

Population dynamics of goby *Paragobiodon echinocephalus* and host coral *Stylophora pistillata*

Tetsuo Kuwamura¹, Yutaka Yogo², Yasuhiro Nakashima³

¹Biological Laboratory, Faculty of Liberal Arts, Chukyo University, Nagoya 466, Japan

²Showa Women's High School, Hita, Oita 877, Japan

³Department of Zoology, Faculty of Science, Kyoto University, Kyoto 606-01, Japan

ABSTRACT: The goby *Paragobiodon echinocephalus* is an obligate associate of the branching coral *Stylophora pistillata*. Population fluctuations of both species were observed over 3 yr on the reef flat of Sesoko Island, Okinawa, Japan. Coral growth was negatively correlated with size, because partial death or destruction often occurred in large corals. The number and maximum size of gobies in a coral were positively correlated with coral size. Small corals (<5 cm diameter) were seldom used, while large corals (>15 cm) were almost always inhabited by 2 or more fish. The goby spawned from April to November, and juveniles (7 to 15 mm) increased in summer. The number of gobies and the corals occupied by gobies increased with the influx of juveniles. The goby population declined during winter and spring except in a year when corals >5 cm became abundant. When the number of large corals decreased, large gobies (30 to 40 mm) decreased in number and the occupation rate of smaller corals increased. Mortality of marked fish (>15 mm) was correlated with that of corals. Thus the population fluctuation of the goby was affected by both the availability of host coral and the goby's seasonal reproductive cycle.

KEY WORDS: Coral-dwelling goby · *Paragobiodon* · *Stylophora* · Growth · Mortality · Reproductive seasonality · Population dynamics

INTRODUCTION

The distribution and abundance of many reef fishes are affected by scleractinian corals (Hiatt & Strasburg 1960, Smith & Tyler 1975, Sale 1980, 1991, Lowe-McConnell 1987, Sano et al. 1987). Two genera of small gobies, *Gobiodon* and *Paragobiodon*, strongly depend on the branching corals *Acropora* and pocilloporids respectively for food, shelter and spawning sites (Tyler 1971, Kuwamura 1976, Lassig 1976, 1977, Yamamoto 1980). The number of *Paragobiodon* individuals in a coral is positively correlated with coral size (Lassig 1976), and so goby population fluctuations should be influenced by the growth and mortality of their host corals. However, there have been no long-term studies linking the population dynamics of gobies with that of their host corals.

We focused on the coral *Stylophora pistillata* and its associated goby *Paragobiodon echinocephalus*. Although Lassig (1976, 1977) designated the goby

species inhabiting *Pocillopora damicornis* as *Paragobiodon echinocephalus*, it is probably *Paragobiodon modestus* and Lassig's '*Paragobiodon* sp.' in the coral *S. pistillata* is probably *P. echinocephalus*, according to the recent literature (Yoshino & Yamamoto 1984, Winterbottom & Emery 1986, Myers 1989). This paper describes population fluctuations of the coral *S. pistillata* and the consequences for its goby associate.

METHODS

We conducted field research using SCUBA on the fringing reef of Sesoko Island (26° 38' N, 127° 52' E), Okinawa, southern Japan (Fig. 1). Preliminary observations showed that *Paragobiodon echinocephalus* inhabited only living *Stylophora pistillata* which, except for a few juvenile *P. melanosomus*, were not used by other *Paragobiodon* spp. *P. melanosomus* and *P. xanthosomus* were found in *Seriatorpora hystrix*, and *P. lacunicolus* and *P. modestus* in *Pocillopora damicornis*.

