

## Reproductive Behavior and Patterns of Sexuality in the Japanese Labrid Fish *Thalassoma cupido*

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(Received January 25, 1977)

**Abstract** The reproductive behavior and sexual organization of *Thalassoma cupido* (Temminck et Schlegel) were studied at the island of Miyake-jima, Japan, from June 1974 to autumn of 1975. Spawning begins in mid-June, continuing until the middle of September, in sea temperatures ranging from 20.0°C~28.0°C. Spawning was observed only in the morning, although courtship was rarely seen in the afternoon.

Of 195 specimens examined, 52.8% were males, 44.6% were females, while the remainder were undetermined. Both males and females have a wide size distribution, with males outnumbering females in the uppermost size range. *Thalassoma cupido* is a protogynous, diandric species. Initial and terminal color phases were noted. The initial phase includes juveniles, females, primary males, and secondary males. The terminal phase appears to be restricted to primary and secondary males.

Both pair and aggregate spawning were observed, the latter more frequently in Miyake waters. Courtship and spawning behavior are described and compared with congeners.

The current literature contains considerable information on the reproductive behavior and sexual organization of members of the labrid genus *Thalassoma* Swainson. Various aspects of the reproductive behavior and biology of the Atlantic species, *T. bifasciatum* (Bloch), have been investigated independently by numerous authors (Stoll, 1955; Randall and Randall, 1963; Zumpe, 1963; Feddern, 1965; Reinboth, 1967, 1970, 1972, 1973, 1975; Roede, 1972; Warner et al., 1975; Robertson and Hoffman, in press; Warner and Robertson, in press). The comprehensive study by Choat (1969) on the biology of labroid fishes at Heron Island, Australia, includes information on the sex structure of *Thalassoma hardwickei* (Bennett), *T. lutescens* (Lay et Bennett), *T. lunare* (Linnaeus) and *T. janseni* (Bleeker). In a subsequent study, Robertson and Choat (1974) provided further details on hermaphroditism in *T. lunare*, placing special emphasis on social and mating systems. Reinboth (1962) originally reported on diandry in *T. pavo* (Linnaeus). In a compilation of data on 16 labrid species, Reinboth (1975) summarized his findings on the sexual organization of *T. pavo*, *T. lucasanum* (Gill), *T. bifasciatum* and

*T. cupido* (Temminck et Schlegel). Aggregate spawning of *T. lucasanum* was described by Hobson (1965), and Randall and Randall (1963) briefly discussed monochromatism in *T. ballieui* (Vaillant et Sauvage).

Although *Thalassoma cupido* is one of the most abundant fishes along the Pacific coast of central Japan, no one has attempted to study the reproduction of this wrasse in detail. Matsuoka (1972) reported a single observation of aggregate spawning at Ryugu Island in a short ecological note. Moyer (1974) described and discussed the reproductive behavior of *T. cupido* on the basis of observations made over a five day period. To date, Reinboth (1975) has been the only person to examine the gonads of this species. In his small sample of nine specimens, he found no indication of spontaneous sex-inversion and stressed the need for additional studies. Noting also that dichromatism in the species had not been recorded, he stated: "Further investigations are highly desirable since it appears somewhat irritating that *Th. cupido* should be an exception within the genus *Thalassoma* with regard to its uniform coloration and its eventual gonochorism."

This paper deals principally with the sexual behavior of *Thalassoma cupido* and provides

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additional information on the reproductive ecology and physiology of the species. The occurrence of sex-inversion is reported and sexual dichromatism is described for the first time.

### Materials and methods

The reproduction of *Thalassoma cupido* was studied at Miyake-jima (34°5'N, 139°30'E), one of the Izu Islands of Japan. Using SCUBA, daily observations were made from June through September of 1974 and 1975, with less intensive studies continued throughout the remainder of each year. Field observations were supplemented with aquarium observations. Specimens used for this purpose were placed in a 158 l aquarium, illuminated by natural sunlight shining through two large glass doors adjacent to the tank. Water temperature was maintained at approximately 28.0°C. Spawning by captive fish were observed on two occasions.

Intermittent collections of specimens were made throughout the study period for examination of their gonads. A variety of methods was employed in collecting these specimens, including hook and line, fish trap, spear, and screen net. Collections were made at a number of locations around the island. A total of 220 specimens were dissected and selected gonads were prepared for histological sections. 10% formalin was used for fixation. The gonads were sectioned at 7  $\mu$  and stained with haematoxylin and eosin.

Specimens selectively collected from spawning aggregates are excluded in the sex ratio and related figures.

