

Temporal Patterns of Breeding and Larval Settlement in a Temperate Population of the Tropical Anemonefish, *Amphiprion clarkii*

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Abstract The breeding of the anemonefish, *Amphiprion clarkii*, and the settlement of larvae were observed in temperate Japan. Spawning had two peaks near the first and the third quarter of the moon in 1983, but did not in 1984. The clutch size varied greatly during the breeding season, with a peak from the second half of June to the second half of July. Adult fishes inhibited larval settlement. The proportion of disappeared 0-year olds to the total was higher in 1984 than in 1983. This difference might be mainly due to the difference in the degree of crowding in each sea anemone. The period of larval settlement closely paralleled the breeding season. The larvae settled abundantly around the first quarter and the third quarter of the moon in 1983, and did from the third quarter to the first quarter in 1984. In both years, the number of settled larvae was more from the full moon to the new moon than the new moon to the full moon. The daily pattern of larval settlement did not reflect that of breeding.

Most coral fishes have a pelagic larval stage lasting scores of days after spawning or hatching, after which larval settlement to the reef population occurs (the term "larvae" in the present paper refers to the life stage between hatching and settlement) (Leis and Miller, 1976; Sale, 1980; Brothers *et al.*, 1983). Therefore, larval recruitment plays an important role in the population dynamics of reef fishes, especially those like strongly site-attached pomacentrids which rarely migrate after settlement. Some recent works suggest that the study of larval recruitments important in understanding the dynamics of the coral reef fish community (Russell *et al.*, 1977; Talbot *et al.*, 1978; Williams and Sale, 1981; Williams, 1983).

The reef fishes have various temporal patterns of larval recruitment: year to year variation (Kami and Ikehara, 1976; Russell *et al.*, 1977; Talbot *et al.*, 1978; Williams and Sale, 1981), a seasonality (Yamamoto, 1976; Russell *et al.*, 1977; Luckhurst and Luckhurst, 1977; Williams and Sale, 1981), a lunar periodicity (for review, see Johannes, 1978), and a brief and sporadic occurrence (Victor, 1983). There are two different ideas as to which factors determine such temporal patterns. One is that recruitment pattern closely parallels spawning pattern (Randall, 1961; Luckhurst and Luckhurst, 1977; Russell *et al.*, 1977). Another is that some process occurring in the planktonic life is respon-

sible for the recruitment pattern (Victor, 1983; Williams, 1983). There have been no studies which simultaneously investigated the temporal patterns of both spawning and larval settlement.

Anemonefishes also have a pelagic larval life followed by a reef-resident life (Allen, 1972; Ross, 1978). In this paper I describe the daily, seasonal and year to year variation of both breeding and larval recruitment in a temperate population of the tropical anemonefish, *Amphiprion clarkii*, and discuss the relationships between the two processes. In addition, I discuss the relationships between the adult fish and the settling larvae.

Materials and methods

Amphiprion clarkii is the most widespread species in the genus; its northern limit of distribution in the Pacific is southern Japan (Allen, 1975). This investigation was carried out at Murote Beach, Uchiumi Bay (33°00'N, 132°30'E), west of Shikoku Island, Japan. The bottom at depths shallower than 10 m consisted of a rocky reef with many patches of coral, to which *A. clarkii* is confined. Here I set up a 50 m × 50 m study area including 121 anemones (*Parasicyonis maxima*). This area contained 30 adult pairs and about 28 juveniles over one year old in 1983, and 24 adult pairs and about 26 juveniles over one year old in 1984. The

