

## Resource Limitation Underlying Reproductive Strategies of Coral Reef Fishes: A Hypothesis

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**Rong-Quen Jan (2000)** Resource limitation underlying reproductive strategies of coral reef fishes: a hypothesis. *Zoological Studies* 39(3): 266-274. A wide variety of complex spawning systems occurs in coral reef fishes. Among them, the demersal spawners and pelagic spawners are dominant in terms of both numbers of taxonomic groups and individuals. Here I propose a hypothesis to explain the reproductive strategies of these demersal and pelagic spawners. This hypothesis is based on 2 primary assumptions: that coral-reef fishes are selected to spawn demersal eggs; and that the nesting resource (i.e., substrate) is limited in the environment. Thus resource limitation is assumed to be the prime factor accounting for different spawning strategies. This hypothesis postulates that fishes which succeed in obtaining appropriate nesting substrates will spawn demersally, whereas those that fail to obtain suitable sites tend to spawn pelagically. Predictions from this resource-limitation hypothesis are in accord with many aspects of the available data. Therefore this hypothesis might be proposed as an alternative to established hypotheses to explain how different spawning patterns of coral reef fishes have occurred.

**Key words:** Damselfish, Nest, Reproduction, Spawning, Territoriality.

The spawning patterns of coral reef fishes have been documented from various points of view, particularly in relation to usage of ecological resources (Balon 1975 1978 1981 1982, Johannes 1978, Barlow 1981, Baylis 1981, Robertson 1991, Sadovy 1996). Despite the fact that a wide variety of complex spawning systems has been found in reef fishes, and also that gradations between major spawning types occur (Table 1), it is useful to discuss spawning strategies by reference to 3 major spawning groups: demersal spawners which deposit demersal eggs; pelagic spawners which produce pelagic eggs; and bearers which retain fertile eggs externally or internally (Balon 1981, Thresher 1984, Leis 1991). Among these, the demersal spawner and pelagic spawner are relatively dominant in terms of both numbers of taxonomic groups (Table 1) and individuals (Thresher 1984).

Many features of these spawning patterns differ. For example, most demersal spawners invest in on-site parental care of fertilized eggs, which is generally not associated with pelagic spawning (Ridley 1978, Blumer 1979, Thresher 1984). Furthermore,

the average size of demersal spawners has been found to be lower than that of pelagic spawners (Thresher 1984). This size difference has been the focal point in the synthesis of explanations of reproductive strategies developed in the last 2 decades (Johannes 1978, Barlow 1981, Baylis 1981, Robertson 1991, Sadovy 1996).

There have been various hypotheses proposed to explain the occurrence of various spawning patterns in terms of natural selection (Johannes 1978, Barlow 1981, Baylis 1981, Robertson 1991). However, few have been generally accepted (Balon 1978, Shapiro et al. 1988). Stability of the marine environment over time has been assumed to be a key factor in some hypotheses to infer that reef fishes are selected to spawn pelagically to favor offspring dispersal. For example, Baylis (1981) assumed that the ocean environment is uniform and temporally stable, while freshwater environments are more variable. It is therefore predicted that freshwater fishes as a rule should deposit demersal eggs because pelagic eggs risk being washed out of their suitable microhabitats; marine