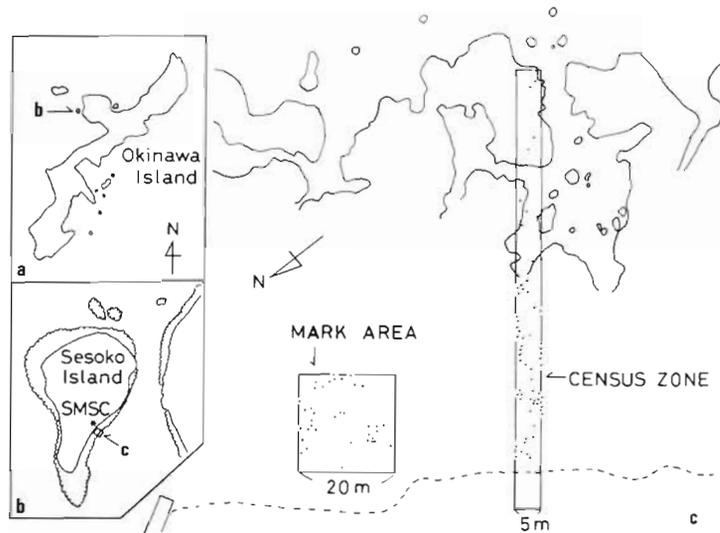


Fig. 1. Map of study area (c), with location at Sesoko Island (b) and Okinawa Island (a). —: reef margin; - -: shoreline at low water of spring tides. Positions of the coral *Stylophora pistillata* (>5 cm AD) given by dots in (c)

Two study areas were chosen on the reef flat near the Sesoko Marine Science Center (SMSC) of the University of the Ryukyus: the Census Zone was a 5 × 90 m area extending from the shore to the reef edge, and the Mark Area was a 20 × 20 m plot near the Census Zone (Fig. 1). Only underwater observations were made in the Census Zone so as not to disturb the coral, but in the Mark Area coral was collected so that gobies could be accurately counted and measured. Water depth was about 5 m at the offshore base of the reef edge and averaged about 2 m in the middle of the reef flat at high tides.

In the Census Zone observations were made every 2 to 4 mo from April 1987 to April 1989; additional observations were made in March 1990 and 1991. All *Stylophora pistillata* >9 cm in their major axis were plotted on a map (Fig. 1). The length (L), width (W) and height (H) of corals were measured to the nearest cm. When a part of a coral colony was dead, the size of the living part was measured. Instead of the geometric mean diameter [$GMD = (L \times W \times H)^{1/3}$; see Loya 1976a, b], the simple average diameter [$AD = (L + W + H)/3$] is used as an indicator of coral size in this paper. Of course, these 2 indicators are strongly correlated (e.g. $AD = 0.260 + 1.026 GMD$, $r = 0.994$, $n = 57$ in April 1987). The larger the difference among L, W and H, the larger the difference between AD and GMD; AD represents the effect of the major axis more directly than GMD. When the size of the living part of a large coral decreased below 5 cm AD by partial death or destruction, it was regarded as dead because such corals never grew larger during the study period.

Gobies associated with each coral were counted and the presence of egg clutches noted. *Paragobiodon echinocephalus* spawns adhesive eggs on branches of the coral and the clutch is guarded by the male parent for about 5 d (Kuwamura et al. 1993). Gobies and corals on 3 patch reefs (2, 3.5 and 3.5 m in diameter) situated 10 to 25 m off the reef edge were also surveyed using the same methods.

In the Mark Area observations and collections were conducted every 1 to 3 mo from May 1988 to March 1991. *Stylophora pistillata* >5 cm in their major axis were measured by the same method as described above. After the survey of gobies and their egg clutches, corals inhabited by gobies were detached from the substrate by hammer and chisel, put into a plastic bag and returned to the laboratory. There all gobies were removed from each coral, anaesthetized with quinaldine solution and measured to the nearest 0.1 mm total length (TL). Gobies >15 mm TL were marked by subcutaneous injection of colored dye

(Alcian Blue) at 1 or 2 positions on the body for individual discrimination. Then the fish with their host coral were returned to the collection sites, the coral being fixed by string attached to nails driven into the bottom around it. Subsequent collections of the corals were easily made by cutting the string.

The number of large corals decreased in the Mark Area during the study period, and 14 corals (11.7 to 25.3 cm AD) without gobies were transplanted from other sites; 2 in May 1989 and 4 in September–October 1990 were exchanged for nearly dead corals, and 1 in August 1988, 4 in May 1989 and 3 in September 1990 were newly set. Thereafter, these corals were studied by the same method as mentioned above.

In this paper coral growth and mortality in the 2 study areas are compared to evaluate the degree of disturbance by the collection–return method, and results from the Mark Area are used to analyze the population dynamics of the goby.