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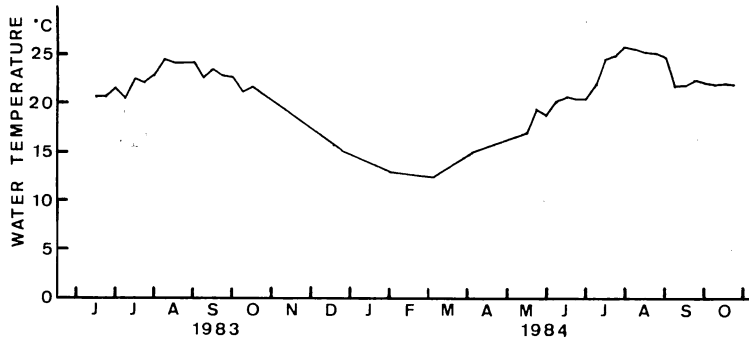


Fig. 1. Water temperature at about five meters depth.

nearest distance between sea anemones was 2.0 ± 1.1 S.D. ($n=76$). A preliminary observation showed that all these sea anemones were controlled by adult pairs. All anemonefishes in the study area, except very small 0-year olds immediately after settlement, were tagged after measuring. The tagging method was according to Thresher and Gronell (1978).

Data were collected between May 1983 and October 1984. Daily observations were made May 18 to June 1, June 15 to October 22 (except 6 days), December 24 to 29 in 1983, February 4 to 5, March 14 to 16, April 14 to 17, and May 15 to October 25 (except 15 days) in 1984. At each observation, I visited all sea anemones to examine the spawnings, the hatchings, the larval settlement, the survival of 0-year olds, and so on. Eggs were deposited densely on flat rock surfaces under the tentacles of the sea anemones. The deposition areas were measured with a 2 cm \times 2 cm-mesh quadrat on the day when I found them for the first time.

In May 1983, the smallest anemonefish (probably recruited the previous year) within the study area was 26 mm in standard length. I distinguished between 0-year olds (settled in 1983) and one-year olds and older by comparison with this anemonefish. The distinction was very easy to make because almost all 0-year olds were about 7 or 8 mm in standard length when they appeared on the sea anemones for the first time. There were some anemonefishes which were obviously larger than this size but smaller than the smallest one-year olds. They were considered to be 0-year old which immigrated after settling elsewhere. The small 0-year olds were not tagged until October in 1983. Therefore, if a 0-year old which was

seen during one observation was as large as that on the same sea anemone during the previous observation, the two were considered to be the same individual.

Results

Reproduction. At Murote Beach, the water temperature ranged from 12.5°C to 27.0°C during the period of investigation (Fig. 1). Spawning started at the beginning of June (about 20.5°C) and ended at the beginning of October (about 22.5°C) both in 1983 and 1984. Within the study area, 31 females deposited 177 clutches in all in 1983 and 24 females produced 126 clutches in all in 1984. The annual number of clutches per stable pair in 1983 and 1984 was 6.6 ± 0.9 S.D. (5 to 9 clutches, $n=24$) and 5.4 ± 1.1 S.D. (4 to 8 clutches, $n=23$), respectively. An annual fecundity per pair in 1983 and 1984 was estimated about 15,000 eggs and about 11,000 eggs, respectively.

Females repeated spawning at approximately semimonthly intervals ($14.4 \text{ days} \pm 0.3$ S.E., $n=143$ in 1983 and 14.7 ± 0.3 S.E., $n=105$ in 1984) throughout the breeding season (Table 1). The size of the individual deposition areas varied greatly during the breeding season, with a peak from the second half of June to the second half of July both in 1983 and 1984 (Fig. 2). This seems to show that during the breeding season each female changed her clutch size considerably because egg density in the second half of June was not smaller than that in the second half of August and September (the mean of three clutches was 313 eggs \pm 44.4 S.D. per 4 cm in the second half of June and that of nine clutches was 286 eggs \pm

Table 1. Semimonthly inter-spawning intervals: days±S.E.