### Results

#### Reproductive activity as related to environmental factors

##### a. The spawning grounds

Observations of spawning were focused in Igaya Bay, on the west side of the island. Although reproductive activity was noted at various locations in the bay, it was consistently found to be highly concentrated at one area, about 150 m offshore. This spawning site encompasses an area of approximately 1460 m<sup>2</sup>, ranging in depth from 9 to 11.5 m. The bottom consists of sand with overlying

volcanic rocks and boulders, covered primarily with the brown alga *Sargassum*, a high diversity of fleshy and filamentous red algae, and intermittent growths of coral. The flow of a weak current can occasionally be felt as it passes through the spawning site.

There is some evidence to suggest that the depth at which spawning takes place varies with different size groups. Small adults showed little preference for depth, whereas larger fish appeared to be more selective. Fish of all sizes, including some as small as 50 mm TL, were commonly seen in spawning aggregates at the site described above. Aggregates observed at depths of less than 7 m consisted primarily of fish in the lower size range. Spawning was observed in water as shallow as 1 m.

##### b. The spawning season

The spawning season of *T. cupido* at Miyake-jima is restricted to a period of approximately three months, beginning in June and ending in September. The first spawning observed in 1974, was on June 17. As dives were not made previous to this date, it cannot be stated whether this was in fact the first spawning of the year. However, the following year, the spawning site was visited daily for some time before spawning was first observed, again on June 17. Reproductive activity was noted for the last time on September 15, in 1974, and on September 10, in 1975. These dates did not correspond in either year to marked changes in temperature or photoperiod.

##### c. Diurnal periodicity in spawning

Reproductive activity in Igaya Bay occurred only during a period of several hours in the morning from about 0830 to 1200. On dives made before 0800, very few wrasses were found at the spawning site. Solitary fish began to appear around 0700. Between 0800 and 0830 the formation of aggregates began and pre-spawning or courtship behavior could be observed. The number of fish at the spawning site decreased noticeably between 1100 and 1200; the latest observed spawning occurred at 1215. On rare occasions courtship behavior was noted in the afternoon, although subsequent spawning acts were not observed. However, Mr. Y. Yogo (personal communication) has witnessed mid-afternoon spawnings

by this species at Amakusa, Kyushu, on at least two occasions. At Miyake-jima no correlation was found between the timing of reproductive activities and the daily tidal rhythm.

#### d. The influence of temperature

Spawning was observed at water temperatures of 20.0°C to 28.0°C. Reproduction did not occur on the few days when the temperature fell below 20.0°C, suggesting that low temperatures inhibit reproductive activity. Yet the overall influence of temperature during the spawning season is probably slight, as periods of cold sufficient to inhibit spawning are minimal at this time. Temperature during the spawning season of 1974 ranged from 19.0°C to 27.5°C but averaged a moderate 23.3°C. The 1975 temperature range during the spawning season was 16.0°C to 28.0°C, averaging 24.8°C.

#### e. The influence of heavy rainfall

Frequently, spawning was not observed during and soon after periods of heavy rainfall. Such weather conditions resulted in an appreciable amount of silt and freshwater runoff from the cliffs surrounding the bay. Heavy overcast in combination with turbid waters noticeably reduced the visibility, on occasion making field observations difficult or impossible. Whether the lack of spawning observed during heavy rains was a direct response to such conditions remains uncertain. An intriguing question is whether mating fish are negatively influenced by chemical alterations of the water which might affect the viability of freshly fertilized eggs.

### Reproductive physiology

#### a. Size at sexual maturity

The smallest mature female collected was a 42 mm SL specimen containing fully developed ovaries with ripe eggs. The smallest mature male specimen measured 44 mm SL. Spawning aggregates comprised exclusively of these very small adults were occasionally encountered.

#### b. Sex ratio

Of 195 specimens examined, 103 (52.8%) were found to be males, 87 (44.6%) were females and the sex of 5 specimens (2.6%) could not be determined by macroscopic in-

spection. Both males and females had a wide distribution in terms of size, maintaining a ratio which closely approximated unity throughout most of the size range. However, among the largest specimens, males heavily outnumbered females (Fig. 1).

#### c. Diandry

*Thalassoma cupido* is a diandric species, its males having two types of ontogenetically, and thus morphologically, distinct testes. As

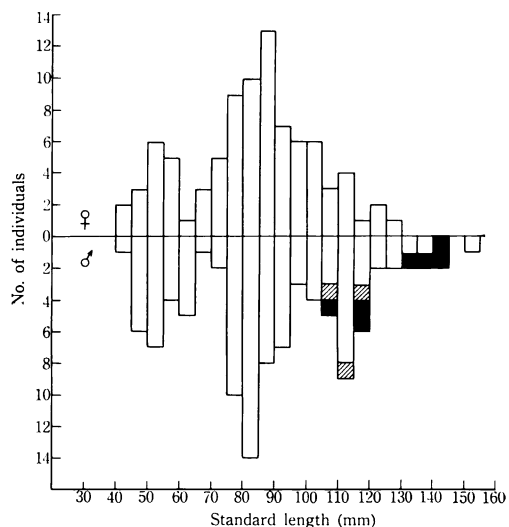


Fig. 1. Size and color distribution as related to sex of *Thalassoma cupido* collected at Miyake-jima. □, Initial color phase; ▨, intermediate color phase; ■, terminal color phase.