RESULTS

Growth and mortality of host coral

Stylophora pistillata was not found in the intertidal zone, but was common on the reef flat and patch reefs. Distribution of corals >5 cm AD in the Census Zone in April 1987 and Mark Area in May 1988 are shown in Fig. 1. Density was 0.13 and 0.12 m⁻² respectively. On the 3 patch reefs 9 corals (>5 cm) were present at a density of 0.20 m⁻² in April 1987. Coral density on the

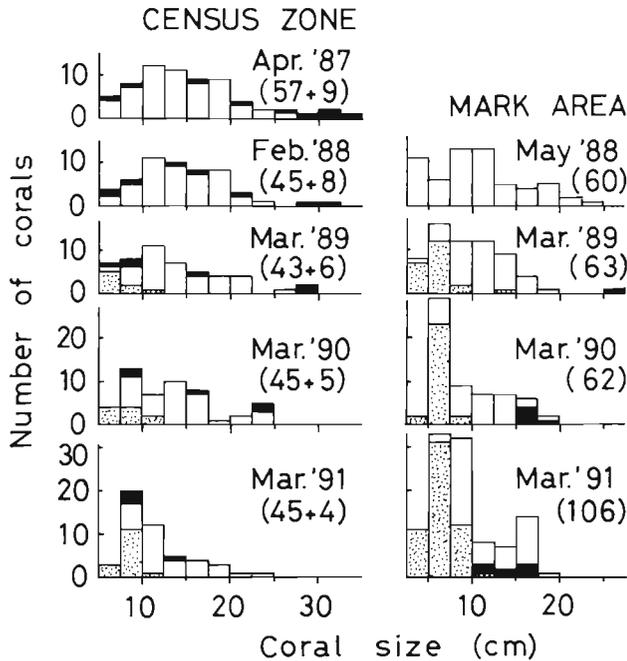


Fig. 2. *Stylophora pistillata* size-frequency distribution. Total no. of corals in parenthesis (+n: patch reefs). Solid bars: corals on the patch reefs (left) or those transplanted (right); dotted bars: newly measured corals. Corals <9 cm and <5 cm in their major axis were not counted in the Census Zone and Mark Area, respectively

patch reefs was higher than on the reef flat, but no *S. pistillata* were found on some other patch reefs in the vicinity. Maximum coral size was greater on the patch reefs (36 cm) than on the reef flat (26 cm).

Table 1. *Stylophora pistillata*. Growth rate of coral. Increase in average diameter (AD; mean \pm SD cm) per year is shown with no. of corals in parentheses. r: correlation coefficient between original size and growth increment; a: intercept; b: slope of regression line. *p < 0.05, **p < 0.01, ***p < 0.001

| Size class (AD, cm) | Feb 1988 ^a -Mar 1989 | Mar 1989 -Mar 1990 | Mar 1990 -Mar 1991 |
|---------------------|---------------------------------|--------------------|--------------------|
| Census Zone | | | |
| 5 - 15 | 0.7 \pm 2.0 (20) | 1.8 \pm 1.9 (26) | 0.9 \pm 1.5 (21) |
| 15 - 26 | -1.4 \pm 4.5 (15) | -0.2 \pm 2.3 (9) | -1.7 \pm 3.8 (9) |
| r (n) | -0.271 (35) | -0.425* (35) | -0.435* (30) |
| a | 3.173 | 3.778 | 3.550 |
| b | -0.230 | -0.192 | -0.260 |
| Mark Area | | | |
| 2.5 - 5 | 2.6 \pm 0.3 (4) | 2.1 \pm 0.9 (3) | 3.8 (1) |
| 5 - 15 | 1.1 \pm 1.7 (29) | 1.9 \pm 1.3 (24) | 2.6 \pm 1.4 (38) |
| 15 - 25 | -3.8 \pm 4.6 (7) | -3.0 \pm 5.2 (3) | -0.1 \pm 1.9 (5) |
| r (n) | -0.774*** (40) | -0.472** (30) | -0.532*** (44) |
| a | 5.491 | 4.077 | 4.390 |
| b | -0.480 | -0.290 | -0.227 |

^aMay 1988 for the Mark Area

Table 2. *Stylophora pistillata*. Survival rate of coral. Annual survival rates (%) are shown, with no. of corals at the beginning of each period in parentheses

| Size class (AD, cm) | Feb 1988 ^a -Mar 1989 | Mar 1989 -Mar 1990 | Mar 1990 -Mar 1991 |
|---------------------|---------------------------------|--------------------|--------------------|
| Census Zone | | | |
| 5 - 15 | 74.1 (27) | 86.7 (30) | 65.6 (32) |
| 15 - 26 | 83.3 (18) | 69.2 (13) | 69.2 (13) |
| Mark Area | | | |
| 2.5 - 5 | 36.4 (11) | 37.5 (8) | 50.0 (2) |
| 5 - 15 | 78.4 (37) | 49.0 (49) | 73.1 (52) |
| 15 - 25 | 58.3 (12) | 50.0 (6) | 62.5 (8) |

^aMay 1988 for the Mark Area

During the study period larger corals decreased in number in both study areas (Fig. 2). The number of corals which were newly measured, i.e. recruited into the smallest size classes, was largest in March 1991 in both study areas (Fig. 2). This resulted in a considerable increase in the total number in the Mark Area during 1990-91.