**Table 1.** Reproductive patterns of bony coral reef fishes

Pattern <sup>a</sup>	Family <sup>b</sup>	No. of species <sup>c</sup>
Live-bearers (2 families)	Bythitidae	90 <sup>e</sup>
	Clinidae	73
Demersal eggs (16 families)	Batrachoididae	69 <sup>e</sup>
	Plotosidae	32 <sup>f</sup>
	Sciaenidae	242 <sup>e</sup>
	Pholidichthyidae	1
	Gobiesocidae	120 <sup>e</sup>
	Pseudochromidae	98
	Pomacentridae	315
	Tripterygiidae	115
	Chaenopsidae	56
	Blenniidae	345 <sup>e</sup>
	Schindleriidae	2
	Gobiidae	1,875 <sup>e</sup>
	Microdesmidae	60 <sup>e</sup>
	Siganidae	27
	Balistidae	40
	Tetraodontidae	121 <sup>e</sup>
Brooded eggs (6 families)	Solenostomidae	3
	Syngnathidae	215
	Grammatidae	10
	Apogonidae	207 <sup>e</sup>
	Opistognathidae	60
Dactyloscopidae	41	
Pelagic eggs (54 families)	Moringuidae	6 <sup>e</sup>
	Chlopsidae	16
	Muraenidae	200 <sup>e</sup>
	Ophichthidae	250 <sup>e</sup>
	Congridae	150
	Synodontidae	55
	Ophidiidae	209
	Carapidae	32
	Lophiidae	25
	Monocentridae	4
	Anomalopidae	6
	Pegasidae	5
	Aulostomidae	3
	Fistulariidae	4
	Dactylopteridae	7
	Scorpaenidae <sup>d</sup>	388 <sup>e</sup>
	Platycephalidae	60
	Serranidae	449 <sup>e</sup>
	Priacanthidae	18
	Malacanthidae	39
	Carangidae	140
	Lutjanidae	125 <sup>e</sup>
	Gerreidae	40 <sup>e</sup>
	Haemulidae	150 <sup>e</sup>
	Inermiidae	na
	Sparidae <sup>d</sup>	100 <sup>e</sup>
	Lethrinidae	39
	Nemipteridae	62
	Mullidae	55
	Monodactylidae	5 <sup>e</sup>
	Pempheridae	25

**Table 1.** (Continued)

Pattern <sup>a</sup>	Family <sup>b</sup>	No. of species <sup>c</sup>	
Pelagic eggs	Kyphosidae	42	
	Ephippidae	20	
	Chaetodontidae	114	
	Pomacanthidae	74	
	Cirrhitidae	32	
	Cheilodactylidae	18	
	Cepolidae	19	
	Mugilidae	66 <sup>e</sup>	
	Sphyraenidae	20	
	Polynemidae	33 <sup>e</sup>	
	Labridae <sup>d</sup>	500	
	Scaridae	83	
	Uranoscopidae	50	
	Creediidae	16	
	Pinguipedidae	50	
	Callionymidae	130 <sup>e</sup>	
Semi-pelagic eggs (3 families)	Acanthuridae	72	
	Psettodidae	3	
	Bothidae	115	
	Cynoglossidae	110 <sup>e</sup>	
	Soleidae	89	
	Ostraciidae	33	
	Diodontidae	19	
	More than 1 type (4 families)	Hemiramphidae	85 <sup>e</sup>
		Belonidae	11 <sup>e</sup>
		Atherinidae	165 <sup>e</sup>
	Unknown (10 families)	Clupeidae (P,D)	181 <sup>e</sup>
		Antennariidae (P,B)	43
		Plesiopidae (B,D)	47
		Labrisomidae (L,D)	102
		Pseudotriconotidae	1
		Ogcocephalidae (P?)	62
Notocheiridae		6	
Holocentridae		65	
Centriscidae		4	
Caracanthidae		4	
Aploactinidae	37		
Kuhliidae	8		
Trichonotidae	6		
Kraemeriidae	8 <sup>e</sup>		

<sup>a</sup> Reproductive patterns for each family are principally based on Thresher (1984) and Leis (1991).

<sup>b</sup> Families are based on Nelson (1994). L (live-bearers), D (demersal eggs), B (brooded eggs), and P (pelagic eggs) refer to the reproductive pattern.

<sup>c</sup> Number of species in the entire family is based on Nelson (1994). It is footnoted when there are members occurring in freshwater environments. The number may also include species from marine environments other than coral reefs. na: data not available.

<sup>d</sup> Some members from temperate waters show other patterns (Potts 1984; Thresher 1984).

<sup>e</sup> From rarely to some in freshwater.