		June	July	Aug.	Sept. ^a
First half	1983	16.3±0.3 n=12	17.3±0.4 n=23	13.5±0.6 n=31	12.3±0.9 n=4
	1984	16.5±0.6 n=13	12.8±0.5 n=24	12.0±0.4 n=17	13.0±0 n=1
Second half	1983	15.4±0.4 n=21	14.3±0.4 n=31	15.1±1.1 n=21	
	1984	16.5±0.5 n=19	15.0±0.6 n=25	19.8±1.7 n=6	

^a First and second half combined.

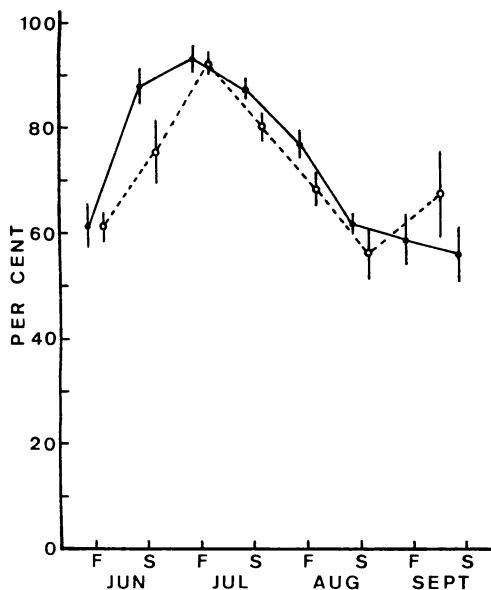


Fig. 2. Semimonthly changes in clutch size throughout the breeding season. Clutch sizes were estimated from deposition areas. Points indicate semimonthly averages of the ratio of each female's clutch size at each interval to her maximum clutch size. F and S refer to first and second half, respectively. Bars indicate standard error of the mean. Solid line, 1983; dotted line, 1984.

25.7 S.D. per 4 cm in the second half of August and September). The average of the maximum deposition areas in 1983 and 1984 was 41.7cm±2.1 S.E. (n=27) and 38.5 cm±2.0 S.E. (n=24), respectively.

Temporal patterns of hatching and spawning. Spawning activity extended over a period of four lunar cycles (Fig. 3). In 1983, spawning occurred continuously but had two peaks around the first

and third quarter of the lunar cycle. The distribution of total spawnings in quarter of the lunar cycle was significantly different from an equal distribution ($\chi^2=22.6$, $P<0.001$). A run test for trends data (Sokal and Rohlf, 1969) also showed that the distribution of total spawnings was significantly different from random (n=25, r=12, ts=-2.134, $P<0.05$). In 1984, spawning occurred continuously and showed no obvious trends. The distribution of total spawnings in each quarter of the lunar cycle was not significantly different from an equal distribution ($\chi^2=5.870$, $0.10 < P < 0.20$).

As the water temperature changed during the breeding season (Fig. 1), the incubation period varied from 6 days to 12 days (Table 2). Hatching did not show more obvious trends than spawning in 1983. A run test did not find out any trends either in 1983 or 1984. The total of hatchings near the full and new moon, however, was more than that around the half moon in 1983 ($\chi^2=12.2$, $P<0.01$). Hatching started about 30 minutes after sunset.

Larval settlement. The first larvae recruited in the study area on 16 June in 1983 and 15 June in 1984. After that time, 53 0-year olds appeared by 22 October in 1984 (the last settlement occurred on October 3) and 292 did by 25 October in 1984 (the last settlement occurred on October 18). Of them, 45 and 225 0-year olds which measured 7 mm to 8 mm in standard length when first observed were considered to be just-settled juveniles. Most of the others were considered to be 0-year olds which had immigrated into the study area after settling elsewhere. Larval recruitment seemed to be negligible after October because only three 0-year olds were newly observed after that time.

