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# Sympatric Spawning of the Damselfishes *Chromis fumea* and *Pomacentrus coelestis* on the Northern Coast of Taiwan

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**Rong-Quen Jan (1997)** Sympatric spawning of the damselfishes *Chromis fumea* and *Pomacentrus coelestis* on the northern coast of Taiwan. *Zoological Studies* **36**(1): 26-32. The damselfishes *Chromis fumea* and *Pomacentrus coelestis* are both free-ranging demersal spawners; they generally do not occupy a permanent substrate. A total of 2 149 nests of *C. fumea* and 890 nests of *P. coelestis* were found in the study area on the northern coast of Taiwan in the spawning season of 1986. Both species spawned in groups. Sympatric spawnings, which involved about 1/3 of *C. fumea* nests and 12.1% of *P. coelestis* nests, occurred at some of the spawning sites. The 2 damselfish species nested mainly on different substrates: *C. fumea* on open substrate, with *P. coelestis* in small burrows or depressions excavated beneath boulders. However, interference occurred whenever they spawned sympatrically. When the interactions involved only 1 individual of each species, *C. fumea* (which is larger in size and built nests first) was able to prevent the competitor from building a nest in the neighboring area by active aggression. In comparison, when the 2 species encountered each other in groups, harassment from *P. coelestis* was observed to force *C. fumea* to abandon their nests. *P. coelestis* subsequently built nests at the site taken over from the latter fish.

Key words: Nesting substrate, Pomacentridae, Resource partitioning, Spawning season.

For demersal spawning fish, a suitable spawning site represents an important external resource, the procurement of which is essential for successful reproduction (Barlow 1981, Baylis 1981). In freshwater environments, optimal spawning sites for some demersal spawners have been suggested to be limited, leading to intense competition for spawning sites (Moodie and Power 1982, McKaye 1984, Cochran and Lyons 1986). In the marine reef environment, nest-site size is also reported to act as a constraint on the reproductive success of paternal fishes which do not defend permanent territories (DeMartini 1988, Hastings 1992).

Limited particular substrate may induce usepartitioning to decrease competition (Ogden 1986, Roberts 1986, Clarke 1988, Mapstone and Fowler 1988, Jan 1996), and low overlap between different species in the utilization of spawning substrates has been reported (Jan and Chang 1993, Ormond et al. 1996).

For species whose spawning sites do overlap, it is of interest to know how this spatial resource is shared and the relationships between these spawning fishes when they spawn at the same time (Jan 1996). By assuming spawning substrate as a resource dimension additional to the conventionally recognized habitat and food, such findings may then help explain the diversity of fishes in the reef environment. In the present paper the sympatric spawnings between 2 damselfishes in the northern waters of Taiwan are described, along with information on behavioral interactions between these 2 fish species whose spawning grounds intermingle. In addition, the implications of interspecific interaction on resource utilization among damselfishes in the local waters are discussed.

# MATERIALS AND METHODS

Field observations were made in a small embayment at Kueihoe on the northern coast of Taiwan (121°41'E, 25°12'N) (Fig. 1) from late April to mid-October 1986. The shoreline is composed of massive sandstone rocks and it accommodates

a fishing harbor. Near the shoreline, the sea bed to the north is composed of reef framework while the southern section is generally sandy. Two demersal-spawning damselfish species (Chromis fumea and Pomacentrus coelestis) were studied. However, as mid-water plankton feeders (Allen 1975, Randall et al. 1981, Chang and Jan 1983), they do not hold territories during the non-spawning period. Like most demersal spawners, when they are ready to spawn they build nests within previously established territories. In both species the male is responsible for egg-caring, which includes egg-cleaning and nest-defending behaviors. The 2 damselfishes tend to nest on different substrates. C. fumea builds nests on the open surface of the reef, whereas P. coelestis utilizes small burrows or depressions, usually excavated beneath boulders (Jan and Ormond 1992a). Their average nest sizes are similar (78 cm<sup>2</sup> vs. 78 cm<sup>2</sup>). Incubation of the fertilized eggs of C. fumea takes 3 days in May (Thresher 1984, Jan and Ormond 1992a), whereas that of P. coelestis takes 5 days (Lin 1992).

Spawning of both species was observed by scuba diving almost daily during the period between late April and mid-June; the survey was continued till mid-October, but with intervals between dives varying between 1 and 5 days. Data were not available during June 13-23 due to heavy rains,



**Fig. 1.** Map of northern Taiwan showing the location of the study area. Note the 10 m isobath passes through the eastern part of the study area.

nor between August 24 and September 1 when a typhoon occurred.