<sup>f</sup> Half of the species are in freshwater.

fishes should, on the contrary, spawn pelagic eggs. By contrast, Barlow (1981) did not consider the marine environment to be stable. However, his dispersal hypothesis also suggested that the reproductive tactics of coral reef fishes have been driven largely by selection for effective dispersal in a patchy environment, as it is generally agreed that a fluctuating environment should favor strategies for dispersal. He also suggested that larger fish may have higher individual fecundity and so are selected to spawn pelagic eggs. Alternatively a small fish with its comparatively low individual fecundity must spawn demersal eggs since it cannot afford losses due to dispersal. Some other hypotheses suggest that the reproductive strategies of reef fishes are heavily governed by egg-predation pressure, which in turn provokes adaptation to different patterns of spawning (Johannes 1978). Moreover, it has also been suggested that the range of spawning patterns, from pelagic spawning through demersal spawning to live-bearers, expresses a phylogenetic sequence from more primitive to better-adapted strategies, and from the energetically more wasteful to the less so (Balon 1978).

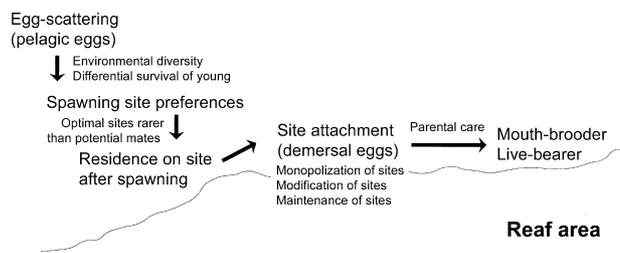
More recently, however, most of these viewpoints have been questioned due to the lack of supporting evidence (Thresher 1984, Shapiro et al. 1988). A similar argument has also arisen over the dispersal hypothesis in relation to marine invertebrates which have much in common with coral reef fishes (Grahame and Branch 1985, Scheltema 1986). As an alternative, Thresher (1984) proposed the size-disadvantage hypothesis to explain the size difference normally observed between demersal and pelagic spawners. According to this hypothesis, small fishes would have little difficulty in finding a secluded and easily defended spot to tend eggs. With increasing body size, however, such defensible spawning sites become more difficult to find. So, it suggests that because of this size disadvantage, larger fishes must spawn pelagically.

While the size-disadvantage hypothesis might explain the relationship between large sizes and pelagic spawning in reef fishes, we are left, however, with the problem of explaining pelagic spawning in many small-sized fishes (Barlow 1981, Robertson 1991). It is likely that the selective forces which mold the structuring process of the fish community may also operate on, and subsequently change, the life history of a fish species (Mapstone and Fowler 1988, Ebeling and Hixon 1991, Sale 1991). Thus, an alternative hypothesis, which mainly focuses on resource availability in the environment, is proposed to explain the reproductive strategies of demersal and pelagic

spawners.

## ASSUMPTIONS

This resource-limitation hypothesis shares the view that egg-predation pressure is the major selective force molding reproductive strategies of reef fishes (Robertson and Hoffman 1977, Johannes 1978, Jones 1981) and that reef fishes are selected to spawn demersally and care for eggs. However, it emphasizes that the nesting resource (substrate for nesting) in the environment is not sufficient for all fishes. Thus, this hypothesis is based on 2 primary assumptions: (1) that coral-reef fishes are selected to spawn demersal eggs; and (2) that the nesting resource (i.e., substrate) is limited. The first assumption follows Baylis's (1981) notion of the evolution of parental behavior (Fig. 1), along with Thresher's (1984) comparative analysis of the advantages of various spawning patterns. The second relies principally on the observation that, on the 2-dimensional coral reef surface where many sessile organisms live sympatrically (Jan and Chang 1991, Jan et al. 1994), not all the fish species electing to build nests are able to obtain optimal nesting substrates. Moreover, the implication that nesting substrates for coral reef fishes are limiting has also arisen from various studies (Hastings 1992, Jan and Chang 1993) and lends support to this notion. Parallel to this, substrates for the demersal spawning of freshwater fishes are generally acknowledged to be limited (McKaye 1979 1984). DeMartini (1988) has also provided considerable evidence to show that spawning sites are in short supply for the temperate marine fish, *Porichthys notatus*. Moreover, competition for suitable nesting substrates may be enhanced, as in the same area, the spawning seasons of different species generally overlap or at least the spawnings peak at about the same time (Fig. 2; Pressley 1980, Robertson 1991, Sadovy 1996).