The number of settled larvae per sea anemone

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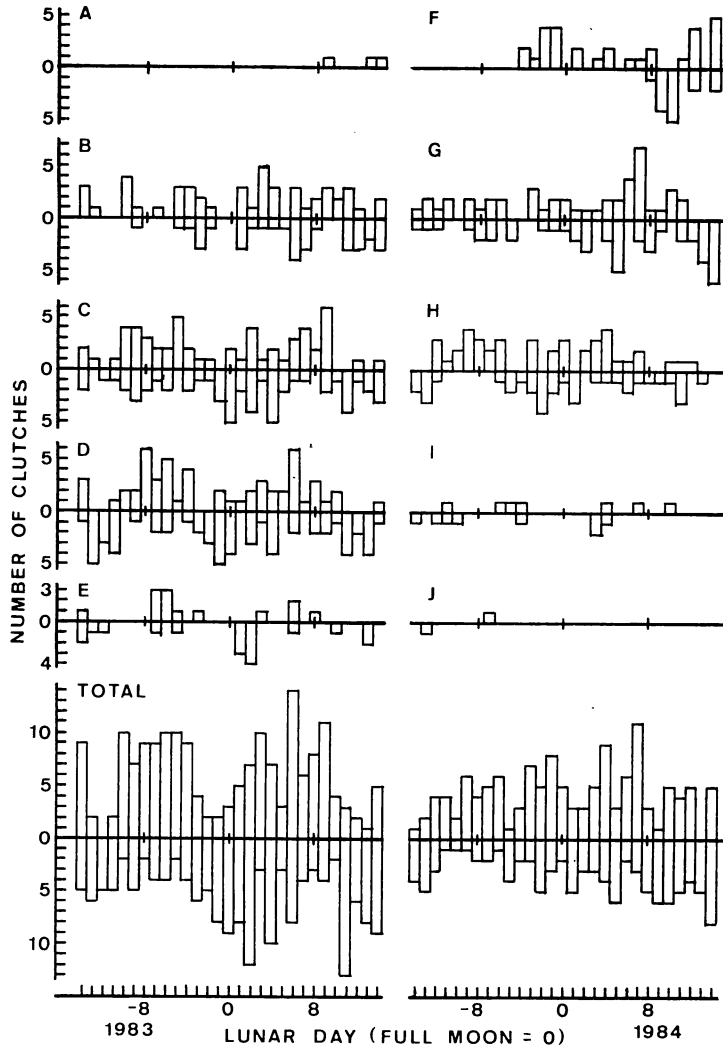


Fig. 3. Spawning and hatching at each lunar cycle throughout the breeding season. Spawning is represented above the line and hatching below the line. Days of the full moon during lunar cycle A to J are 27 May, 25 June, 25 July, 23 August, 22 September, 13 June, 13 July, 12 August, 10 September and 10 October, respectively. Spawning days prior to 14 June 1983 were estimated from hatching days.

did not follow a Poisson distribution (Fig. 4, G -test for goodness of fit, $G=39.850$, $P<0.001$, Sokal and Rohlf, 1969). One cause for this badness of fit seemed to be an inhibitory effect of adults on larval settlement because the number of settled larvae per sea anemone was significantly different between the sea anemones used as spawning sites (0.79 ± 0.21 S.E. per anemone) and the unused ones (2.16 ± 0.23 S.E. per anemone) (Table 3, Mann-Whitney U -test, $U=768$, $P<0.001$). Adults

spent $36.5 \text{ days} \pm 1.8$ S.E. ($n=24$) on the care of eggs (spawning to hatching) between June 15 and August 31 in 1984 during which time breeding was active. Although all sea anemones were controlled by adult pairs (anemones were close enough together that individual adult fish were resident in several neighbouring anemones), parents spent more time near the spawning sites than near other sea anemones during the breeding season (pers. obs.). The sea anemones used as

Table 2. Change of incubation periods in 1983. Incubation period=days±S.E.
F, first half; S, second half.