Annual growth rates were calculated excluding 'dead' corals (Table 1). Coral growth rate was negatively correlated with size. The regression parameters, slopes and intercepts, did not differ significantly among years or between the 2 study areas (p > 0.05, Table 1). Partial destruction sometimes occurred while collecting corals in the Mark Area; the large decrease (-7.6 cm \pm 4.7, n = 3) in the largest size class (20 to 25 cm) in 1988-89 can be attributed to this. The maximum growth observed was 6 cm yr⁻¹ (from 10.0 to 16.0 cm).

Survival rate of the coral in each year is shown in Table 2. In the Census Zone survival rate did not differ significantly among size classes (>5 cm) nor among years (p > 0.05, χ^2 test or Fisher's exact probability test). The average annual survival rate was 75%. Similar survival rates were observed on the patch reefs (67 to 89%, n = 4 to 9). In the Mark Area the survival rate of the smallest size class (2.5 to 5 cm) was lowest every year but significantly only in 1988-89 (p < 0.05, χ^2 test). The survival rate of corals >5 cm was 74% and 72% in 1988/89 and 1990/91, similar to the rates in the Census Zone, but it was much lower (49%) in 1989-90 (p < 0.05, χ^2 test). This was a result of mass predation (25 of 33 dead corals in that year) by the crown-of-thorns starfish *Acanthaster planci* during April 1989.

Although causes of coral death could not always be determined, there are several

possible sources of mortality other than predation by *Acanthaster planci*. Typhoons often caused heavy waves during July and October, and some corals were detached from the substrate, destroyed by collision with rolling rocks and stones or buried under sand and rubble. Predation by another starfish, *Culcita novae-guineae*, was also observed. Some corals were overgrown by neighboring corals *Montipora aequituberculata* and *Seriatopora hystrix*, softcorals *Lobophytum crassum* and *Sarcophyton glaucum*, or algae cultivated by the territorial damselfish *Stegastes nigricans*. Partial death also occurred from the overgrowth of algae used for the nest tube of the snapping shrimps *Alpheus* spp. (mostly *A. pachychirus*), which were associated with the coral.

Seasonal fluctuation of goby population

The smallest *Paragobiodon echinocephalus* found in a coral was 6.9 mm TL, and the largest adult 41.5 mm. The size-frequency distribution of the goby in the Mark Area showed seasonal change (Fig. 3). The frequency of smaller fish increased in summer and

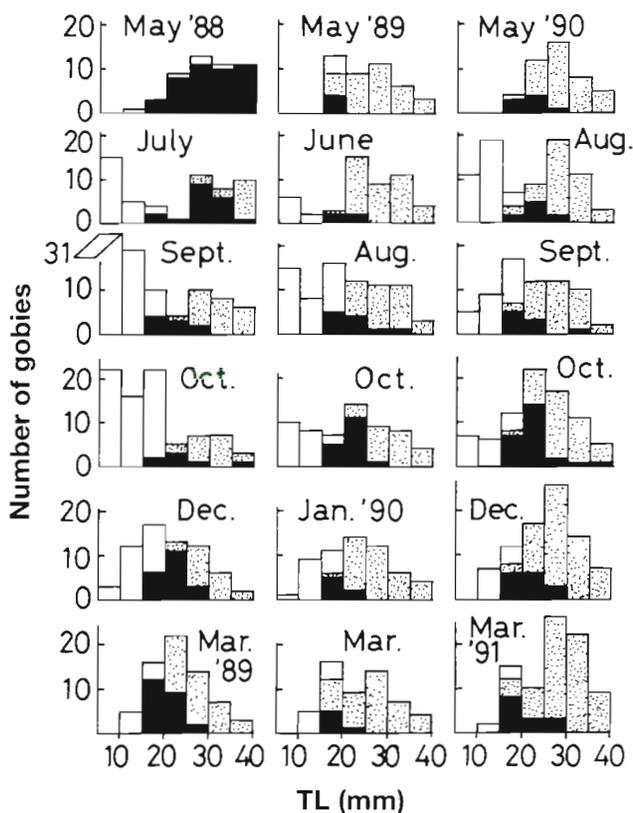


Fig. 3. *Paragobiodon echinocephalus* size-frequency distribution in the Mark Area. Solid and dotted bars indicate newly and already marked fish, respectively