**Fig. 1.** Hypothesized sequence of events in the evolution of parental behavior of fishes on coral reefs. (After Baylis (1981), with egg types and reef diagram appended).

## HYPOTHESIS TESTING

This hypothesis postulates that fishes which succeed in obtaining nesting substrates will spawn demersally, whereas those that fail to obtain suitable sites will tend to spawn pelagically. Possession of spawning substrate can be achieved either by long-term territoriality or by temporary exploitation. Accordingly, some ecological characteristics of demersal spawners and pelagic spawners can be predicted as follows.

1. Long-term nesting substrate holders spawn demersally.

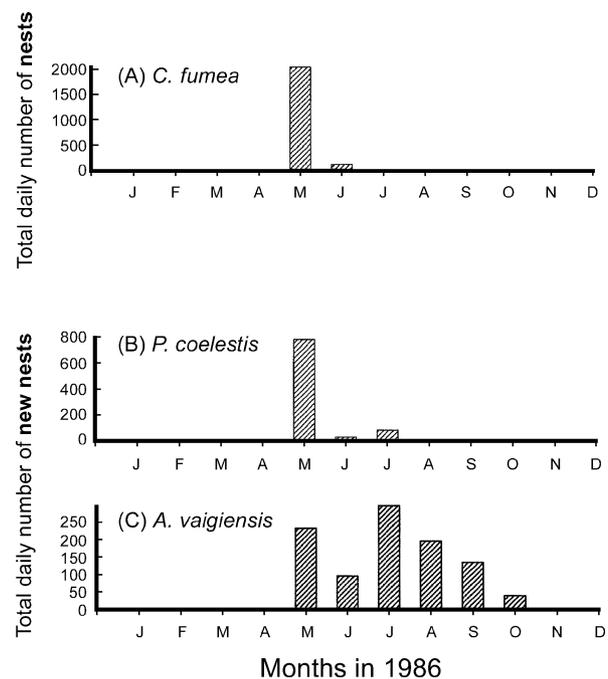
Suitable nesting substrates can be secured by long-term sustained territoriality, as found in *Stegastes* spp. and other territorial damselfishes (Clarke 1971, Williams 1978, Wellington and Victor 1988, Hoelzer 1990, Peterson and Hess 1991, Karino 1995), some gobies (Miller 1984, Cole and Shapiro 1992), and blennies (Thresher 1984, Hastings 1992). The securing of a food resource, particularly benthic algae, is generally believed to be the main value of the territoriality of many damselfishes (Ebersole 1980, Losey 1982, Jones and Norman 1986, Foster 1987, Roberts 1987). However, the defended substrate also provides fish with essential nesting substrate (Clarke 1971, Williams 1978, Wellington and Victor 1988). For example, in northern Taiwan most territories defended by mature male *Stegastes fasciatus* include large mounts and clefts, the typical nesting substrate used by this species; by contrast, territories defended by females and juveniles usually do not include such types of substrate (Jan 1989). In Curacao, Netherlands Antilles, *Chromis cyanea* was found to defend long-term territories which did not seem to be associated with its food resource (De Boer 1980 1981). In this case the male *C. cyanea* established territories on the reef slope both in- and outside the spawning period, while the females roamed freely over the reef framework. The nest was built on suitable substrate within the territory. Since only the male defends long-term territory, it is possible that this damselfish defends the substrate against others solely for the purpose of spawning.

This prediction does not apply to the territoriality of some male bluehead wrasse, *Thalassoma bifasciatum*, because it is the mating site rather than the substrate which is defended. These sites tend to be upward projections on the downcurrent periphery of a reef and serve as egg-launching sites for the pelagic eggs (Warner and Hoffman 1980a, b, Warner 1984 1991). Also not included are some surgeonfishes which are known to be territorial but

which spawn pelagically (Nursall 1974, Robertson et al. 1979, Robertson 1983). Robertson and Gaines (1986) studied resource utilization of 13 surgeonfish species at Aldabra, Indian Ocean to demonstrate that those territorial surgeonfishes are actively competing for food. Otherwise the possibility of competition for and defense of shelter sites of any type in these surgeonfishes is remote (Robertson et al. 1979, Choat 1991). Because their territoriality does not seem to involve the defense of any specific type of potential nesting substrate, the present hypothesis would not predict demersal spawning for these species.

