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SPAWNING OF DAMSELFISHES ON THE NORTHERN COAST OF TAIWAN, WITH EMPHASIS ON SPAWNING SITE DISTRIBUTION[1]

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Rong-Quen Jan and Rupert F.G. Ormond (1992) Spawning of damselfishes on the northern coast of Taiwan, with emphasis on spawning site distribution. *Bull. Inst. Zool. Academia Sinica* **31**(4): 231-245. In this paper we describe, with emphasis placed on spawning site distribution, the spawning characteristics of seven damselfish species, including *Abudefduf bengalensis, Abudefduf coelestinus, Abudefduf vaigiensis, Chromis fumea, Neopomacentrus taeniurus, Pomacentrus coelestis,* and *Stegastes fasciolatus*. Observations on these damselfishes were made off the northern coast of Taiwan (Northern West-Pacific) in 1986. All of these damselfishes spawn demersally, but with eggs deposited on a variety of substrates. The influence of local territorial species on the availability of spawning substrate for non-territorial damselfishes, and factors affecting spawning site selection of these damselfishes are discussed.

Key words: Damselfish, Nest size, Nesting site, Spawning behavior, Reproduction

The spawning behavior of demersally spawning fishes has attracted the attention of many ethologists; most of these fishes are strongly associated with coral reefs, and most exhibit conspicuous motor patterns during courtship (Abel, 1961; Myrberg, 1972; De Boer, 1980; Chang and Jan, 1983). Information on the ethology of demersal spawners — for example, parental care extended to fertilized eggs — has been accumulating (Blumer, 1979; Keenleyside, 1979; Perrone and Zaret, 1979; Potts, 1984). However, the ecological constraints associated with this type of spawning pattern, particularly the availability of the nesting substrate, have been overlooked (Jan, 1991; see Potts, 1984, 1985 for temperate marine teleosts). Unlike pelagic spawners, which broadcast eggs in the water column, demersal spawners need to acquire suitable nesting substrate to deposit eggs (Thresher, 1984). Since the securement of suitable substrate is critical to the reproductive success of demersal spawners, it is crucial to learn how substrate is utilized by these species when spawning.

In this paper we report our results from a survey of spawning sites, nests, and courtship behaviors of damselfish — one of the major coral reef fish families known to be

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demersal spawners — conducted in northern Taiwan. Our results are arranged in two parts; firstly, the spawning characteristics of each of the seven damselfish species are described. Second, the distribution of spawning sites and some observed interspecific interactions between sympatric spawning species are described. The implications of these observations are discussed along with the findings.

MATERIALS AND METHODS

Underwater observations were made in a small embayment at Kuei-hoe village, east of Yeh-liu Peninsula (121°41'E, 25°12'N) on the northern coast of Taiwan (Fig. 1) during late April and mid-October, 1986. Except for a fishing harbor near the village, the shoreline is made up of giant sandstone rocks. The northern part of the study area is