Spawning day	June		July		Aug.		Sept.	
	S	F	S	F	S	F	S	
Average °C	20.6	21.1	22.3	23.3	24.2	23.1	23.2	
Incubation period	10.3±0.2 n=23	10.2±0.2 n=20	8.9±0.1 n=34	7.8±0.2 n=28	7.3±0.1 n=32	8.1±0.3 n=7	8.0±0.2 n=7	

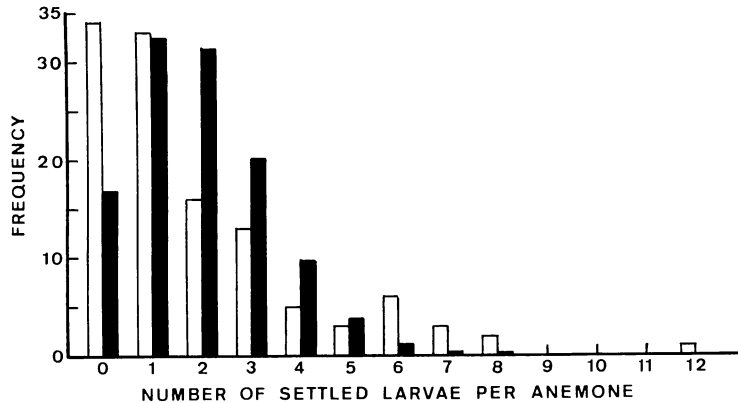


Fig. 4. Frequency distribution of the number of settled larvae per sea anemone. The ordinate means the number of sea anemones. Hollow bars indicate the observed numbers. Solid bars indicate the expectation estimated from a Poisson distribution.

Table 3. The number of settled larvae per sea anemone. Data were gathered between June and August in 1984 during which the breeding was active.

Number of settled larvae	0	1	2	4	5	6	7	8	9	Total
Number of anemones:										
used for spawning	17	11	3	1	0	0	1	0	0	33
unused	19	22	14	11	4	5	4	1	3	83

the spawning site were larger than the unused ones (used: 50.2 cm±1.8 S.E. diameter in major axis, n=31 and unused: 36.5 cm±1.3 S.E. diameter in major axis, n=78).

Temporal pattern of settlement. Larval settlement extended over a period of four lunar cycles (Fig. 5). The period closely paralleled the breeding season. The pattern of larval settlement had two peaks. It was significantly different from an equal distribution (Kolomogorov-Smirnov one-sample test: $D_{10}=0.5022$, $P<0.01$ for lunar cycle B, $D_{19}=0.3394$, $P<0.05$ for C, $D_{45}=0.4008$, $P<0.01$ for the total of 1983, $D_{148}=0.5268$, $P<0.01$ for F, $D_{36}=0.3908$, $P<0.01$ for G, $D_{16}=0.4116$, $P<0.01$ for H, $D_{12}=0.5374$, $P<0.01$ for I and

$D_{225}=0.3263$, $P<0.01$ for the total of 1984).

In 1983, larvae settled abundantly around the half moon. In 1984, they settled abundantly from the third quarter to the first quarter. In both years, the number of settled larvae was small around the full moon, and more from the full moon to the new moon than from the new moon to the full moon (about 2.8 times). Sixty-one point three percent of larvae settled from 15 to 27 July in 1984.

Figure 6 shows the fluctuation in the numbers of 0-year olds within the study area. They increased steadily throughout most of the period of settlement in 1983. On the other hand, they reached a maximum (146 0-year olds) at the