Table 1. Color, size, and sexual derivation of 13 male specimens of *Thalassoma cupido*.

Color phase	Standard length (mm)	Testes
Initial	112	Primary
	112	Primary
	112	Secondary
	114	Primary
	114	Primary
	119	Primary
	155	Secondary
Intermediate	108	Primary
	114	Primary
	118	Primary
Terminal	109	Primary
	144	Secondary

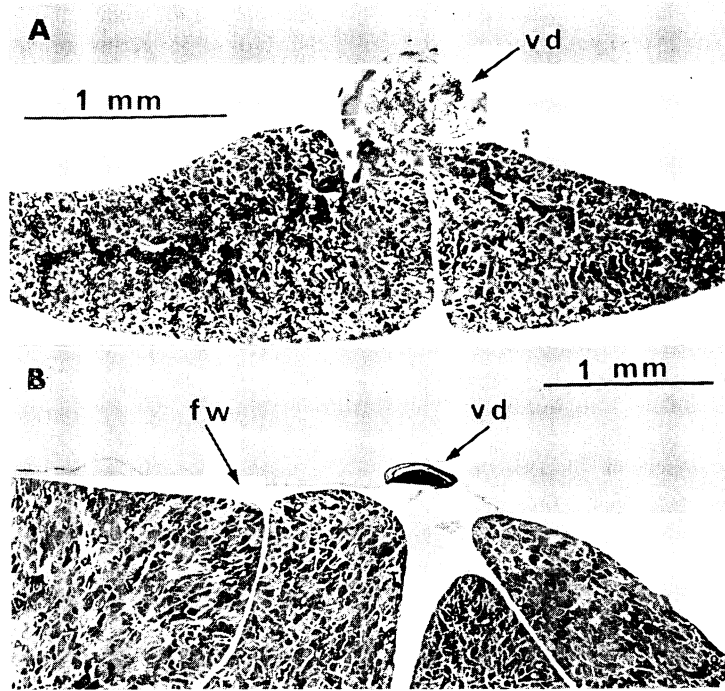


Fig. 2. Cross sections of primary testis (A) and secondary testis (B) of *Thalassoma cupido*. fw, former ovarian wall; vd, vas deferens. Photos by Dr. A. Nakazono.

shown in Table 1, histological examination of 13 testes revealed ten primary testes and three secondary testes (Fig. 2). In the latter, the testicular lobes are surrounded by a thin membrane derived from the ovarian wall. The vas deferens develops as a ramified system within this membrane. In contrast, the primary testes have a cylindrical vas deferens between the right and left lobes. Further evidence for the ovarian origin of secondary gonads lies in the arrangement of the testicular tissue, which surrounds the former ovarian cavity. Cross sections of the primary and secondary testes of this species are shown in Fig. 2.

#### Sexual dichromatism

Two color phases are found among the adults of *Thalassoma cupido*. While not sharply contrasting, these color phases are nevertheless clearly distinct. Characteristic of the more common form is the prevailing green coloration. Running along the entire body length are two broad, brick-red, irregular, longitudinal bands. These bands may be tem-

porarily broken into two series of quadrate dark blotches, or they may become very dark, appearing as two distinct black bands. A third narrower longitudinal band runs backward from the lower pectoral base, becoming somewhat faded posteriorly. The head and median fins are also green with brick-red markings. A prominent black blotch covers the second interspinous membrane of the dorsal fin. The thorax and abdomen are pale blue. The ventral and pectoral fins are hyaline, the latter with blackish tips. The intensity of this black coloration varies considerably, fading and darkening within seconds.

The color phase described above is most prevalent among fish in the lower size ranges (Fig. 1) but has a wide distribution in terms of sexual identity; it is found among juveniles, females, primary males, and secondary males. The two secondary males which were found among specimens included in this color group were fully transformed, functional males. This form will subsequently be referred to as the "initial" color phase in accordance with

the terminology proposed by Reinboth (1975).

A small minority of fish (estimated to be less than 1% of the population) undergo a color transformation to the "terminal" color phase. This is achieved primarily by a change in the green pigmentation. The ground color of the head, the body, and median fins change from green to deep blue. The pectoral fins assume a blue tinge, while the thorax and abdomen darken their original blue color. Color transformation, however, is not accompanied by the disappearance of existing markings or the addition of new traits. The final impression is that of a brightly colored, predominantly blue fish, as opposed to the drab greenish coloration peculiar to the initial phase. The terminal phase was found only among large adult males (Fig. 1). Because fish with this color pattern are scarce, the sample size is correspondingly small. However, the sexual behavior of other terminal phase fish observed in the field strongly suggests that all are males. These may be either primary or secondary in derivation.