Data on the temporal spawning patterns of both species were collected. The overlap of spawning sites between the damselfishes was traced on a map drawn on a water-resistant notebook. Because the color of the fertilized eggs of both species was pale throughout the development period, no attempt was made to distinguish newly spawned eggs from others in the data set. Similarly, the numbers of nests used in the analysis of temporal spawning overlap were derived from the number of nests found each day rather than the number of nests where newly spawned eggs were found.

Behavioral interactions among individuals of the 2 species which spawned at the same site were monitored daily. The differences between the spawning success of *C. fumea* at sites with and without the co-occurrence of *P. coelestis* were also compared. To do this, a sympatric spawning site (Site E, as shown on Fig. 2) was divided into 2 parts: an area where nests of both damselfishes co-occurred (Site Y1) and an adjacent area where only nests of *C. fumea* were found (Site Y2).

#### RESULTS

In this study 2149 nests of *Chromis fumea* and 890 nests of *Pomacentrus coelestis* were found at 7 sites (Sites A-G, Fig. 2; daily counts of nest, Fig. 3). The spawning period of *C. fumea* lasted



Fig. 2. Sketch map showing the distribution of spawning sites of *Chromis fumea* and *Pomacentrus coelestis* within the study area.

for less than 1 mo. The 1st nest was observed on May 8. A spawning episode followed — nearly 200 nests were observed daily during May 8-11. Spawning activity decreased thereafter. The last nests were observed on June 3.

Spawning of *P. coelestis* also occurred mainly in May. However, there was an additional brief spawning session in early July (Fig. 3). Thus, temporal overlap of spawning between *C. fumea* and *P. coelestis* was considerable, but not complete.

Nests of the 2 damselfishes were distributed erratically at different sites. Though nests of *C. fumea* were found at Sites A, D, E, and G, most occurred at Site D, a site consisting of small, isolated barren reefs. In comparison, *P. coelestis* mainly built its nests on the sea bed in troughs or channels between reef outcroppings (Sites A, B, C, E, F) (Fig. 2). Only at Sites A and E did nests of both species occur (Fig. 3). About 1/3 of *C. fumea* nests and 12.1% of *P. coelestis* nests were sympatric.

## Interspecific interactions

Two different types of individual interactions were observed during sympatric spawning at Sites A and E. At Site A only 1 individual of each species was involved in the confrontation, while at Site D groups of individuals of both species were encountered. These interactions are described below.

## Site A

Sympatric spawnings occurred in early May, when a group of 30-35 individuals of *P. coelestis* arrived at the underwater embayment, where individuals of *C. fumea* had already built nests and spawned for 2 days. On the afternoon of May 10, these *P. coelestis* dispersed and began to prepare nests. Two individuals of *P. coelestis* which chose to build nests at an up-current site close to *C. fumea* nests were confronted and vigorously attacked by the nearest nesting *C. fumea*. Meanwhile, sediments agitated by the tail-fanning of *P. coelestis* were observed to settle on a *C. fumea* nest 25 cm away (Fig. 4). Confrontations continued till dusk.

By the next morning, the previously engaged *P. coelestis* had disappeared, while the neighboring *C. fumea* remained. The missing *P. coelestis* did not return during the following 3 days of observation. A 2nd *P. coelestis* involved in a similar situation also disappeared. In contrast, no interactions



**Fig. 3.** Daily number of nests of *Chromis fumea* and *Pomacentrus coelestis* found at 7 sites in the study area during the spawning season of 1986. The broken time axis indicates the period for which data were not available.

were observed when *P. coelestis* built its nest down current of a *C. fumea* nest. Four such *P. coelestis* individuals succeeded in their nest preparation and spawned in the next 3 days. Overall, at this spawning site nests of *C. fumea* were only found during May 8-13, while nests of *P. coelestis* were observed in the periods of May 11-18 and May 25-31 (Fig. 3).

# Site E

On May 6, hundreds of individuals of *C. fumea* aggregated over Sites D and E, and nest-preparation commenced the next day. A total of 24 nests were counted at Site E on the 3rd day (May 8). Also, a group of *P. coelestis* gathered at the northwestern corner of Site E on the morning of May 9. Then mixed groups of *C. fumea* and *P. coelestis* occurred. Nest-preparation by *P. coelestis* commenced that afternoon.