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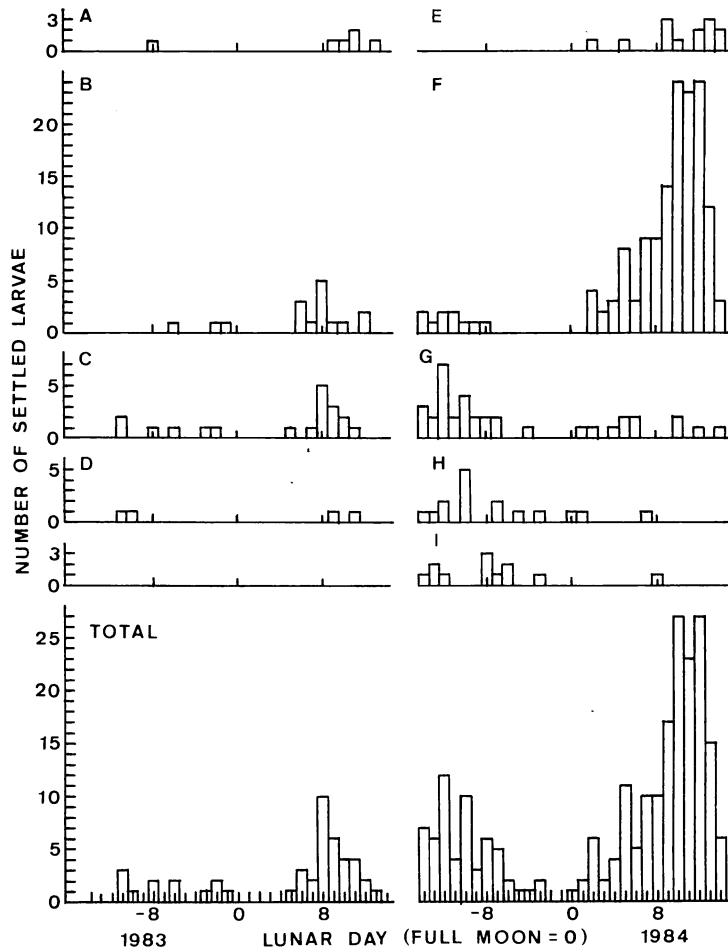


Fig. 5. Daily pattern of larval settlement during each lunar cycle. Days of the full moon during lunar cycle A to I are 25 June, 25 July, 23 August, 22 September, 13 June, 13 July, 12 August, 10 September and 10 October, respectively.

beginning of August, and then decreased gradually in 1984.

Discussion

Temporal patterns of spawning and hatching. The clutch size varied considerably during the breeding season, with a peak from the second half of June to the second half of July (Fig. 2). On the other hand, the interval between spawnings remained fairly constant at about two weeks throughout the breeding season (Table 1). This means that females maximized their reproductive output around July. Two factors might result in the variations in fecundity. One is the variation in the environmental conditions for adults

(e.g. the amount of food, Wootton, 1973, 1977, 1979). The other is that for survival of offspring (e.g. water temperature and the amount of food). It would cause changes to adult fecundity if there was evolutionary time enough for reproductive effort to be best tuned to environmental cycles. Qasim (1955) has stated that the larvae hatch during the season which is most favourable for finding food. Russell *et al.* (1977) suggest that breeding cycles may be timed to ensure that larval settlement occurs at the time of year most favourable for growth. In addition, Lobel (1978) suggests that reproduction may be synchronized with ocean currents favoring return of larvae to home reefs among fishes adapted to unique situations.