Individuals with an intermediate color pattern were often observed underwater. However, in the sample obtained there were only three such specimens. All of these proved to be primary males.

### Reproductive behavior

In common with many labroid fishes, *Thalassoma cupido* exhibits both pair and aggregate spawning (Randall and Randall, 1963). Groups comprising only initial phase fish engage in aggregate spawning. Pair spawning is performed by a terminal phase male and an initial phase female or, more rarely, by two initial phase fish. Males displaying an intermediate color pattern also participate in pair spawning activities. Aggregate spawning is the preponderant type in the waters around Miyake-jima and may be readily observed on most days during the spawning season. Pair spawning is conspicuously less common.

#### a. Aggregate spawning

During periods of reproductive activity, large numbers of *T. cupido* gather in groups of varying sizes at the spawning site. It is estimated that the largest of these groups

comprise as many as 150 individuals. Collections from among spawning aggregates revealed a heavy preponderance of males. In one aggregate of 14 fish, 4 fish proved to be females and in another aggregate of 11 fish, only one female was found.

The groups observed at the spawning site may be best described as loose aggregations of milling fish. The aggregating fish swim an irregular path, frequently changing direction so that individual members often vary in their orientation. The characteristic motor pattern among these fish is a peculiar bobbing motion in which the entire body is moved steadily up and down by simultaneous vertical strokes of the pectoral fins. Bobbing fish swim slowly, sometimes barely moving forward at all, and often brush against the bodies of others swimming below or nearby. Also characteristic of aggregate members is a uniform change in coloration, typified by a darkening of the two broad longitudinal bands on the body which appear as dominant features.

Spawning aggregates are not always well-defined, isolated entities; aggregates may merge with neighboring groups or may break into yet smaller units. In addition to frequent departures and the arrival of new fish, mild chases contribute to the unstable nature of the aggregations. Most groups contain a single individual that behaves quite differently towards the other aggregate members, often treating them aggressively. These individuals are positioned at the periphery of the aggregation and have a greater range of movements, swimming around and above the others. They exhibit individualistic behavior, typified by more forceful movements and a distinctive manner of swimming whereby the pectoral fins are fluttered rapidly, conspicuously displaying their blackened tips. Despite their unique prespawning behavior, these fish normally participate in the spawning act in a manner identical to that of the other group members.

Occasionally, more highly organized groups may be observed, in which the fish are similarly orientated, swim at a uniform pace, and exhibit coordinated movements. In these groups, the foremost position is maintained by a single fish which appears to lead the others.

Spawning in the milling aggregations is preceded by greater cohesiveness and uniformity of movements. Immediately prior to spawning, three or more fish abruptly break away from the aggregation, move forward with accelerated fin movements, and come together in a tight group, tilting their bodies upward in a diagonal position. Sometimes this abrupt forward movement is repeated several times in rapid succession. The upward spawning dash then follows, the apex at which the eggs and sperm are released. The height of the upward dash varies considerably, from a minimum of approximately 13 cm to a maximum of about 1.5 m. Immediately after spawning, the fish move slightly apart and swim downwards with great rapidity. The wrasses may reassemble upon returning to the bottom or they may disperse. The entire spawning sequence occurs within the span of about one second.

**b. Pair spawning**

Mating pairs are temporary associations, enduring for only the short period of fertilization. Pair formation begins when the male encounters a female or isolates one by chasing and driving her into the algae. A conspicuous courtship display follows. Although the courtship sequence is not entirely rigid, it nevertheless has a characteristic pattern which can be described as follows: the male swims

back and forth or in a roughly circular path above the female, propelled primarily by a rapid fluttering of the pectoral fins. After a series of such circuits, he dips downward as he approaches the female so that he is positioned directly above her. This downward movement is accompanied by an acceleration of pectoral fin fluttering and the onset of a high speed beating of the caudal fin, a combination which creates an impression of the entire body quivering. Continuing this display, the male hovers a few centimeters above the female for several seconds, his body variously positioned in a lateral arch (Fig. 3, A) or slanted slightly upwards (Fig. 3, B). When in the former position, he may turn tight semicircles around the female, displaying alternately to her left and right sides.