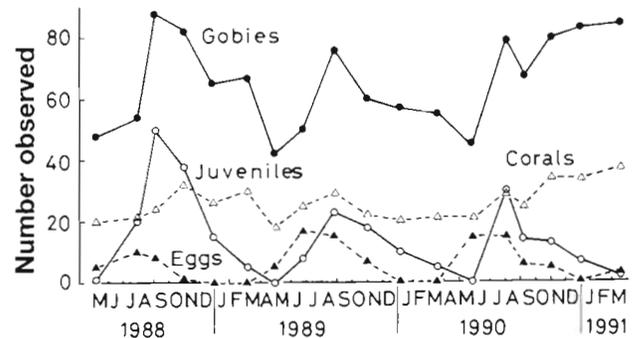


Fig. 4. *Paragobiodon echinocephalus*. Seasonal population fluctuation in the Mark Area. Total no. of gobies (●); no. of juveniles < 15 mm TL (○); no. of corals inhabited by gobies (Δ); and no. of corals with goby eggs (▲) are shown

autumn and decreased in winter and spring. Since a 10 mm juvenile grew to 17 mm in 2 mo in a tank with flowing seawater (unpubl. data), small gobies < 15 mm can be regarded as newly settled after the previous census. Most fish grew to over 20 mm by May (Fig. 3).

Egg clutches were found from late April (late March in 1991) to early November, and most frequently in summer (Fig. 4). The water temperature on the bottom of the reef flat was 21 to 24 °C in April, 28 to 32 °C in August, and 22 to 25 °C in early November; the goby bred only during the warmer season. The peaks of juvenile settlement occurred a few months later than those of breeding (Fig. 4). There were fewer egg clutches observed in 1988 than in 1989, but more juveniles settled in 1988 than in 1989 (Fig. 4). Apparently reproductive output in the study area was not directly reflected in juvenile recruitment.

The total number of gobies increased during summer and autumn as a result of juvenile recruitment, and then usually decreased during winter and spring (Fig. 4). The number of corals inhabited by gobies was relatively stable, but increased slightly during summer and autumn (Fig. 4), because juvenile gobies sometimes settled into corals smaller than those used by adults (see Fig. 5). The number of corals occupied was positively correlated with the total number of gobies ($r = 0.824$, $n = 18$, $p < 0.001$).

Growth rates of marked gobies (> 15 mm TL) during the breeding season ($0.49 \text{ mm} \pm 0.38 \text{ SD mo}^{-1}$, $n = 37$) did not differ from those in the rest of the year ($0.55 \text{ mm} \pm 0.57$, $n = 118$) ($p > 0.05$, Mann-Whitney *U*-test). The maximum growth rate observed in a shorter period was 5.0 mm mo^{-1} (from 16.6 mm at the end of July to 22.8 mm at the beginning of September). The growth rates suggest that the newly found, unmarked fish > 25 mm, which were observed throughout the year (Fig. 3), must have immigrated from corals outside of the study area.

Effects of host coral on goby population

Small corals <5 cm AD were seldom inhabited by *Paragobiodon echinocephalus*, and the rate of occupation by the goby increased with coral size (Table 3). The number of gobies in a coral was also positively correlated with coral size (Fig. 5). Up to 16 gobies occupied a single coral in summer, when many juveniles settled. The average number of gobies in a coral in the Mark Area varied from 2.0 (June 1989) to 3.6 (September 1988) with the overall mean of 2.5 ± 0.35 SD ($n = 18$). The density per coral was weakly correlated with the total number of gobies ($r = 0.409$, $n = 18$, $0.1 > p > 0.05$) but not with the number of corals occupied ($r = -0.176$, $p > 0.05$).

Large corals >15 cm were almost always inhabited by 2 or more gobies (Fig. 5). When the number of large corals decreased during 1988–89 in the Mark Area, the occupation rate of smaller corals increased (Table 3). When empty large corals (14.0 to 25.3 cm, $n = 8$) were transplanted into the Mark Area, all were inhabited by gobies within 2 to 4 mo. Small juveniles settled into 6 corals, and marked fish (>25 mm TL) immigrated into 7 corals.