Direct interactions occurred at Site Y1 between 1430 h and 1700 h, when *P. coelestis* individuals adopted an aggressive posture (i.e., full extension of both dorsal and anal fins, accompanied by a darkening of body color) toward nesting individuals of *C. fumea*. The *C. fumea* group responded to this harassment by chasing back the intruders with fast dashing movements. The chasing rate was 10 bouts (3 min)<sup>-1</sup> on average, with 24 bouts (3 min)<sup>-1</sup> the highest. By contrast, at the adjacent site (Site Y2) where few individuals of *P. coelestis* 



**Fig. 4.** Photograph showing sympatric nesting of *Chromis fumea* (Cf) and *Pomacentrus coelestis* (Pc) at Site A. The *C. fumea* individual is guarding its nest, including 3 boulders on which egg batches (indicated as e) are visible, while the *P. coelestis* individual is building its nest by excavating the substrate under another 2 boulders. (Meanwhile, the *C. fumea* individual was also vigorously attacking the nest-preparing *P. coelestis*.) (Nikon F2/Nikko 55 mm micro lens).

occurred, no such interactions were observed. In addition, the *C. fumea* nesters at Site Y2 would, though infrequently, cluster in mid-water. This behavior was not observed at Site Y1 (Table 1).

Two *C. fumea* nesters were removed by spearing at each of the 2 sites at 1700 h, leaving their eggs unprotected. Egg-predators appeared instantly after the removal and the exposed eggs were completely consumed within 15 min at both sites. All the predators were other *C. fumea*, most being holders of neighboring nests. Individuals of *P. coelestis* at Site Y1 showed no observable reaction to either the exposed eggs, or the eggpredators.

On May 10, four nests of C. fumea were abandoned at Site Y1 while all the nests, except the 2 whose holders were removed, remained at Site Y2. By contrast, 4 new P. coelestis nests were added to Site Y1. On May 11, no C. fumea nests were observed at Site Y1. Three new P. coelestis nests appeared on the site. By comparison, 8 old and 5 new C. fumea nests occurred at Site Y2. The old nests were improved and expanded and newly laid eggs were observed. Overall, during this whole spawning aggregation, nests of C. fumea occurred daily during May 8-13, while those of P. coelestis occurred during May 10-16. However, more C. fumea nests occurred at Site Y2 than at Site Y1 during May 11-14 when the group interaction at Site Y1 prevailed, while more P. coelestis nests were, on the contrary, found at Site Y1 than at Site Y2 (Table 1).

# DISCUSSION

In the study area the overlap of either spawning seasons or spawning sites between *C. fumea* and *P. coelestis* is considerable but incomplete. However, whenever spawning occurred sympatrically, interspecific interactions were observed.

In freshwater environments, interactions, competition in particular, for spawning sites have been recorded between substrate-spawning fishes such as cichlid fishes. Cichlid fishes spawn in shallow water with distinct breeding seasonality (McKaye 1984), and competition for space in terms of territory turnover is intense. Pairs of cichlid fishes will aggressively evict another pair in order to establish a breeding territory (McKaye 1979). In the marine environment, spawnings of different damselfishes within a confined area have been reported (Albrecht 1969, Mapstone and Wood 1975). However, there was no information on whether the spawning site was partitioned, nor on interspecific interactions between these damselfishes.

In the present study the confrontation between 2 individuals of different species took place at Site A. In this case, C. fumea, with its relatively larger size (75 mm vs. 58 mm in maximum standard length, Jan and Ormond 1992a), was able to exclude P. coelestis from nesting in the neighborhood. In comparison, at Site Y1 of Site E the continual challenge from a group of P. coelestis seems to have forced the C. fumea to abandon their nests. The aggressive behavior of C. fumea towards P. coelestis at Site Y1 was not simply a response for securing egg protection, because P. coelestis did not take the unprotected eggs of C. fumea at all. Overall, it is more than likely that P. *coelestis* benefited by acquisition of the substrate, upon which they subsequently nested. Therefore, even if the 2 damselfishes use different types of nesting substrate, interference competition could occur when spawning sites overlap.

The function of grouping in fishes seems to vary according to the situation (Robertson et al.

1976, Loiselle and Barlow 1978, Potts 1980 1981, Dominey 1981, Robertson 1981, Warner 1982, Foster 1985, Jan 1991 1995). It is possible that both damselfish species used the group tactic to acquire substrate for nesting. *P. coelestis* was more successful in the application of this tactic, since at Site A the solitary individuals which confronted *C. fumea* apparently failed to build nests, while those that formed the group at Site E were able to take over the entire substrate.