There are many reef fishes whose spawning

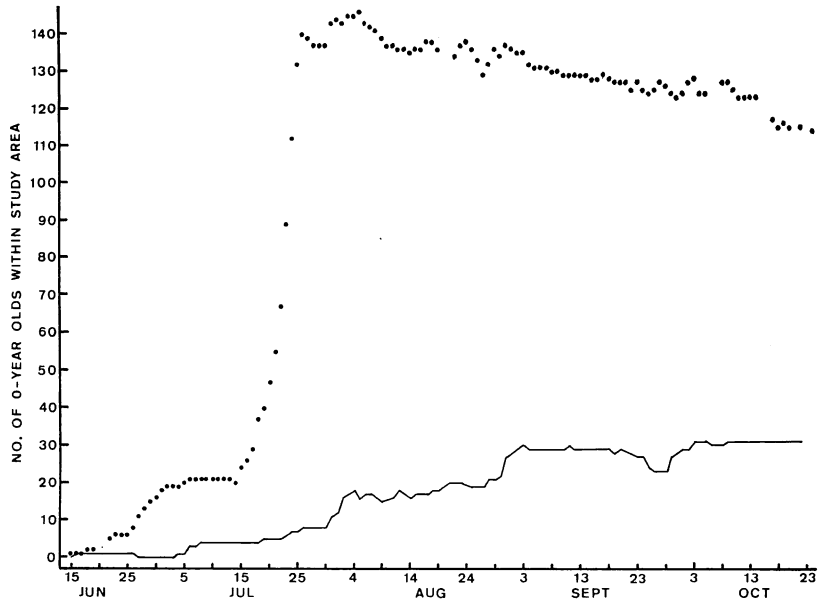


Fig. 6. Fluctuations in the number of 0-year olds within the study area. Solid line, 1983; dotted line, 1984.

behavior is synchronized with the lunar or tidal cycle, and this spawning behavior, it is inferred, has some selective advantage (for review, see Johannes, 1978). An influential hypothesis is that reef fishes reduce the intense predation pressure on their eggs or larvae by synchronizing spawning (in species with pelagic eggs) or hatching (in species with demersal eggs) with the strong outgoing current around the new and/or full moon (Johannes, 1978; Ross, 1978).

Among the anemonefishes, *A. melanopus* at Guam has two spawning peaks around the half moon with hatching peaks near full and new moons since the incubation period is 7.5 to 8.5 days (Ross, 1978). On the other hand, *A. chrysopterus* and *A. perideraion* at Enewetak (Allen, 1972), and *A. bicinctus* in the Red Sea (Fircke, 1947) have one spawning peak around the full moon. In the present study, it could not be concluded whether *A. clarkii* showed lunar periodicity in reproductive behavior or not, because reproductive behavior, was synchronized with the lunar cycle in 1983 but not in 1984 (Fig. 4). At Murote Beach high spring tides occur twice a day, shortly after sunrise and near sunset around the new and full moon as at Guam. Therefore, as suggested by Ross (1978), the synchronization of hatching with

spring tides in *A. clarkii* where hatching occurred shortly after sunset might reduce predation on the newly hatched larvae by carrying them in the strong outgoing current. If so, the constant inter-spawning intervals of about two weeks would be useful for a female to synchronize spawning with the lunar cycle. In contrast with the stable incubation period at Guam, the changing incubation periods from 6 days to 12 days at Murote Beach might make it difficult for a female to spawn so as to synchronize hatching with a suitable tide throughout the breeding season.

A. clarkii at Miyake-jima has some reproductive characters different from present findings, e.g. a weak lunar periodicity (Bell, 1976; Moyer and Bell, 1976) and a random variation in clutch size (Bell, 1976). These differences might be due to unknown geographical differences between two study sites.

Year to year variations of larval settlement and early death rate of 0-year olds. Some recent studies show that the number of recruits differed greatly from year to year for many coral reef fishes (Kami and Ikehara, 1976; Russell *et al.*, 1977; Talbot *et al.*, 1978; Williams and Sale, 1981). There also existed a 5-fold difference in numbers of settled larvae between 1983 and 1984 in the present study.

One could attribute such a difference to variations in breeding, interactions between residents and settling larvae, or some process occurring in the larval life. Variations in breeding were, however, unlikely to be a cause because neither the number of females, the number of spawnings per female, nor the clutch size in 1984 were larger than those in 1983. Interactions of larvae with residents could not be a primary cause because although adults had an inhibitory effect on larval settlement (Fig. 4, Table 3) and the number of adult pairs was smaller in 1984 than in 1983 by four pairs, only 30 of 225 larvae which had been occupied by those four pairs.