2. Non-territorial fishes may be demersal spawners if they adopt specific tactics in their exploitation of nesting substrates, or have developed specific features in their reproductive biology to cope with the availability and/or quality of nesting substrate.

Nesting substrates are essential in demersal spawning for depositing eggs. Free-ranging fish generally do not defend nesting substrates in the non-spawning season. However, some fish are capable of exploiting suitable substrate from the open



**Fig. 2.** Number of nests of 3 damselfish species, namely (A) *Chromis fumea*, (B) *Pomacentrus coelestis*, and (C) *Abudefduf vaigiensis*, found on an area of approximately 9000 m<sup>2</sup> on the northern coast of Taiwan in 1986, showing the overlap of spawning seasons. (A) and (B) based on Jan (1997) and (C) based on Jan and Chang (1992b). Note that in (B) and (C) only new nests were counted.

environment for demersal spawning. Acquisition of the substrate is achieved by different strategies under different environmental conditions. For example, in the Maldives, a group of *Abudefduf vaigiensis* exploited their spawning substrates by aggressive exclusion of the former substrate users including *Acanthurus lineatus*, *Acanthurus* sp. and *Plectroglyphidodon lacrymatus* (Jan 1989), whereas in northern Taiwan, where substrates were commonly dominated by territorial *Stegastes fasciolatus*, the utilization of nesting substrate by *A. vaigiensis* was related to complex interspecific interactions (Jan 1995). In the case of low availability of suitable substrate, while some fishes are capable of modifying a sub-optimal substrate into an optimal one (Thresher 1984), others may adopt alternative strategies to ensure successful spawning. The latter is shown by damselfishes such as *Chromis fumea* (Jan 1997) and *Dascyllus trimaculatus* (Jan 1989). Both species tend to spawn in sub-optimal conditions on open substrates which are subject to heavy sedimentation. However, the hatching time of their eggs is reduced (compared with those of other damselfishes), thus reducing their dependence on the substrate. The balistids, which have large body sizes and hence should experience difficulties in obtaining nesting substrate, also have a short egg-incubation period (Thresher 1984). Egg-brooders seem to have adopted similar strategies. Eggs of brooders such as cardinal fishes, jawfishes, or longfins are generally deposited on a defended area of substrate (with the exception of *Phaeoptyx* sp. and some *Apogon* spp.) before they are moved and incubated in the brooder's mouth (Thresher 1984, Kuwamura 1985). Moving eggs from the substrate obviously also lessens their dependence on the substrate.

3. If the spawning of a fish can be achieved either in association with substrate or without it, then spawning in association with the substrate would be favored.

This is shown by the spawning of *Thalassoma* spp. (Warner and Hoffman 1980a, b, Dawson-Shepherd 1981, Warner 1984) and some other wrasses (Robertson and Hoffman 1977). *Thalassoma bifasciatum* chooses to spawn at sites on the downcurrent edges of reefs over some vertical projections (Warner 1987), while *Pseudolabrus celidotus* exhibits a preference for spawning at a small number of sites in deeper areas (Jones 1981). The mating sites, rather than those occupying males, appear to be the objects of female choice in these wrasses (Jones 1981, Warner 1985, 1987).

This spawning-site fidelity exhibited by females may be interpreted to be an adaptation for increasing