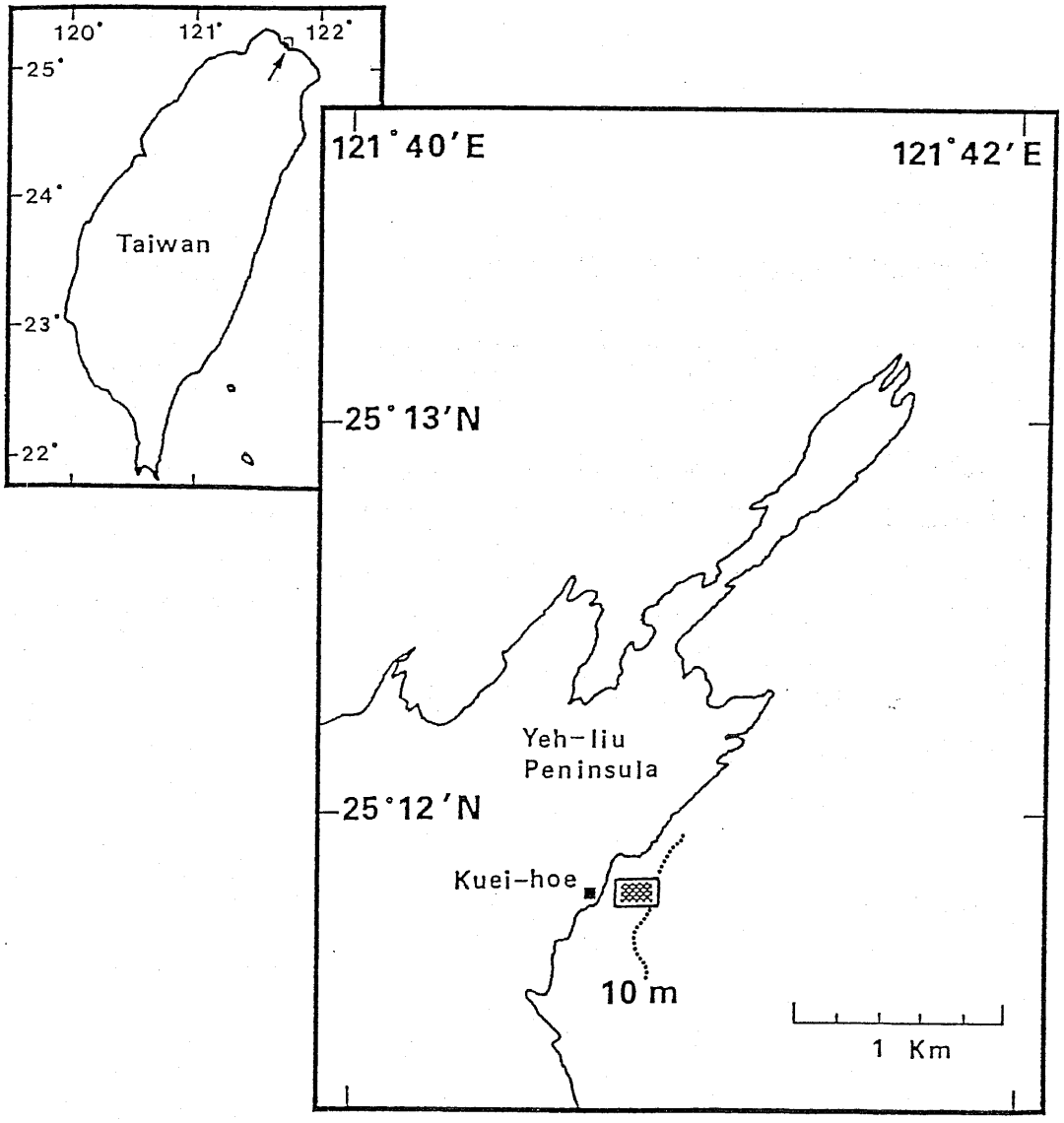

Fig. 1. Map of northern Taiwan showing location of the study area. Note that a 10m isobath passes through the western part of the study area.

composed of reef framework, while the southern part (adjacent to a beach) is generally sandy. The study was undertaken in an area approximately 9,000 m^2 in size.

The reef framework is composed of sandstone and coral rubble; on the reef framework there are a few small coral patches, irregular knobs, and mounds. Coral reefs are not well-formed in this region. Instead, most coral colonies are found growing on a noncoralline substratum (Randall and Cheng, 1977, 1979). The sea bed slopes gently, but this slope is generally interrupted by a number of low cuestal ridges. The shoreward sides of these ridges are steep to vertical and frequently interrupted by short protruding ledges, while the seaward sides form a gently dipping slope. There are also low troughs and furrows penetrating the reef framework. A few rocky islets, boulders, large angular blocks, gravels, and sands cover the sea floor in these troughs and furrows. Grooves excavated by sea urchins such as *Echinometra* sp. occur throughout parts of the sandstone substratum. Particularly noticeable on the reefy ridges are tufts of 5-10 cm high red algae *Corallina*. Long strands of *Sargassum* sp. are present in the shallow shoreward regions, while the intertidal zone is dominated by *Ulva* spp., *Chaetomorpha* spp., and *Enteromorpha* spp.; this gives the area a bright green color from winter to early summer (Wang and Chen, 1980). For the most part, the reef framework is dominated by the territorial damselfish *Stegastes fasciolatus*.

In the southern part, a sandy beach extends seaward, forming a limited sandy sea bed. Adjacent to and away from the sandy floor is a broad submarine terrace made up of an emergent part of the reef framework. The long slope between shoreline and reef terrace is also gentle, with reef outcrops occurring sporadically. These outcrops, which lack massive coral colonies, are occasionally linked by mounds.

Nine damselfishes are commonly found in the study area. These are *Abudefduf bengalensis, A. coelestinus, A. vaigiensis, Chromis fumea, C. notata, Neopomacentrus taeniurus, Pomacentrus coelestis, Stegastes fasciolatus,* and juvenile *Dascyllus trimaculatus*. Spawning was observed for seven of these nine species.

Except for days of heavy rain or typhoon prevalence, scuba diving was carried out almost daily during the study period. Some dives were made to depths of 25m, but in compliance with safety guidelines for repetitive dives, most were to less than 15m. The standard lengths of specimens (all adults) collected in relation to other projects are used to describe the sizes of damselfish species. Nest sizes were measured as the area of substrate on which eggs were present. Some nest sizes were measured using methods described by Jan (1989).

RESULTS AND DISCUSSION

The nests of most observed damselfish species were formed on patches of hard substrate cleared of algae, sessile organisms, and sediments, on which eggs were subsequently laid (Table 1). Except for *Stegastes fasciolatus*, which spawned within territories scattered over most of the reef framework, the distribution of spawning sites of other damselfish species is shown in Fig. 2. The Habitat, behavior, spawning sites and nesting sites of the fish are given below.

Abudefduf bengalensis

Habitat

The *Abudefduf bengalensis* population was much smaller than those of either *A. vaigiensis* or *A. coelestinus*; it occurred occasionally in small groups in the rocky areas, in or near the surge zone. Maximum SL out of fourteen individuals collected was 128 mm.

Table 1.
Summary chart of our findings.

Species name	Maximum[1] SL (mm)	Body color of adults	Abundance[2]	Social behavior[3]	Main spawning site	Depth of spawning site (m)	Synchronous spawning[4]	Courtship		Main nesting substrate	No. of nests found[7]	Nest size (cm^2)				No. of nests measured	Spawning Month(s)	Photograph
								Occurrence[5]	Color[6]			Max	Min	Avg	SD			
Abudefduf bengalensis	128 (n=14)	whitish, with seven vertical dark bars	O	small groups; solitary	near surge zone	2-4	NA	NA	NA	lateral side of sandstone rocks	4	820	315	625	222	4	May, Jul	Fig. 3
Abudefduf coelistinus	131 (n=7)	same as above, but with black bands on caudal fin	C	small groups	bank of reef trough; reef slope	4-8	+	+	–	clefts; underside of massive coral colony	5+	638	323	444	130	5	May — Jun	NA
Abudefduf vaigiensis	132 (n=15)	whitish, with five vertical dark bars	A	schools; shoals	reef adjacent to sandy sea bed	3-8	+	+	dark blue	lateral surface of reef outcrop	996	3300	1075	2088	478	54	May — Oct	Fig. 4
Chromis fumea	75 (n=49)	grayish yellow	A	aggregation	isolated reef; underwater embayment	3-6	+	+	white tail	open substrate	2149	120	30	78	27	24	Apr — Jun	Fig. 5, 6
Neopomacentrus taeniurus	71 (n=16)	blackish	C	aggregation	emergent reef	3-8	+	+	blotchy	clefts; caves	5+	22	12	17	4	5	May — Jul	Fig. 7
Pomacentrus coelestis	58 (n=11)	blue	A	aggregation	isolated reef; embayment; reef trough	3-8	+	+	dark blue	burrows; depressions	890	81	76	78	2	5	May — Jul	Figs. 8, 9
Stegastes fasciolatus	106 (n=34)	blackish brown	A	territorial	within territory	3-?	NA	NA	NA	caves; crevices; clefts	2+	255	206	232	–	2	May — Jun	Fig. 10