The number of 0-year olds within the study area increased steadily throughout most of the period of settlement in 1983. On the other hand, they reached a maximum in the first half of the period of settlement, and then decreased gradually in 1984 (Fig. 6). The increase was due to larval settlement and immigration; settled larvae accounted for 84.9% and 77.1% of 0-year olds in 1983 and 1984 respectively. The decrease was probably due to death and emigration. If the rate of immigration to the study area was equal to the rate of emigration from the study area, the number of dead 0-year olds would be the number of 0-year olds which appeared within the study area minus the number of existing 0-year olds minus the total of new fishes which were immigrants. The proportion of dead 0-year olds to the total of new 0-year olds for the season was estimated at 26.4% and 38.0% until October 22 in 1983 and 1984 respectively. This difference might be mainly due to the difference in the degree of crowding in sea anemones each year. Agonistic interactions among 0-year olds were so frequent that small 0-year olds were driven away to the outskirts of sea anemones (pers. obs.). This might increase the chance of exposure of small 0-year olds to predation.

Daily pattern of larval settlement and its relationship to the daily pattern of breeding. A characteristic pattern of larval settlement was repeated at each lunar cycle throughout the period of settlement. The number of settled larvae peaked around the first and the third quarter of the moon in 1983, and did between the new moon and the half moon and between the half moon and the new moon in 1984 (Fig. 5). In both years, settlement was low around the full moon.

In some tropical coastal fishes, the inshore

movement of larvae and juveniles are synchronized with a particular lunar phase (for review, see Johannes, 1978). Johannes (1978) noticed that most of these fishes migrate inshore mainly on spring tides and suggested that there is a selective advantage for the young to move inshore at times when they can maintain a maximum distance between themselves and the bottom, thereby minimizing their contact with benthic predators. The timing of larval settlement at Murote Beach did not follow this hypothesis, in that larval settlement peaked rather near neap tides. The temperate population of *A. clarkii* shows many differences in behavior when compared to conspecifics and other anemonefishes from the tropics (Moyer, 1980). This timing of larval settlement also might be influenced by temperate environmental conditions.

One feature of the daily pattern of settlement that might be a product by a selection pressure was that the number of settled larvae was small near the full moon. If the larvae settled at night to avoid diurnal planktivores, the light of the full moon might make it easy for nocturnal planktivores to find out the larvae.

It is possible that the observed daily pattern of larval settlement occurs unrelated to any selective advantage. While some have suggested that settlement patterns are a product of spawning patterns (Randall, 1961; Luckhurst and Luckhurst, 1977; Russell *et al.*, 1977) this can not be the case here because two features of the settlement pattern, two differently sized peaks during a lunar month and the extreme peak between 15 to 27 July in 1984, could not be explained from the spawning pattern (Figs. 3, 5). There are some reports that some process occurring during planktonic life is responsible for the pattern of settlement (e.g. Victor, 1983; Williams, 1983). Processes occurring during larval life which affect larval mortality and larval return to home reef may play an important role in determining patterns of settlement.

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温帯産クマノミの繁殖と定着の時間的パターン

越智晴基

クマノミの繁殖活動を四国の内海で 1983 年と 1984 年に調査した。1983 年には半月の頃に産卵活動のピークがあったが、1984 年には明瞭なピークは認められなかつ

た。1 雌当りの産卵数は繁殖期間中に大幅に変化し、両年共に6月後半から7月後半にかけてピークがあった。50 m×50 m の調査枠内に定着した仔魚の数は1983年には45匹、1984年には225匹であった。成魚は仔魚の定着を阻害するが、この両年の定着数の差は定住魚の阻害効果によるものではない。また、両年の繁殖の違いによるものでもない。定着後まもない0才魚の死亡率は1983年よりも1984年のほうが高く、これは宿主イソギンチャクの込み合い度の違いによるものと推測される。定着

期間は繁殖期間とほぼ一致していた。両年共に1月周期の間の定着数には明瞭なピークが認められ、満月の頃に定着数は減少した。仔魚の定着数の変化パターンは繁殖活動の変化パターンを反映しているとは考えられなかった。

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