The body size of the largest goby in a coral was also positively correlated with coral size (Fig. 5). Large gobies >30 mm were usually found only in large corals >15 cm. The annual change in number of large gobies >30 mm in the Mark Area (22 in May 1988, 10 in March 1989, 11 in March 1990 and 31 in March 1991; Fig. 3) corresponded with that of large corals >15 cm (12, 6, 8 and 15 respectively; Fig. 2) ($r = 0.985$, $n = 4$, $p < 0.05$). Small corals <10 cm were rarely inhabited by gobies >20 mm or by 2 gobies (Fig. 5), and were thus rarely used by the fish for breeding. The smallest was a 7.2 cm coral that was used by the smallest breeding pair observed (17.2 mm female and 17.3 mm male).

The total number of gobies and occupied corals did not decrease in the winter of 1990–91, although the number of juveniles <15 mm decreased as in other years (Fig. 4). The increased number of corals >5 cm that had grown and survived in that year (Fig. 2, Table 3) may have provided additional habitats for growing fish.

Survival rate of marked gobies (>15 mm) was higher in the non-breeding season than the breeding season (Table 4). This was correlated with the survival rate of corals ($r = 0.905$, $n = 5$, $p < 0.05$, Table 4), which was lower during April and October as a result of the mass predation by the starfish and physical abrasion by heavy waves associated with typhoons, as already mentioned.

Table 3. *Stylophora pistillata*. Percentage of corals inhabited by goby *Paragobiodon echinocephalus* (with no. of corals in parentheses) observed in the Mark Area

| AD (cm) | May 1988 | Mar 1989 | Mar 1990 | Mar 1991 |
|---------|-----------|-----------|-----------|------------|
| 2.5 – 5 | 0.0 (11) | 0.0 (8) | 0.0 (2) | 0.0 (11) |
| 5 – 10 | 5.3 (19) | 17.9 (28) | 10.5 (38) | 18.5 (65) |
| 10 – 15 | 38.9 (18) | 85.7 (21) | 57.1 (14) | 73.3 (15) |
| 15 – 20 | 100.0 (9) | 100.0 (5) | 100.0 (8) | 100.0 (15) |
| 20 – 25 | 100.0 (3) | 100.0 (1) | – (0) | – (0) |

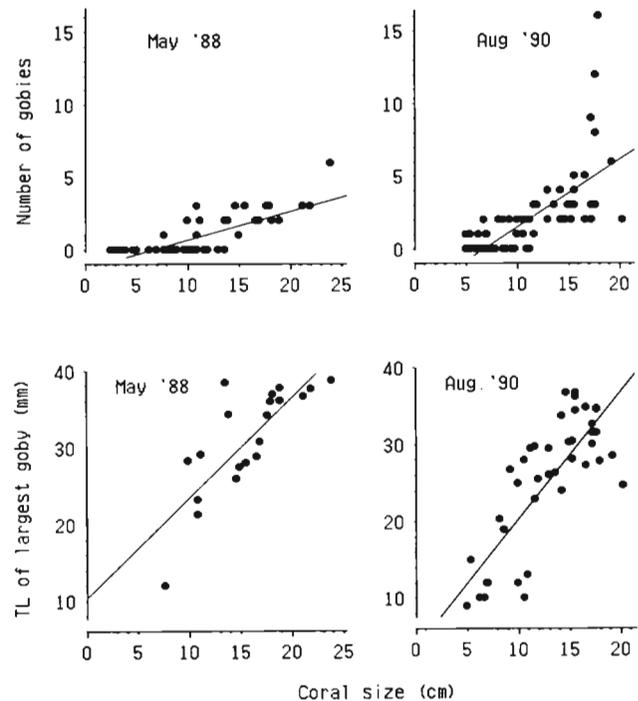


Fig. 5. Relation between no. of gobies, or TL of the largest goby, and coral size in the Mark Area. Examples at the beginning (May 1988) and in the middle of the breeding season (August 1990; including 12 corals around the Mark Area) are shown. Top left: $r = 0.796$, $n = 60$, $p < 0.001$; top right: $r = 0.699$, $n = 72$, $p < 0.001$; bottom left: $r = 0.798$, $n = 20$, $p < 0.001$; bottom right: $r = 0.797$, $n = 42$, $p < 0.001$