1 Maximum SL —
No. of specimens for which measurements were taken is indicated as n in parentheses.

2 Abundance —
A: Abundant; more than 320 individuals observed at a site.
C: Common; 80 - 320 individuals observed at a site.
O: Occasional; 20 - 80 individuals observed at a site.
R: Rare; less than 20 individuals observed at a site.

3 Social behavior —
For descriptions of each social behavioral pattern, refer to Fishelson (1970).

4 Synchronous spawning —
+: confirmed
NA: no spawning observed or data insufficient

5 Courtship, Occurrence —
+: courtship observed
NA: data not available

6 Courtship, Color —
–: no color change observed during spawning
NA: no courtship observed or data insufficient

7 No. of nests found —
+: more nests than the given number were present

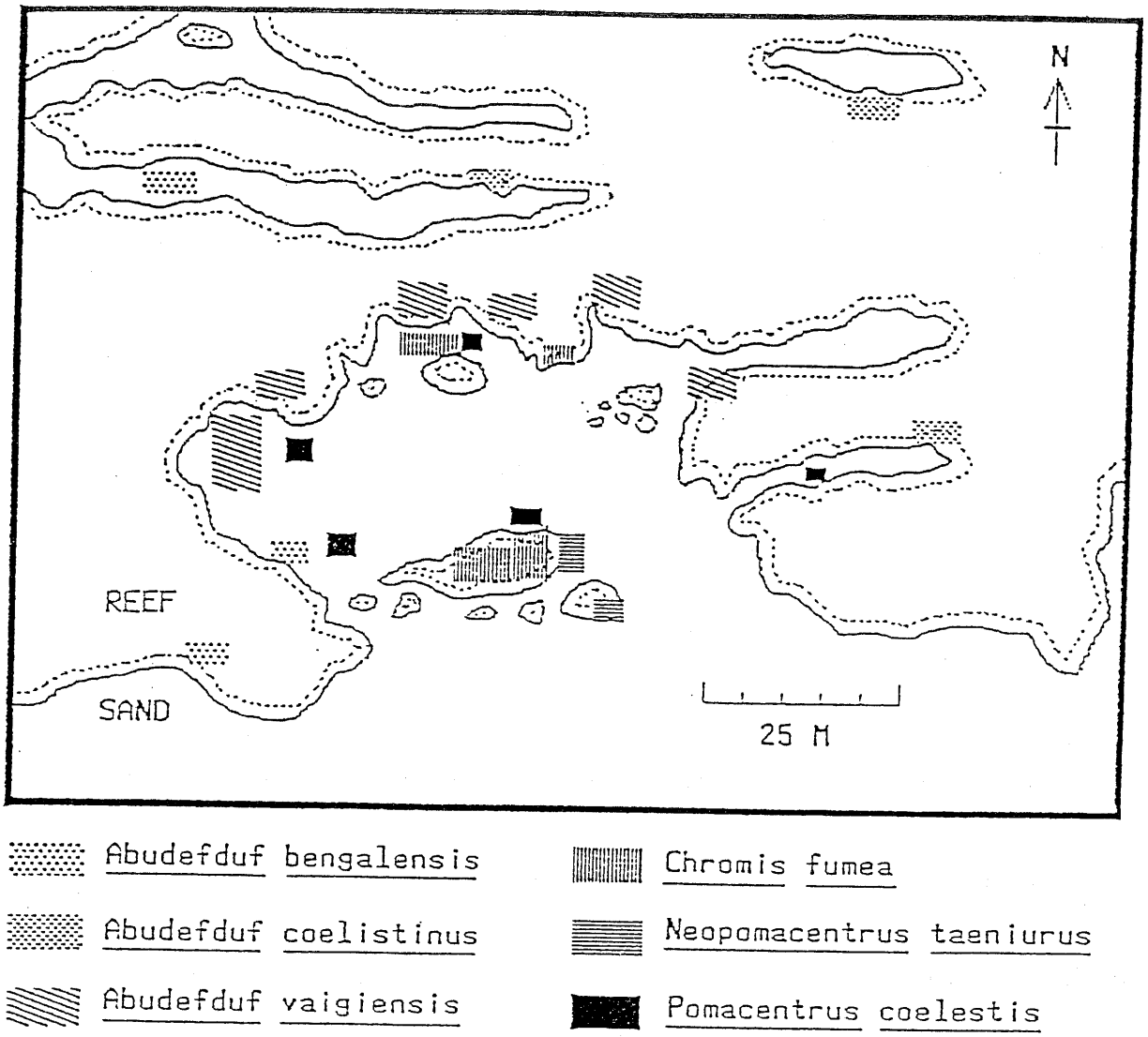

Fig. 2. · Sketch map showing the distribution of spawning sites of six damselfish species within the study area in 1986. Spawning sites of *Stegastes fasciolatus* are not shown on this graph because this damselfish spawned ubiquitously within territories on the reef framework.