If the female is not immediately receptive, the male will resume his original position and repeat the entire sequence. Most often the display is repeated a number of times before the female responds. Usually she lies nearly motionless in the algae with only her head protruding until emerging to spawn. As in aggregate spawning, the pair dash rapidly upward, usually about 25~50 cm, where the eggs and milt are released. The cloud of reproductive material is less obvious than that observed during aggregate spawning. The female appears to initiate the upward

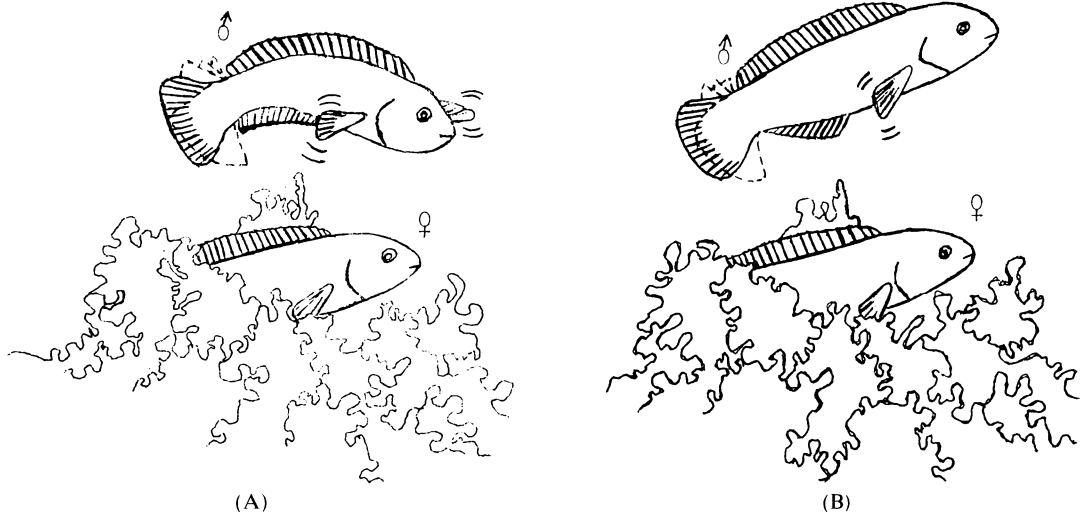


Fig. 3. Variations of the courtship display performed by pair spawning males of *Thalassoma cupido*. See text for details.

dash. During the onset she holds the leading position, with the male following closely behind.

Rarely, pair spawning is not preceded by the typical courtship display. In these instances, the male vigorously chases the female. The chase terminates when the female abruptly ceases to flee, and spawning immediately follows.

During periods of reproductive activity, individually recognized pair spawning males were found daily at the spawning site. Although these males roam widely, familiarity with individual fish revealed that select areas were visited repeatedly and occupied for lengthy periods of time. These areas are usually situated immediately within the aggregate spawning grounds or in close proximity. Often they are located along the outskirts. These areas lack rigid boundaries but usually cover a distance of about 6~10 m<sup>2</sup>. Generally they surround some natural landmark of notable stature. Spawning by such pair spawning males are largely restricted to these sites. The male dominates the area during his presence, actively chasing away some conspecifics. The tolerance with which other conspecifics are treated upon intrusion suggests that territories are defended against competitive males only, in defense of potential spawning partners. Fish that are not attacked apparently pose no threat to the reproductive success of the male. Agonistic interspecific encounters were never witnessed.

#### Response of predators to reproductive activities

Five species of pomacentrid fishes, *Pomacentrus coelestis* Jordan et Starks, *P. nagasakiensis* Tanaka, *Chromis flavomaculata* Kamohara, *C. chrysura* (Bliss), and *C. miyakeensis* Moyer et Ida, regularly fed on the pelagic eggs of this species. These damselfishes gathered above the spawning aggregations and ate the eggs as soon as they were released. Egg predation by these fishes has been described in greater detail by Moyer (1975). In addition to the above, I once also witnessed the anemonefish *Amphiprion clarkii* (Bennett) feeding on eggs released by the wrasses just outside of the host anemone. In the aquarium, egg

predation by the juvenile damselfish, *Dasycyllus reticulatus* (Richardson), was also observed. Matsuo (1972) reported an observation of *T. cupido* feeding on the fresh spawn of conspecifics in the sea. However, this probably occurs only rarely as I have never witnessed such behavior in the field.

Mating fish are also vulnerable to predation. The large concentrations of fish in spawning aggregations and conspicuous sexual displays of this species seemed to attract predators to the spawning site. The lizardfish *Synodus variegatus* (Lacepède) was the most common of these predators. On at least 30 occasions, this lizardfish was observed to attack with great speed just as the wrasses formed the characteristic close-knit group immediately prior to the upward dash. Similar attacks by *S. variegatus*, directed at pair spawning fish, were also frequently observed. The serranid *Epinephelus fasciatus* (Forsskal) also appeared to show interest in the spawning aggregations (Moyer, personal communication). Other successful predators were *Muraena pardalis* Temminck et Schlegel and an unidentified scorpaenid. When attacked, the wrasses quickly dispersed, seeking refuge under the algae where they remained for about 30 seconds.

### Discussion

#### a. Sex-inversion

It is well known that protogynous sex-inversion is common among labrid fishes. Within the family Labridae, protogyny is expressed in a variety of forms, from species in which all males are derived secondarily from females, to species in which varying numbers of individuals are born as males and never undergo a sex change. Reinboth (1975) has emphasized the extreme variability which exists between protogynous wrasses in regards to the particulars of sex and color transformation and their interrelationships. His data indicate differences even among congeneric species. Table 2 provides a comparative summary of some pertinent information currently available on members of the genus *Thalassoma* for which protogynous sex-inversion has been demonstrated.