egg survival by assuming that eggs spawned at these sites are vulnerable to fewer egg predators or have a higher possibility of being swept away from the reef where planktivores are based. However, as suggested by Shapiro et al. (1988), the assumption that spawning sites are selected specifically to speed the egress of pelagic eggs off the reef remains questionable because there is little information known of current flow at specific spawning and non-spawning sites. Similarly, the assumption that pelagic spawning is selected to occur at the site where egg predators are fewer is also unproven (Colin and Bell 1991). Furthermore, Colin and Clavijo (1988) and Colin and Bell (1991) studied the time, location, seasonality, and behavior of pelagic spawning species from different oceans, and found that predation by piscivores on spawning adults was rare. By contrast, the function of territorial behavior in the male cunner, *Tautoglabrus adspersus* (another pelagic spawning labrid) from north temperate waters is suggested to provide an area in which courtship and spawning can occur with relatively little risk of interference by rival males (Pottle and Green 1979, Pottle et al. 1981). Apparently, this spawning-site fidelity remains open to interpretation. Here with the relatively small body sizes of *Thalassoma bifasciatum* and *Pseudolabrus celidotus*, this phenomenon is considered to be a behavioral adaptation toward demersal spawning according to the assumption of the present hypothesis.

4. Taxonomic groups of fish currently engaging in pelagic spawning might adapt to demersal spawning if suitable nesting substrate is available.

Information that would test this prediction in coral reef fishes is unavailable. However, even though almost all tropical wrasses are known to spawn pelagically (*Anampses* spp. are the possible exception to this; Thresher 1984), in temperate regions, where the diversity (e.g., number of species) in the fish community is comparatively low, many wrasses spawn demersally (Taborsky et al. 1987). For example, among the 5 common wrasses in British coastal waters, four (including *Labrus bergylta*, *L. mixtus*, *Centrolabrus exoletus*, and *Symphodus (Crenilabrus) melops*) are demersal spawners (Potts 1985). Furthermore, these wrasses build nests and care for their eggs, as do the tropical damselfishes (Warner and Lejeune 1985, Taborsky et al. 1987). Also, in temperate waters some members of the Sparidae and Scorpaenidae are demersal spawners, despite their coral reef confamilials spawning pelagically (Potts 1984, Thresher 1984).

5. Large-sized fishes are selected to spawn pelagically; specific behavioral adaptations to avoid

egg predation should occur in small-sized pelagic spawners.

The first part of this prediction is parallel to that based on Thresher's (1984) size-disadvantage hypothesis. In demersal spawning, nest size is expected to be related to the body size of the nesting species (as found in damselfishes, unpubl. data). In an environment where open substrate is limited, suitable nesting sites (substrate) become less available for fishes with increasing body size. Thus, while fishes are basically electing to guard their eggs, large-sized fishes, because they are unable to obtain nesting substrate, should use the alternative of spawning pelagically.

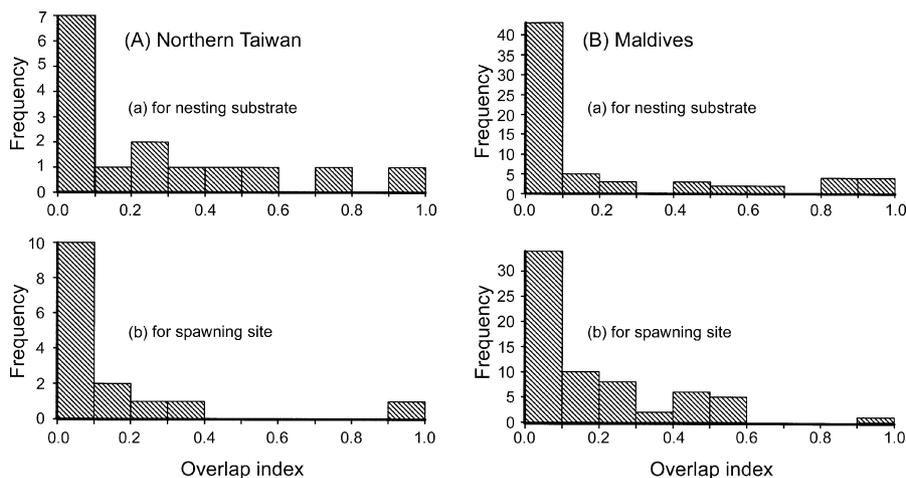
Conversely, small-sized pelagic spawners, with their assumed relatively low fecundity (Sadovy 1996), would face difficulties of losing more eggs in the water column than they could afford. Thus, some specific adaptation for egg-predator avoidance would be essential to ensure their survival. A common example of this is spawning at dusk or during the night. For instance, spawning of the sandperch, *Parapercis snyderi* and the hawkfish, *Cirrhichthys falco* (both pelagic spawners) commences just after sunset and continues until darkness (Nakazono et al. 1985, Donaldson 1986 1987). Possible advantages of such timing include reduced planktivore activity and thus reduced levels of planktivory upon pelagic eggs.