Spawning sites and nests

Only four nests were observed in May and July. They were found at depths of 2-4m on the reef area near the surge zone. These nests were formed on the lower part of the lateral sides of sandstone rocks. Nest sizes were 315, 622, 745 and 820 cm^2. These nests occurred in isolation; each nesting fish stayed close to and defended its nest against trespassers such as *Pomacentrus coelestis, Stegastes fasciolatus, Halichoeres melanochir, Thalassoma lunare,* and *Pterocaesio diagramma.* No *A. bengalensis* spawning was witnessed. One of the nests with its owner is shown in Fig. 3.

Abudefduf coelestinus

Habitat

Abudefduf coelestinus was observed to be a common damselfish species mostly occur-

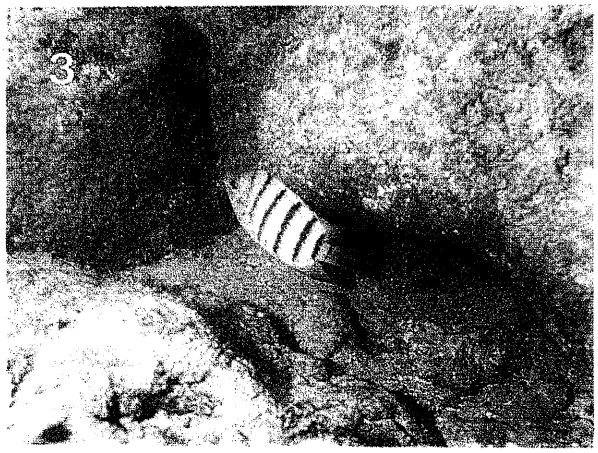

Fig. 3. An *Abudefduf bengalensis* and its nest. The nest was formed on the lateral side of a boulder in shallow water. The fish stayed in the vicinity of the nest and guarded its eggs. Eggs of two different colors, (red and orange) were found in this nest. (Nikon F2 / Nikko 55 mm micro lens).

ring on the outer slopes of the reef framework. However, some also lived in small groups along troughs between reefs. Adults were generally distributed deeper than *A. vaigiensis* adults. In contrast, juveniles of both damselfishes lived sympatrically in shallow water. Maximum SL out of seven individuals collected was 131 mm.

Spawning sites and nests

Spawning was observed at depths of 4-8m in May and early June, 1986; nests were formed on sheltered substrates. Along troughs, nests were found underneath table-like coral colonies protruding from the upper reef bank; on the outer slopes of the reef, nests were built in clefts or crevices in the sloping substrate.

Group spawning was observed in a trough between two reef sections. Invitations from males consisted of brief lateral courtship displays, in which no distinct color changes appeared. Individuals staying near the nest and being invited to spawn were often smaller than nesting males. Spawning was frequently interrupted by the departure of females. However, these females frequently returned to the nest within minutes and continued spawning. Five nests were measured; their sizes were 323, 345, 408, 506 and 638 cm^2.

After spawning, males remained in the vicinity of their nest. Most of the time they did not stay very close to its nests, but instead roamed over nearby substrate. No egg predation occurred despite the appearance of trespassers such as *Pterocaesio diagramma* and *Halichoeres melanochir*.

As a result of this behavior, the substrate with which the fish associated did not usually indicate the location of nests. This uncommon egg-caring behavior and almost invisible nest sites may help explain why little is known about the spawning of this damselfish — despite the fish's wide range.

Abudefduf vaigiensis

Abudefduf vaigiensis (Quoy and Gaimard) is the Indo-Pacific form of Atlantic *Abudefduf saxatilis* (Linnaeus) (Randall, 1968; Fishelson, 1970; Allen, 1975; Allen, 1976; Thresher, 1980). Hensley (1980) studied the morphology of these two species and suggested that there are two subspecies of *Abudefduf saxatilis* (*i.e.*, *Abudefduf saxatilis vaigiensis* and *Abudefduf saxatilis saxatilis*) rather than two distinct species (see also Randall, 1983). To avoid confusion, however, their traditional names have been adopted for use in the present study.

Habitat and general behavior

Abudefduf vaigiensis was found to be very abundant at the study area. In many aspects, the diurnal behavior of adult *A. vaigiensis* resembled that exhibited by *A. saxatilis* in both the Atlantic Ocean (Albrecht, 1969) and Red Sea (Fishelson, 1970; Fishelson *et al.*, 1974). Briefly, we found the adult *A. vaigiensis* generally lived in shoals; that is, individuals lived in groups, within

which they swam in all directions and behaved more or less independently, moving only partially in accordance with other members of the group (Fishelson *et al.*, 1974). Shoal size varied from a few to approximately 80 individuals. The maximum SL of this damselfish (fourteen individuals collected) was 132 mm.

Spawning sites, nests and courtship

A. vaigiensis spawning was observed between May and mid-October, 1986. They spawned in groups on reefy substratum at depths of 3-8 m. Individuals within the same group spawned synchronously.

Spawning sites were scattered on reef adjacent to sandy sea bed (Fig. 2). Most nests were formed on the lateral side of hard substrates such as reef furrows, cuestal ridges, ledges protruding from the reef, and giant underwater blocks. Nevertheless, some nests were formed in shaded areas beneath overhangs. The sizes of fifty-four nests measured ranged between 1,075 cm^2 and 3,300 cm^2; average size was 2,088 cm^2 (SD=478). A photo of a nest formed on a section of reef is presented as Fig. 4; in this plate, a nesting male guarding the nest is also shown.

Fig. 4. An *Abudefduf vaigiensis* and its nest. The fish was guarding its nest, which had been formed on the vertical surface of a reef outcrop. The pink area on the substrate behind the fish is the egg patch. Note the densely laid eggs on the substrate. (Nikon F2 / Nikko 55 mm micro lens).