An outstanding feature of protogynous hermaphroditism in Miyake-jima populations of

Table 2. Summary of selected information on sex and color schemes for protogynous species of the genus *Thalassoma*. Sources are given in parenthesis: 1, Choat (1969); 2, Kuhn (1976); 3, Reinboth (1962); 4, Reinboth (1967); 5, Reinboth (1970); 6, Reinboth (1972); 7, Reinboth (1973); 8, Reinboth (1975); 9, Robertson and Choat (1974); 10, Roede (1972); 11, Stoll (1955); 12, Warner and Robertson (in press); 13, Present study. \*, no distinction made between primary (1°) and secondary males (2°). Data listed under the headings "initial color phase" and "terminal color phase" are derived only from the samples examined by the authors cited and may, in some cases, be incomplete.

Species	Distribution	Diandry	Dichromatism	Initial color phase			Terminal color phase			Degree of synchronization between color change and sex change
				♀♀	1° ♂♂	2° ♂♂	♀♀	1° ♂♂	2° ♂♂	
<i>bifasciatum</i>	Bermuda, West Indies Caribbean Sea	+	+	+	+	+	-	+	+	None Sex change precedes color change (4, 6, 7, 8, 12)
<i>cupido</i>	Japan, Taiwan	+	+	+	+	+	-	+	+	Appears similar to <i>bifasciatum</i> but further investigation needed (13)
<i>hardwickei</i>	Indo-Pacific	+	+	+	+	+	-	-	+	No conclusive studies to date
<i>janseni</i>	Indo-Pacific	+	+	+	+	+	-	+	+	No conclusive studies to date
<i>lucasanum</i>	East Pacific	+	+	+	+	+	-	+	+	Appears similar to <i>bifasciatum</i> but studies to date inconclusive (8)
<i>lunare</i>	Indo-Pacific	+	+	+	+	-	-	-	+	No conclusive studies to date
<i>pavo</i>	Mediterranean Sea	+	+	+	+	+	-	+	+	Appears similar to <i>bifasciatum</i> but studies to date inconclusive (8)

*Thalassoma cupido* is that the secondary male component appears to be very small. Even in those species in which primary males contribute significantly to the population, the protogynous state is often reflected in unequal sex ratios and an unbalanced distribution of the sexes with size. For example, in a study of seven protogynous labrid species from the Caribbean, Roede (1972) found that in every species females prevailed at small sizes, while males predominated at large sizes. Furthermore, in six of the seven species, the total

number of females was significantly higher than that of males. Choat (1969) obtained similar results in his survey of labrid fishes at Heron Island, Australia. That a biased sex ratio is evident in *T. cupido* only in the uppermost size range suggests that most males enter the population during juvenile stages. Though limited, histological investigations provided further evidence for the paucity of secondary males in this species. Although 23% of the specimens examined histologically were secondary males, these specimens were



intentionally selected on the basis of their large size, and in some cases, their intermediate or terminal color pattern in order to obtain a sample which one would expect to be biased towards sex-inversed males. Taking into account this biased method of sampling, secondary males would seem to be very scarce.

Recent studies (Warner et al., 1975; Warner and Robertson, in press) have shown that in *Thalassoma bifasciatum* the proportionate number of primary males varies in populations of different sizes; they are common in large populations and rare in small ones. It has been suggested that this is the result of selective pressures against initial phase males, and thus primary males, in small populations where terminal phase males are better able to control the entire spawning area and effectively reduce the spawning activity of initial phase males. How these and other factors might interact in determining the relative number of primary and secondary males in *T. cupido* requires further study to explain the apparent scarcity of secondary males in Miyake-jima populations. The physiological process of sex-inversion in this species also deserves further attention and an extensive histological survey is needed.

**b. Comparison of reproductive behavior with congeneric species**

A high degree of similarity is found in comparing the sexual behavior of *Thalassoma cupido* with that of *T. lunare* and *T. bifasciatum*, the two congeneric species for which detailed studies have been made.

A basic characteristic common to these three species is the existence of a loosely organized social system in which permanent dominance relationships are lacking, thus denying males direct access to and control over females. This is in contrast to the system seen in *Labroides dimidiatus* (Valenciennes), in which harems are established and a rigid hierarchy is maintained based on the dominance of a single male over a group of females (Robertson and Choat, 1974). Robertson and Hoffman (in press) have suggested that, in *T. bifasciatum*, free female mate choice and the need for males to compete for spawnings has led to the development of specific male sexual displays and

coloration, and an active role of males in courtship activities. Females, on the other hand, lack a special sexual color pattern and well-developed sexual displays, and play a quiescent role in courtship. This scheme is also well suited to the mating systems of *T. lunare* (see Robertson and Choat, 1974) and *T. cupido*. It should be added that basic to this system is the existence of two differing modes of reproduction; aggregate and pair spawning.