#### 6. Additional predictions for demersal spawning.

According to the second assumption of the present hypothesis, i.e., optimal spawning substrate on the reef is limiting, the following features of de-

mersal spawning may be expected: (1) nesting substrate specificity (Fisherson 1970, Thresher 1984, Jan and Ormond 1992a), (2) nesting substrate partitioning (Jan and Chang 1993, Ormond et al. 1996), and (3) polygamy, a result of pressure to reduce the number of nests (Thresher 1984, Davies 1989 cf. Donaldson 1989, for monogamy).

Nesting substrate specificity is expected because differentiation in utilization of nesting substrate may occur when substrates are selected by demersal spawners in accordance with their powers of nest defense and their potential for using the substrate to avoid egg predation. In damselfishes, for example, the selection of spawning in burrows, pockets, or excavations by small-sized species such as *Chrysiptera* spp. and *Pomacentrus* spp. (Jan and Ormond 1992a) may be a behavioral adaptation to assist egg protection. By contrast, large-sized species such as *Abudefduf* spp., which are capable of nest-defense, normally spawn on uncovered substrates (Jan 1991, Jan and Ormond 1992b). Interestingly, predation pressure is likely to provoke interspecific competition by imposing a common requirement among fishes for shelters for egg protection, and the capability of performing substrate modification may, in return, help to relieve the seriousness of the situation. Nesting substrate partitioning is expected following the niche-diversification hypothesis which predicts that coexisting fishes differ in their resource use (Ebeling and Hixon 1991). Data collected from damselfishes, with the relatively low pairwise overlap in the utilization of nesting substrate between non-territorial fishes (Fig. 3), appear for the



**Fig. 3.** Frequency histogram showing positively skewed distributions of overlap indices for spawning resources of damselfish species, where (A) includes data from northern Taiwan, with 6 species nesting at 5 substrate types and in 5 different zones (i.e., spawning sites), based on Jan and Chang (1993), and (B) includes data from the Maldives, with 12 species nesting at 8 substrate types and in 7 different zones, derived from Ormond et al. (1996). Pianka's (1973) overlap index is used.

most part to agree with this prediction.

Concluding remarks: This resource-limitation hypothesis is proposed as an alternative to established hypotheses to explain how the spawning patterns of reef fishes have been selected. Research findings support various aspects of the predictions stemming from this hypothesis. Since the present resource-limitation hypothesis mainly deals with resource utilization among demersal spawners, it apparently lacks the power of predicting the selection of spawning sites and timing for pelagic spawning. A close look at the hypotheses which assume that spawning behaviors of pelagic spawners are adaptive (Johannes 1978, Barlow 1981, Thresher and Brothers 1989, Robertson 1991 cf. Shapiro et al. 1988, Planes et al. 1998) may stimulate a synthesis that can satisfactorily explain the full range of fish species spawning patterns. That is to say, although the assumptions adopted by various hypotheses may differ, it is possible that the different hypotheses may not be totally incompatible.