Time spent in nest preparation and egg hatching varied over the spawning season. In May, when the spawning season commenced, males aggregated at spawning sites and started nest preparation three days before spawning occurred. In September, it took less time — only one or two days — for the fish to build their nests. In May, when the water temperature was 22-24°C, hatching took six days; it took only five days in the period between June and October, when the water temperature was 24-28°C.

The courtship occurred when groups of females approached the spawning site. Male behavior was mainly composed of invitations to the females. That is, males swam quickly in an undulating manner towards the group of female fish, but before reaching them, turned around and swam slowly back to his nest. At first, most females responded to such invitations by turning away, most nesting males eventually succeeded in their invitations. During spawning, the coloring of both males and females turned dark; this color change only lasted for a short while, but occurred frequently. After spawning, males stayed on their nests and cared for the eggs. Egg-caring behaviors such as skimming, fanning, and nipping the eggs (Jan and Chang, 1984) were commonly seen in nesting fish.

A total of 996 nests were found, mostly at six spawning sites (Fig. 2). Furthermore, we noted that of these nests, 767 (77%) were located within territories of another damselfish, *Stegastes fasciolatus*. In contrast, no *A. vaigiensis* nests were found on the flat reef framework, even though most of that area was also defended by *S. fasciolatus*.

Chromis fumea

Chromis fumea is a damselfish which mainly occurs in the northern West-Pacific,

especially in Taiwan and southern Japan. In Taiwan, Shen and Chen (1978) described this fish as *Chromis caudofasciata*. The holotype was later examined by Randall *et al.* (1981), who concluded that it was conspecific with *C. fumea*.

Habitat and general behavior

C. fumea and another congeneric species, *i.e. C. notata*, occurred sympatrically. Both species were observed in shallow water but the surge zone. When the water was calm, hundreds of *C. fumea* aggregated in mid-water above the sandy bottom adjacent to the reef framework, where they fed on plankton. The entire aggregation moved slowly around and sometimes met aggregations of *C. notata* in the water column; the two aggregations never intermingled, since in most cases *C. notata* moved to a position above *C. fumea* in the water column. When the sea was rough, *C. fumea* formed small groups and stayed in troughs between reefs. Some individuals, struggling against the currents, stayed close to the submerged reefs. The maximum SL out of forty-nine individuals of this damselfish species collected by gill-net was 75 mm.

Spawning sites, nests and courtship

C. fumea spawning occurred episodically at depths of 3-6m in the period between late April and early June of 1986. In total, 2,149 nests were found during this period; while some nests were found in a small embayment adjacent to the reef framework, most of spawning occurred on the isolated reef in the sandy southern area (Fig. 2). At the latter nesting site, spawning aggregations involved hundreds of individuals, and spawning occurred daily for several days. Nests consisting of small patches cleared of sediment on the open surface of the reef (Fig. 5) were densely distributed. (On 10 May the average distance to the nearest neighbor measured from nine nests was 49 cm.) The sizes of twenty-four nests measured ranged between 30 cm^2 and 120 cm^2; average size was 78 cm^2 (SD=27).

Fig. 5. Spawning of *Chromis fumea*. The fish pressing its abdomen against the substrate is the spawning female. Eggs were deposited on a part of the substrate which had been cleared of sediment. Note that the male, whose tail color is turning to white, is nudging the female while she is laying eggs. (Nikon F2 / Nikko 55 mm micro lens).

Both the isolated reef and underwater embayment — the main spawning sites of *C. fumea* — were subject to heavy sedimentation in the severe weather; it was common to find nests of *C. fumea* covered by a layer of sediment on rainy or windy days (Fig. 6). Nests were abandoned if heavy sedimentation lasted for more than two days. Most nests on the isolated reef were buried by the displacement of sand from surrounding areas on 14-15 May and on 21 May, when seas were rough.

Nests were prepared by males; substrates were cleaned — mainly by trembling of the body trunk and by mouth-carrying — during the course of nest-preparation. When groups of conspecific fish approached the nesting ground, most nesting males moved quickly towards the aggregation in mid-water to court gravid females; females then followed males to the prepared nest. After a short

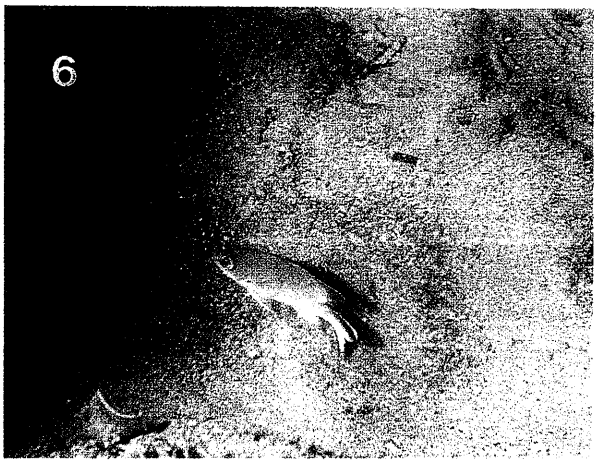

Fig. 6. *Chromis fumea* nest covered by sediment. Most *C. fumea* nests were formed on open substrate subject to heavy sedimentation, hence sea conditions had a strong influence on egg survival. This nest was deserted the day after this picture was taken. (Nikon F2 / Nikko 55 mm micro lens).

while, the female started to press her abdomen against the substratum, upon which eggs were deposited (Fig. 5). While this was underway, the male stayed to one side, circling or nudging the female; the males' caudal fin frequently turned bright white. The fertilization of eggs is assumed to happen during this circling behavior. Female spawning of often terminated abruptly without any noticeable prior signals; nevertheless, on many occasions individual females were repeatedly courted by the same male, and consequently they spawned at the same nest repetitively. After spawning, males stayed on their nests and took care of the eggs; while guarding the eggs, most males also continued to modify the adjacent substrate and enlarge their nests. The eggs normally hatched on the third day after fertilization.