The interactions between *C. fumea* and *P. coelestis* found in the present study also indicate the significance of the availability of suitable spawning substrate to free-ranging demersal spawners, which generally do not occupy a permanent substrate (unlike territorial fishes). There were 7 species of damselfish found spawning in the study area during the study period. Most of these spawned in May and June (Jan and Ormond 1992a,b). Most parts of the reef substrate were aggressively defended by just 1 species, namely, *Stegastes fasciolatus*. Among other damselfishes in this area, only *Abudefduf vaigiensis* was able to build

**Table 1.** Information on interspecific interactions between *Chromis fumea* and *Pomacentrus coelestis* nesting sympatrically at Site E. Site Y1: the site where overlap of spawning occurred; Site Y2: a control site for Site Y1. The standard deviation is shown in parentheses

	Site Y1	Site Y2
Observations started on	May 6	May 6
Area	2.4 m × 4 m	3 m × 3 m
Water temperature	23 °C	23 °C
Date: May 9		
C. fumea		
Number of nests	12	12 + 1 <sup>a</sup>
Density of nest (No. m <sup>-2</sup> )	1.25	1.33
Age of eggs in nest (day)	2	2
Average area of egg batch (cm <sup>2</sup> )	72(20) <sup>b</sup>	84(30) <sup>b</sup>
Inviting females (bout (3 min) <sup>-1</sup> )	7(5) <sup>b</sup>	7(4) <sup>b</sup>
Chasing rate (bout (3 min) <sup>-1</sup> )		
Toward conspecific nest holder	1(1) <sup>b</sup>	1(2) <sup>b</sup>
Toward P. coelestis	10(7) <sup>b</sup>	0 <sup>b</sup>
Midwater clustering (bout (3 min) <sup>-1</sup> )	0 <sup>6</sup>	1.7 <sup>b</sup>
P. coelestis		
Number of individuals	50-60	2-5
Number of nests	0	0
Date: May 10		
Number of nests of C. fumea	6 <sup>c</sup>	10 <sup>c</sup>
Number of nests of P. coelestis	4	0
Dates: May 11-14		
Total number of nests of C. fumea	3	15
Total number of nests of P. coelestis	30	5

<sup>a</sup>One nest was prepared but no eggs were laid in it throughout the observation.  ${}^{b}n = 12$ .

<sup>c</sup>Two nesters were speared out on May 9.

nests in *S. fasciolatus* territories (Jan 1995). Consequently the other 5 species (i.e., *C. fumea*, *P. coelestis*, *Neopomacentrus taeniurus*, and 2 species of *Abudefduf*) had to share the remainder of the reef substrate during spawning (Jan and Chang 1993).

If competition for spawning substrate is a reality, it would be advantageous for a damselfish to avoid, as far as possible, competition with other species for this extrinsic reproductive resource (Giller 1984). One way to do this is by keeping each nesting session as short as possible, thereby reducing the overall demand on the substrate for reproduction. This strategy might be particularly favored by the species nesting on open substrate such as C. fumea. This damselfish was found to spawn in a period of 1 month, which is relatively short compared with spawning seasons of other damselfishes (Jan and Ormond 1992b). In addition, this species nests on open surfaces rather than constructing more sophisticated modifications such as burrows underneath boulders (as did P. coelestis). It was thus able to spend only 1 day, rather than the 2 days normally invested by other damselfishes (Jan 1989), in the preparation of the nest. Moreover, C. fumea only takes 3 days (the shortest among damselfishes (Thresher 1984)) to incubate its fertilized eggs. In consequence, all these adaptations considerably reduce the amount of time that C. fumea requires the substrate during spawning.

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# 臺灣北部海岸燕尾光鰓雀鯛與變色雀鯛間同域生殖現象及交互作用

# 詹榮桂'

燕尾光鰓雀鯛(Chromis fumea)和變色雀鯛(Pomacentrus coelestis)兩種魚類都是底棲性產卵者,不過 牠們平時並未在海域中佔據領域。在1986年的生殖季節裡,於臺灣北部海岸附近海域內的一個研究區域,共 觀察到2149個燕尾光鰓雀鯛的以及890個變色雀鯛的生殖巢。兩種雀鯛都是產卵時聚集成群的群性產卵 者。在調査區內,燕尾光鰓雀鯛的巢分布在四個產卵區,而變色雀鯛則在五個區。其中有兩個產卵區是兩者 都利用到的,亦即牠們的產卵區有相重疊的現象。其中1/3的燕尾光鰓雀鯛以及12.1%的變色雀鯛的巢出現 在重疊區域內。這兩種雀鯛的巢分別築在不同的基質上:燕尾光鰓雀鯛築在平坦空曠的海底基質(礁石)的上 表面,而變色雀鯛則在礁石下挖掘出洞穴並在裡面產卵。當此二種雀鯛同時在同一區域產卵時,之間會發生 一些互相干擾的現象:在單純的個體與個體之間的相遭遇間,燕尾光鰓雀鯛會被迫放棄牠們已建的巢,而變色 雀鯛則會從原來燕尾光鰓雀鯛築巢的地點築起巢來。

關鍵詞:築巢基質,雀鯛科,資源分配,生殖季節。

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