Table 4. Survival rates of marked goby *Paragobiodon echinocephalus* (>15 mm TL) and host coral *Stylophora pistillata* (>5 cm AD) in the Mark Area. Survival rate (%) per 6 mo is shown with no. at the beginning of each period in parenthesis. ** $p < 0.01$, *** $p < 0.001$ (χ^2 test between values to the left and right of the asterisks)

| | Oct 1988 –Mar 1989 | Mar 1989 –Oct 1989 | Oct 1989 –Mar 1990 | Mar 1990 –Oct 1990 | Oct 1990 –Mar 1991 |
|-------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|
| Goby | 71.1 (24) ** | 37.1 (58) *** | 88.3 (45) *** | 47.0 (54) *** | 79.4 (69) |
| Coral | 87.3 (45) ** | 59.5 (55) *** | 92.9 (37) | 80.9 (60) | 92.7 (54) |

DISCUSSION

The numbers of both species and individuals of reef fishes severely decrease after the complete death and destruction of corals in a wide area (Sano et al. 1987). However, few studies have considered how less-catastrophic mortality and normal growth of coral species affect the population dynamics of associated fish.

The host coral *Stylophora pistillata* is known to have characteristics of an *r*-strategist such as high rates of settlement, growth and mortality (Loya 1976a, b). These studies (and also Sakai & Nishihira 1991) focused on small corals (<10 cm diameter), but we studied larger corals also. Large corals >15 cm often decreased in size due to partial death or destruction. The growth rate was negatively correlated with size, as has been reported in some other coral species (Hughes & Jackson 1985, Hughes & Connell 1987), even though the linear extension rate of branches is independent of colony size (Kinzie & Sarmiento 1986). Survival rates of *S. pistillata* did not differ among size classes except for the smallest (2.5 to 5 cm). Mass predation by the starfish *Acanthaster planci* occurred in one of the study areas, and except for that year the survival rate of corals did not differ between the 2 areas. Growth patterns did not differ either between the 2 study areas, though partial destruction sometimes occurred while collecting large corals in the Mark Area. Thus the collection-return method adopted in the Mark Area seems to have caused little disturbance of the growth and mortality of the coral. So this method, which enables accurate counting and measuring of the associated fish, is useful for a long-term study on the population of coral-dwelling fish.

We found that the number and maximum size of the goby *Paragobiodon echinocephalus* were correlated with size of the host coral *Stylophora pistillata*. The goby seldom inhabited small corals <5 cm, and rarely bred in those <10 cm. Small corals may not provide enough food, nest space or stable shelter for the goby. Growth rate of small corals (2.5 to 5 cm) was 2 to 3 cm yr⁻¹, suggesting that if a fish settles on a small coral, the host will not grow large enough to provide a suitable nesting site by the time the goby attains reproductive size (17 mm TL). As only the largest 2 fish breed monogamously in a coral (Kuwamura et al. 1993), the abundance of large corals may limit the reproductive output of the goby population.

Seasonal increases in abundance of *Paragobiodon echinocephalus* were associated with reproductive activity in the goby population. Peaks of juvenile settlement occurred a few months after those of breeding activity, but the abundance of recruits did not always correspond with the reproductive output. We know little about the goby's pelagic larval stage and the

recruits into the study population may have included those produced by other populations (Robertson 1991). Goby density per coral and the number of corals inhabited by the goby increased during summer and autumn because juveniles settled into corals occupied by adults as well as unoccupied smaller corals.

Changes in the coral population also influence goby abundance. When the number of corals >5 cm increased, the total number of gobies did not decrease even in winter and spring. When large corals decreased in number, the number of large gobies decreased and the occupation rate of smaller corals increased. The goby may try to move into another colony after death or destruction of its host, but predation pressure outside the coral seems to be high (Lassig 1976) and the lower survival rate of the marked gobies >15 mm in the breeding season was correlated with that of corals >5 cm.

Population dynamics of *Paragobiodon echinocephalus* are driven by the combined effects of changes in the host coral population and the goby's reproductive seasonality.

Acknowledgements. We are grateful to the staff of Sesoko Marine Science Center of the University of the Ryukyus, which provided the facilities for the field research. Naomi Tanaka provided an original map of the study area. We also thank Robert Kinzie III, Kazuhiko Sakai and 2 anonymous reviewers for comments on the manuscript. This work was supported in part by the fund to T.K. as the visiting researcher of SMSC (1988) and the Grant-in-Aid for Scientific Research on Priority Areas (# 02248216, 03234108, 04218108) from the Japan Ministry of Education, Science and Culture. This is Contribution # 258 from Sesoko Marine Science Center.