In pair spawning, transient mating pairs are formed which endure for only the short period of fertilization. Hence, males mate promiscuously with many females. In each species, pair spawning males hold temporary territories during periods of reproductive activity which they defend from other males and in which they perform sexual displays and fertilize the eggs of individual females. In a comparative analysis of courtship patterns in three species of tropical labrids (*Clepticus parrae*, *Labroides dimidiatus*, and *Thalassoma bifasciatum*), Robertson and Hoffman (in press) and Robertson (personal communication) distinguished two types of sexual displays; long distance communicative displays and short distance displays. For example, in *T. bifasciatum* "loopings" (Reinboth, 1973) are performed even in the absence of females and apparently serve to announce the presence and location of the territorial male. Supplementary to looping is a series of close proximity activities which a male directs to an approaching female as he circles above her. These displays consist primarily of pectoral fin fluttering and tail quivering.

Robertson and Choat (1974) described similar close proximity displays for terminal phase males of *T. lunare*, but gave no account of long range displays analogous to looping. Similarly, only close proximity displays were observed of *T. cupido*. These displays are directed towards isolated individuals, clearly serving a courtship function. In common with *T. bifasciatum* and *T. lunare*, pectoral fin fluttering and tail beating are the basic motor patterns of the courtship display.

Because territories are so poorly defined, it is difficult to ascertain the relative extent to which males of each species are active in

searching for and procuring their spawning partners. It appears, however, that the lack of long range announcement displays in *T. cupido* is compensated for by a more active role on the part of pair spawning males in selecting mates. Female *T. bifasciatum* come to the male's territory when ready to spawn, often waiting there if the male is absent or preoccupied (Reinboth, 1973; Warner et al., 1975). This was very rarely observed of *T. cupido*. More often a male would be forced to stray to the outskirts of his comparatively large territory (roughly 6~10 m<sup>2</sup>, as opposed to the estimated 1~4 m<sup>2</sup> reported for *T. bifasciatum*), and intercept females from passing aggregations. Frequently, a male would spend as long as 20 minutes driving off other males while attempting to isolate a female.

In addition to *T. bifasciatum* and *T. lunare*, aggregate spawning has been reported for *T. hardwickei* (Choat, 1969) and *T. lucasanum* (Hobson, 1965). The spawning sequence as described for these four species does not differ significantly from that of *T. cupido*. A single exception is that "bobbing", which appears to be an important action pattern in *T. cupido*, has not been previously noted in the literature.

The many similarities in sexual behavior among these congeneric species may have facilitated an incidence of interspecific spawning observed during the course of this study. In July of 1975 pair spawning was seen between *T. cupido* and its congener, *T. lunare*. Spawning proceeded in a manner typical of what has been described in this paper and was preceded by the courtship display performed by the former species, a male in the terminal color phase. The isolated *T. lunare* was partially concealed in the seaweed and behaved in a manner identical to that of female *T. cupido* prior to spawning. No other *T. lunare* were seen in the vicinity. Although their patterns differ, the blue coloration of terminal phase *T. cupido* is very similar to that of *T. lunare* and this may have also contributed to this unusual spawning.

Subsequent to this observation another report (Randall, 1972) was discovered in which brief mention was made of spawning between two species of *Thalassoma*. In both of these instances, one species was very abundant while

the other was rare, a factor which Hubbs (1961) suggests may contribute to the breakdown of barriers to interbreeding. Although these are clearly exceptional cases, they provide additional evidence that among members of the genus there exists a high degree of conformity in patterns of reproductive behavior.

#### c. The frequency of aggregate and pair spawning

Reinboth (1973) noted that in *T. bifasciatum* the relative frequency of aggregate spawning and pair spawning varies at reefs of different sizes; aggregate spawning seems to prevail on large reefs, while pair spawning prevails on small reefs. He speculated that, "pair spawning is the most efficient way of reproduction in cases where equal physiological readiness may hardly be attained simultaneously by a number of individuals". These requirements of synchronization are probably satisfied by the short breeding season and extreme abundance of *T. cupido* at Miyake-jima and may contribute to the fact that aggregate spawning greatly exceeds pair spawning in frequency.