Neopomacentrus taeniurus

Habitat and general behavior

Neopomacentrus taeniurus was seen to occur mainly on isolated emergent reefs. They gathered around the reefs and lived in aggregations. Unlike *Chromis fumea* — which moved along the water column — *N. taeniurus* stayed on isolated reefs and seldom moved from one reef to another. The maximum SL out of sixteen individuals collected by gill-net was 71mm.

Spawning sites and nests

N. taeniurus built nests inside crevices or narrow clefts in the emergent reef, particularly on overhanging portions of the substrate. The nests were so well hidden as to be almost invisible from outside the cleft. However, they could be located through observations of courtship, since courtship subsequently led the fish to the nests. Nests were formed on reefs at depths of 3-8 m, but only with the aid of a torch could a nest be occasionally directly examined. Nests were relatively small in size; of the five nests examined, the smallest was 12 cm^2 while the largest was 22 cm^2. Mean size was 17 cm^2 (SD=4). A picture of a nest formed inside a cave is shown as Fig. 7; in this picture, a small egg patch is identified by its distinct white color.

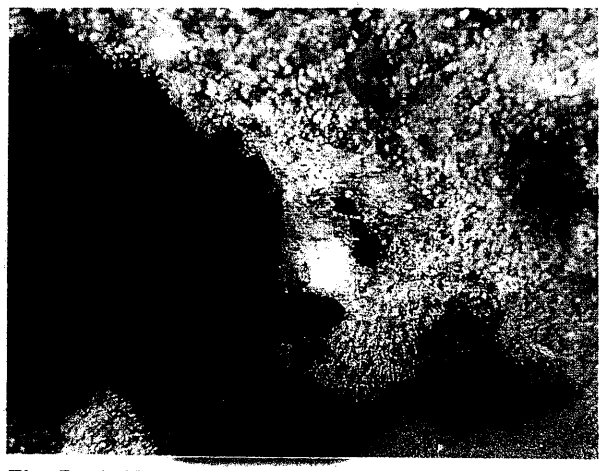

Fig. 7. A *Neopomacentrus taeniurus* and its nest. The nest was built on substrate in a cave which was 45 cm deep. A small egg patch (white) can be seen on the substrate. The fish was rubbing its eggs with its body when this picture was taken. (Nikon F2 / Nikko 55 mm micro lens).

N. taeniurus spawning occurred synchronously in fish of the same group. Courtship took place in the water column rather than inside the crevices. During courtship, males dashed outward from their nests to approximately 1-1.5 m above their nests; they trembled laterally, and their normal dark body color turned intermittently blotchy. In many cases, such displays occurred without the appearance of female. Thus, the eliciting of this behavior did not seem dependent on the appearance of a female. Nevertheless, males would dash toward any female if one arrived. A successful courtship would entice the female to follow the male to the hidden nest and — on many occasions — to start her spawning. During egg-caring, males spent most of their time outside the nest, except at times when disturbances to the nest were evident. Nest eggs were normally of different ages.

Pomacentrus coelestis

Habitat and general behavior

This damselfish was found to be very abundant in the reef area. Individuals formed small groups close to the reef, or else aggregated in mid-water. It has been previously reported that in calm water, the more fish that gather, the higher they tend to ascend in the water column (Chang and Jan, 1983). The maximum SL out of eleven individuals collected by gill-net was 58 mm.

Spawning sites and nests

P. coelestis spawning was found at depths of 3-8 m between May and July, 1986. A total of 890 nests were observed; spawning sites were located on isolated emergent reefs, in embayments adjacent to the reef framework, and in troughs between reef sections. Furthermore, in some places *P. coelestis* and *Chromis fumea* spawnings occurred sympatrically (Fig. 2).

P. coelestis spawned gregariously at spawning sites; nests consisted of small burrows or depressions, usually excavated under rocks or stones (Fig. 8). The nests were packed closely together at spawning sites. Courtship occurred when groups of individuals moved to the spawning site and descended to the nesting ground; males then darted from their nests to the fish clustering above. Meanwhile, the normally bright blue color of males turned dark. After intermingling with the clustered fish for a few seconds, the males swam straight downward, leading females to their prepared burrows or pockets. Eggs were mainly deposited on the roofs of nests. The sizes of five nests measured in an embayment on 12 May ranged between 76 cm^2 and 81 cm^2; the average size was 78 cm^2 (SD=2).

Fig. 8. Nest-preparation of *Pomacentrus coelestis*. This individual has half finished excavating a burrow next to the rock. The nest was subsequently built inside the burrow.

The spawning activity of *P. coelestis* seemed to move from one site to another over the spawning season, but it occurred synchronously at each site. Egg-laying lasted for several days at each site, consistent with our finding of eggs at different developmental stages in one nest (Fig. 9).

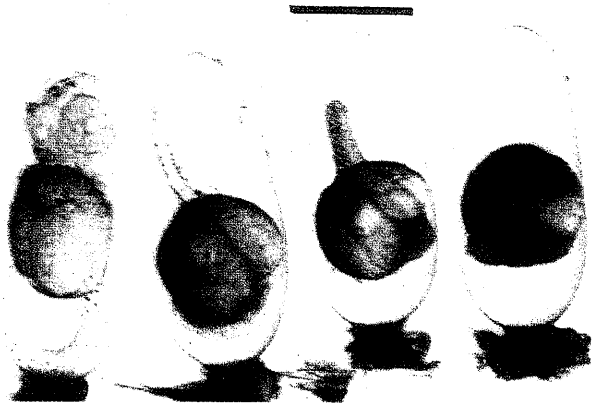

Fig. 9. Eggs collected from a *Pomacentrus coelestis* nest. Differences in developmental stages consistent with observations that the spawning of this *P. coelestis* occurred daily over a three-day period. Bar = 0.5 mm.