LITERATURE CITED

- Hiatt, R. W., Strasburg, D. W. (1960). Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. *Ecol. Monogr.* 30: 65–127
- Hughes, T. P., Connell, J. H. (1987). Population dynamics based on size or age? A reef-coral analysis. *Am. Nat.* 129: 818–829
- Hughes, T. P., Jackson, J. B. C. (1985). Population dynamics and life histories of foliaceous corals. *Ecol. Monogr.* 55: 141–166
- Kinzie, R. A. III, Sarmiento, T. (1986). Linear extension rate is independent of colony size in the coral *Pocillopora damicornis*. *Coral Reefs* 4: 177–181
- Kuwamura, T. (1976). Seasonal occurrence of fishes in the interstice of shrub corals on the rocky reef of Sirahama, Japan. *Nankiseibutu* 18: 15–22 (In Japanese with English summary)
- Kuwamura, T., Yogo, Y., Nakashima, Y. (1993). Size-assortative monogamy and paternal egg care in a coral goby *Paragobiodon echinocephalus*. *Ethology* (in press)
- Lassig, B. R. (1976). Field observations on the reproductive behaviour of *Paragobiodon* spp. (Osteichthyes: Gobiidae) at Heron Island Great Barrier Reef. *Mar. Behav. Physiol.* 3: 283–293

- Lassig, B. R. (1977). Socioecological strategies adopted by obligate coral-dwelling fishes. Proc. 3rd int. coral Reef Symp. 1: 565–570
- Lowe-McConnell, R. H. (1987). Ecological studies in tropical fish communities. Cambridge Univ. Press., Cambridge
- Loya, Y. (1976a). The Red Sea coral *Stylophora pistillata* is an *r* strategist. Nature 259: 478–480
- Loya, Y. (1976b). Settlement, mortality and recruitment of a Red Sea scleractinian coral population. In: Mackie, G. O. (ed.) Coelenterate ecology and behavior. Plenum Press, New York, p. 89–100
- Myers, R. F. (1989). Micronesian reef fishes. Coral Graphics, Guam
- Robertson, D. R. (1991). The role of adult biology in the timing of spawning of tropical reef fishes. In: Sale, P. F. (ed.) The ecology of fishes on coral reefs. Academic Press, London, p. 356–386
- Sakai, K., Nishihira, M. (1991). Immediate effect of terrestrial runoff on a coral community near a river mouth in Okinawa. Galaxea 10: 125–134
- Sale, P. F. (1980). The ecology of fishes on coral reefs. Oceanogr. mar. Biol. A. Rev. 18: 367–421
- Sale, P. F. (ed.) (1991). The ecology of fishes on coral reefs. Academic Press, London
- Sano, M., Shimizu, M., Nose, Y. (1987). Long-term effects of destruction of hermatypic corals by *Acanthaster planci* infestation on reef fish communities at Iriomote Island, Japan. Mar. Ecol. Prog. Ser. 37: 191–199
- Smith, C. L., Tyler, J. C. (1975). Succession and stability in fish communities of dome-shaped patch reefs in the West Indies. Am. Mus. Novit. 2572: 1–18
- Tyler, J. C. (1971). Habitat preferences of the fishes that dwell in shrub corals on the Great Barrier Reef. Proc. Acad. nat. Sci. Philad. 123: 1–26
- Winterbottom, R., Emery, A. R. (1986). Review of the gobioid fishes of the Chagos Archipelago, Central Indian Ocean. Life Sci. Contr. 142, Royal Ontario Museum, Toronto
- Yamamoto, T. (1980). Embryonic development in *Paragobiodon lacunicola* and the spawning sites of *Gobiodon* spp. and *Paragobiodon* spp. (Pisces: Gobiidae). Biol. Mag. Okinawa 18: 17–24
- Yoshino, T., Yamamoto, T. (1984). *Paragobiodon echinocephalus* (Rüppell). In: Masuda, H., Amaoka, K., Araga, C., Ueno, T., Yoshino, T. (eds.) The fishes of the Japanese Archipelago. Tokai University Press, Tokyo, p. 255–256

This article was submitted to the editor

Manuscript first received: January 7, 1993

Revised version accepted: September 23, 1993