#### d. The relationship between dichromatism and sexual behavior

Previous investigators have found a direct correlation between male dichromatism and sexual behavior among members of the genus *Thalassoma*. Initial phase males of *T. bifasciatum*, *T. lunare*, and *T. lucasanum* normally spawn in aggregates while terminal phase males pair spawn. Occasionally spawning aggregations of *T. lucasanum* are joined by individuals clearly transitional to the terminal male form and rarely by some that appear to have attained this form (Hobson, personal communication). However, aggregate spawning by terminal phase *T. bifasciatum* and *T. lunare* appears to be quite rare, as few examples of such spawnings have been reported in the extensive literature on this subject. Occasionally, initial phase males of these two species will participate in pair spawning activities, although this occurs in a rather peculiar fashion. An unusual trio is formed as a second male rushes up to join a pair just as gametes are being shed (Warner et al., 1975). Initial phase males of *T. bifasciatum* may also engage in pair spawning activities by "sneaking" (Warner et al.,

1975). These fish approach the territory of a sexually active terminal phase male and induce spawning with individual females that are waiting to mate with the courting territory holder.

The relationship between color and spawning behavior in *Thalassoma cupido* is similar to that of its congeners. Aggregate spawning by a terminal phase *T. cupido* was witnessed only once throughout the several hundred observations made. Participation in pair spawning by initial phase males of this species is not restricted to trio formation, although this behavior was rarely observed. On several occasions, typical pair spawnings were seen in which both participants were initial phase fish. Perhaps some of these observations can be attributed to poor synchronization on the part of a small group, as was clearly the case when this was seen in the aquarium. However, this is not always the case, as is evidenced by occasional initial phase males which actively pursue, court, and spawn with single females. These males behave in a manner indistinguishable from that of terminal phase males, even defending territories for short periods of time. Pair spawnings by such initial phase males are not directly comparable to the spawnings which result from "sneaking" in *T. bifasciatum*. They may take place in areas removed from the territories of terminal phase males and often do not involve interfering with the activity of terminal phase territory owners.

The most interesting example of this was the case of an exceptionally large initial phase fish which was observed daily throughout the 1975 spawning season engaged in reproductive activity characteristic of terminal phase males. Pair spawning by this individual was usually observed several times each day. This was thought to be its sole mode of reproduction until once, when minutes after pair spawning, it joined and spawned with an aggregate. Such observations indicate that initial phase males possess a versatility in mating systems and that sexual behavior is not fixed, but is variable depending upon the immediate social pressures. Sexual origins appear to have little, if any, influence over spawning behavior as both primary and secondary testes were found

among pair spawning males. Although color is a more reliable index of a male's spawning strategy, this relationship is not absolute. It is suggested that the large size and bright colors of terminal phase males confer an advantage in pair formation, normally to the exclusion of neighboring initial phase males. Yet under favorable conditions, initial phase males will also compete for access to single females.

#### Acknowledgments

I am indebted to Dr. Akinobu Nakazono of the Fishery Research Laboratory, Kyushu University, for his extensive assistance in the histological investigations of gonad samples, and for providing many helpful comments and suggestions throughout this study. Mr. Yutaka Yogo of the Fishery Research Laboratory, Kyushu University, Dr. Edmund S. Hobson of the Southwest Fisheries Center Tiburon Laboratory, Dr. D. Ross Robertson of the Smithsonian Tropical Research Institute, and Prof. Rudolf Reinboth of the Institut für Zoologie, Johannes Gutenberg-Universität, are thanked for sharing valuable observations and information. Further thanks are due to Dr. Robertson for providing two of his unpublished manuscripts. The assistance of Dr. Torao Sato of Tokyo University in locating pertinent literature, and that of Peter A. Hofmann in translating German articles is gratefully acknowledged. Jennifer A. Crooks kindly prepared the drawings of Fig. 3. Dr. K. Mashiko of Teikyo University, Prof. Reinboth, Dr. Robertson, Dr. Nakazono, and Mr. Yogo are thanked for critically reading the manuscript. Finally, I wish to express my gratitude to Jack T. Moyer, John W. Shepard, and Claire E. Sawyers, of the Tanaka Memorial Biological Station, who contributed many valuable observations, ideas, and suggestions, assisted in collecting specimens, and provided encouragement and support.

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ニシキベラの一次雄、二次雄における性徴と生殖行動  
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三宅島において 1974 年 6 月から 1975 年秋にかけて、ニシキベラの生殖行動と性構造を観察した。産卵は 6 月中旬から 9 月中旬まで続き、その間の水温は 20.0~28.0°C であった。求愛行動はまれに午後を観察されることもあるが、産卵は午前だけに限られた。195 尾の調査個体のうち、52.8% は雄、44.6% は雌(残りは不明)であった。雌雄ともに同範囲の体長分布を示したが、そのうち特に大型の個体についてだけみれば、雄の数は雌より多い。本種は雌性先熟現象により雄に 2 型を示す。体色相の変異についても観察し、initial phase は未成魚、雌、一次雄、二次雄に認められるが、terminal phase は一次雄、二次雄に限られる。ペア形成産卵と群れ形成産卵の両型が観察されたが、本研究水域では後者がより頻繁であった。求愛行動および産卵行動の記載を行ない、同属の他の魚種との比較検討を行なった。