatched outside the natural range of cumulative temperatures differed to that of larvae which hatched within the natural range. This was particularly evident in larvae which hatched in lower than natural cumulative temperatures because they were extremely immature with no pigmentation. Thus, the cumulative temperature strongly influenced the devel-

opmental stage of newly hatched larvae. In addition to the cumulative temperature, egg size may also affect the development rate of eggs and embryos, i.e., large eggs having a slower development rate than small eggs (Duarte & Alcaraz 1989, Robertson 1991, but see Knutsen & Tilseth 1985). Egg size in *Oxymonacanthus longirostris* changed seasonally (maximum in May and minimum in August), being negatively correlated with water temperature as reported in other fishes (e.g. Ware 1977, Imai & Tanaka 1987). Larval development in *O. longirostris* was very similar among months, regardless of differences in egg size. These results suggest that the cumulative temperature is the most important factor influencing the development rate of the egg and embryo in this species (also see Pauly & Pullin 1988). Therefore, *O. longirostris* parents control the developmental stage of their newly hatched larvae by attempting to optimize the cumulative temperature.

Oxymonacanthus longirostris is an essentially tropical species and thus subtropical Okinawa Island is close to its biogeographical and sea temperature range limits. If subtropical assemblages of *O. longirostris* spawned shortly before sunset throughout the breeding season as in the tropics, their embryos would be immature at hatching in the early and late breeding seasons, owing to lower cumulative temperatures. There is little doubt that immature larvae are disadvantaged in surviving the early planktonic stage. For example, lower locomotive abilities in immature larvae may increase predation rates (Bailey & Houde 1989, Kerrigan 1997, McCormick 1998, 1999). Therefore, *O. longirostris* parents shift their spawning time to the morning in the early and late breeding seasons to avoid their embryos' hatching at an immature developmental stage. Such parental control may be critically important in *O. longirostris* because newly hatched larvae of monacanthids are less developed than those of other demersal egg spawners (Thresher 1984, Nakazono & Kawase 1993). Environmental pressures of subtropical and temperate waters modify the reproductive biology of other primarily tropical species (Moyer 1980, Richardson et al. 1997). A seasonally variable spawning time in subtropical *O. longirostris* assemblages will also be a local adaptation to strong seasonal variations in water temperature. Whether such an adaptation is the outcome of phenotypic plasticity (reviewed by Warner 1997) or genetic differentiation (reviewed by Conover 1998) remains to be tested.

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