Stegastes fasciolatus

Stegastes fasciolatus is widely distributed across the tropical Indo-west Pacific (Allen, 1975; Allen and Emery, 1985). Its behavior (Rasa, 1969; Losey, 1981, 1982), ecology (MacDonald, 1981; Hourigan, 1986), and genetics (Shaklee, 1984) have been extensively studied. The coexistence of this species with other fishes (including blennies and surgeonfishes) was reported in the western Indian Ocean (Robertson and Polunin, 1981).

Habitat and general behavior

S. fasciolatus inhabited shallow reefs along the study area; it occurred extensively on the reef framework. In a 1983 survey made in the present study area, a total of sixty-two individuals were found in a 600 m^2 area (Chiou, 1984). Adults were found to be highly territorial, generally holding territories on parts of the reef surface suitable for algal growth (Chiou, 1984). Mature fish tended to hold territories within which there were reef outcrops or crevices. Rarely was this damselfish found near the isolated reef islets in the southern sandy area (Fig. 2). The maximum SL from thirty-four individuals collected by gill-net or spearing was 106 mm.

Nests

According to the results of a study undertaken in the same study area during April — December, 1983 on the monthly variation of the gonadal-somatic index of *S. fasciolatus*, the index was high in April and May, dropped in June, and remained low during the following months (Chiou, 1984). Therefore, *S. fasciolatus* in this area probably spawn mainly in May and early June. However, unlike in Hawaii — where *S. fasciolatus* nests are easily recognizable (MacDonald, 1981) — in northern Taiwan nest identification proved difficult since most nests were built inside crevices on reef outcrops. Usually there was not enough space for a diver to be able to inspect the roof of a crevice in a low reef mound. Moreover, when the nesting crevice opening was narrow, or when the egg patch was located in the depths of a crevice, the nests were always inaccessible unless some destructive measures were taken.

A total of twelve nests were observed at depths of 3-5m. However, spawning probably also occurred in deeper waters, where numerous territorial *S. fasciolatus* were observed. Only two nests — both found on the undersides of blocks — were measured; their sizes were 206 cm^2 and 255 cm^2. A photo of one of them is shown as Fig. 10. In the picture, grayish eggs are visible in the left-hand corner above the fish. No courtship behavior was observed during this study, even though clustering and mutual chasing were frequently seen on the reef framework in May and early June.

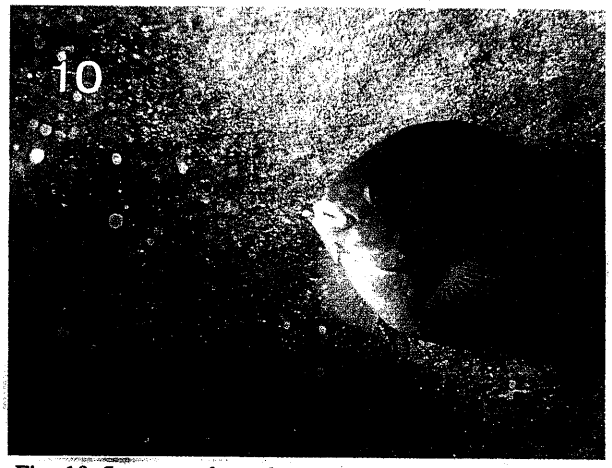

Fig. 10. *Stegastes fasciolatus* and its nest formed on the underside of a sandstone block. The fish was guarding the nest when this picture was taken. Light grey eggs appear in the left hand corner of this picture. (Nikon F2 / Nikko 55 mm micro lens).

OVERALL DISCUSSION

Spatial distribution of spawning sites

Among the damselfishes studied, two distinct patterns of utilization of spawning substrate were observed. One shows that when fish defended a long-term territory, it built a nest within that territory. This behavior pattern was shown by *Stegastes fasciolatus*; food was the usual resource it defended. However, individuals were more aggressive when caring for eggs than they were during non-spawning periods (Chiou, 1984). The other pattern showed that when fish did not hold long-term territories, they exploited open area spawning sites when they were ready to spawn. The spawnings of *Abudefduf vaigiensis, Chromis fumea,* and *Pomacentrus coelestis* clearly demonstrated this pattern.

Most of the reef framework in the study area was dominated by *S. fasciolatus*. For damselfishes whose body sizes are larger than that of *S. fasciolatus*, only *A. vaigiensis* was observed building nests in *S. fasciolatus* territories. The formation of an association between these two damselfishes is unusual; in this case, *S. fasciolatus* tended to prey on *A. vaigiensis* eggs (Jan, 1989). Therefore, a "trade-off" strategy may have been adopted by *S. fasciolatus* in order to achieve a net gain (through feeding on *A. vaigiensis* eggs) by allowing this association. By comparison, nests of two other *Abudefduf* species (*A. coelestinus* and *A. bengalensis*) were not observed on the reef framework (Fig. 2).

Damselfishes of relatively small body size built nests outside the reef framework. For example, *P. coelestis* and *C. fumea* spawned on small barren reefs (see Fig. 2) where aggressive *S. fasciolatus* were rare. These barren reefs are subject to physical disturbance from severe weather conditions, and thus can hardly be considered as optimal spawning sites. When *P. coelestis* and *C. fumea* spawned sympatrically, interference was observed occurring between them (Jan, 1989). Although the factors which govern both spawning site and nesting substrate selection remain mostly unknown, the appearance of the highly aggressive *S. fasciolatus* (Rasa, 1969; Losey, 1981, 1982) may have influenced spawning site selection by other damselfishes.

Territory defence

The long-term territoriality of *S. fasciolatus* in northern Taiwan is of great interest concerning the aspect of resource utilization. It is known that territorial defense has associated costs; it takes time and energy, and also increases the risks of injury and predation (Huntingford, 1984). Territoriality is most likely selected for where a particular resource is limited. In other words, if there are sufficient resources for all competitors, then individuals can adopt exclusive areas without displaying any aggression at all (Davies and Houston, 1984). A significant consequence of territoriality is that within a species those individuals that hold a territory generally have a higher fitness than those

that do not (Begon *et al.*, 1986). For example, in the wrasse *Thalassoma bifasciatum*, territorial (often terminal phase) males — which presumably possess higher competitive abilities — normally gain a higher reproductive success over the non-territorial males (Warner and Hoffman, 1980a, 1980b; Warner, 1984).

The question remains: What principal resource is the fish defending by being territorial? As already mentioned, food is one of the possible resources being defended during the non-spawning season. However, since territorial damselfishes as a rule build nests within territories, it is likely that nesting substrate is a second resource being defended. Direct evidence is very scarce; in Curacao (Netherlands Antilles), *Chromis cyanea* was found to be defending long-term territories which did not seem to be associated with food resources (De Boer, 1980, 1981). In this case the male *C. cyanea* established territories on reef slopes both before and after the spawning period, while the females roamed freely over the reef framework. Nests were built at suitable sites within the territory. Since only males defended long-term territories, it is possible that this damselfish defended substrate against others solely for the purpose of spawning. This inference is consistent with our finding that in northern Taiwan most territories defended by mature male *S. fasciolatus* included large mounts and clefts — the typical nesting substrate used by this species; in contrast, territories defended by females and juveniles usually did not include such types of substrate.

Resources defended by damselfishes showing long-term territoriality are often not open to exploitation by other free-ranging species (Losey, 1982; Jones and Norman, 1986). Therefore, long-term territoriality is likely meant to reduce the possibility of interspecific competition over spawning substrate when interspecific types of nesting substrate are similar. This may allow territorial fishes to share identical resources with other species, consequently allowing these fishes to coexist.

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台灣北部海岸雀鯛科魚類的產卵調查，兼論產卵場的分布

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本文描述 1986 年在台灣北部龜吼附近海域內調查所得的雀鯛科魚類產卵情形。文中分別敍述了七種雀鯛的產卵行為、生殖巢的結構以及大小等特徵。這些雀鯛分別為：孟買雀鯛 *Abudefduf bengalensis*，六帶雀鯛 *Abudefduf coelestinus*，條紋雀鯛 *Abudefduf vaigiensis*，燕尾光鰓雀鯛 *Chromis fumea*，藍帶雀鯛 *Neopomacentrus taeniurus*，變色雀鯛 *Pomacentrus coelestis*，以及太平洋雀鯛 *Stegastes fasciolatus* 等。

這些雀鯛皆是底棲性產卵者，所產的卵為具有黏性的沉性卵，但是用來產卵的巢的構築，在位置上以及結構上卻往往因種而異。文中並描述了研究區域內雀鯛產卵場所的分布情形，此外並以這些產卵場的分布為著眼點，分析影響這些雀鯛產卵場選擇的一些生物因子。同時，在一個區域內，領域性魚種的領域行為可能會導致一些非領域性魚種在生殖時不易獲得築巢用的基質，進而影響後者的產卵場的分布，文中對此點亦加以討論。

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CHEMICAL COMPOSITION OF SEX PHEROMONE GLAND EXTRACT IN FEMALE ORIENTAL ARMYWORM *PSEUDALETIA SEPARATA* WALKER (LEPIDOPTERA: NOCTUIDAE) IN TAIWAN[1]

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Rong Kou, Yien-Shing Chow and Hsiao-Yung Ho (1991) Chemical composition of sex pheromone gland extract in female oriental armyworm *Pseudaletia separata* Walker (Lepidoptera: Noctuidae) in Taiwan. (Z)-11-hexadecenyl acetate (Z11-16:OAc), (Z)-11-hexadecenol (Z11-16:OH), hexadecanol (16:OH), and hexadecanyl acetate (16:OAc) were isolated and identified as major chemical components from the female sex pheromone gland of the oriental armyworm, *Pseudaletia separata*, in Taiwan. The average amount of each component in one female gland was 60.0, 29.3, 9.3, and 9.0 ng/♀, respectively, in a ratio of 56:27:9:8.

Key words: Sex pheromone, *Pseudaletia separata.*

In Japan, the sex pheromone of the female oriental armyworm (*Leucania* (=*Pseudaletia*) *separata* Walker) was identified as a blend of (Z)-11-hexadecenyl acetate (Z11-16:OAc) and (Z)-11-hexadecenol (Z11-16:OH) at a ratio of 8:1 by Takahashi *et al.* (1979). However, in mainland China the male oriental armyworm was not attracted to the sex pheromone identified by Takahashi *et al.* in 1979; instead, (Z)-11-hexadecenal (Z11-16:Ald), hexadecanal (16:Ald), and (Z)-11-hexadecenol (Z-11-16:OH) were identified as the female sex pheromone components in the mainland China research (Zhu *et al.*, 1987). These different results encouraged our investigation of the chemical composition in the sex pheromone glands of the female *P. separata* in Taiwan in order to further determine the existence of pheromone polymorphism or of different species living in different parts of Asia.

MATERIALS AND METHODS

Insects

Mature larvae were collected from corn fields and reared with corn to pupation; after adults mated, eggs were laid. Hatched larvae were reared on an artificial diet modified from Shory and Hale (1965), and sexes were separated at pupal stage. All tested insects were maintained under a 16L:8D light regime at 24-26°C.

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