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## REFERENCES

- Balon EK. 1975. Reproductive guilds of fishes: a proposal and definition. *J. Fish Res. Board Can.* **32**: 821-864.
- Balon EK. 1978. Reproductive guilds and the ultimate structure of fish taxocenes: amended contribution to the discussion presented at the mini-symposium. *Environ. Biol. Fishes* **3**: 149-152.
- Balon EK. 1981. About processes which cause the evolution of guilds and species. *Environ. Biol. Fishes* **6**: 129-138.
- Balon EK. 1982. About the courtship rituals in fishes, but also about a false sense of security given by classification schemes, "comprehensive" reviews and committee decisions. *Environ. Biol. Fishes* **7**: 193-197.
- Barlow GW. 1981. Patterns of parental investment, dispersal and size among coral-reef fishes. *Environ. Biol. Fishes* **6**: 65-85.
- Baylis JR. 1981. The evolution of parental care in fishes, with reference to Darwin's rule of male sexual selection. *Environ. Biol. Fishes* **6**: 223-251.
- Blumer LS. 1979. Male parental care in the bony fishes. *Quart. Rev. Biol.* **53**: 149-161.
- Choat JH. 1991. The biology of herbivorous fishes on coral reefs. *In* PF Sale, ed. *The ecology of fishes on coral reefs*. San Diego, New York: Academic Press, pp. 120-155.
- Clarke TA. 1971. Territory boundaries, courtship and social behavior in the garibaldi *Hypsypops rubicunda* (Pomacentridae). *Copeia* **1971**: 295-299.
- Cole KC, DY Shapiro. 1992. Gonadal structure and population characteristics of the protogynous goby *Coryphopterus glaucofraenum*. *Mar. Biol.* **113**: 1-9.
- Colin PL, LJ Bell. 1991. Aspects of the spawning of labrid and scarid fishes (Pisces: Labroidei) at Enewetak Atoll, Marshall Islands, with notes on other families. *Environ. Biol. Fishes* **31**: 229-260.
- Colin PL, IE Clavijo. 1988. Spawning activity of fishes producing pelagic eggs on a shelf edge coral reef, southeastern Puerto Rico. *Bull. Mar. Sci.* **43**: 249-279.
- Davies NB. 1989. Sexual conflict and the polygamy threshold. *Anim. Behav.* **38**: 226-234.
- Dawson-Shepherd AR. 1981. Diandry in the coral reef wrasse *Thalassoma rueppellii*. Ph.D. dissertation, Univ. of York, UK, 248 pp.
- De Boer BA. 1980. A causal analysis of the territorial and courtship behaviour of *Chromis cyanea* (Pomacentridae, Pisces). *Behaviour* **73**: 1-50.
- De Boer BA. 1981. Influence of population density on the territorial, courting and spawning behaviour of male *Chromis cyanea* (Pomacentridae). *Behaviour* **77**: 99-120.
- DeMartini EE. 1988. Spawning success of the male plainfin midshipman. I. Influences of male body size and area of spawning site. *J. Exp. Mar. Biol. Ecol.* **121**: 177-192.
- Donaldson TJ. 1986. Courtship and spawning of the hawkfish *Cirrhichthys falco* at Miyake-jima, Japan. *Jpn. J. Ichthyol.* **33**: 329-333.
- Donaldson TJ. 1987. Social organization and reproductive behavior of the hawkfish *Cirrhichthys falco* (Cirrhitidae). *Bull. Mar. Sci.* **41**: 531-540.
- Donaldson TJ. 1989. Facultative monogamy in obligate coral-dwelling hawkfishes (Cirrhitidae). *Environ. Biol. Fishes* **26**: 295-302.
- Ebeling AW, MA Hixon. 1991. Tropical and temperate reef fishes: comparison of community structures. *In* PF Sale, ed. *The ecology of fishes on coral reefs*. San Diego, New York: Academic Press, pp. 509-563.
- Ebersole JP. 1980. Food density and territory size: an alternative model and a test on the reef fish *Eupomacentrus leucostictus*. *Am. Nat.* **115**: 492-509.
- Fishelson L. 1970. Behaviour and ecology of a population of *Abudefduf saxatilis* (Pomacentridae, Teleostei) at Eilat (Red Sea). *Anim. Behav.* **18**: 225-237.
- Foster SA. 1987. Territoriality of the dusky damselfish: influence on algal biomass and on the relative impacts of grazing by fishes and *Diadema*. *Oikos* **50**: 153-160.
- Grahame J, GM Branch. 1985. Reproductive patterns of marine invertebrates. *Oceanogr. Mar. Biol. Ann. Rev.* **23**: 373-398.
- Hastings PA. 1992. Nest-site size as a short-term constraint on the reproductive success of paternal fishes. *Environ. Biol. Fishes* **34**: 213-218.
- Hoelzer GA. 1990. Male-male competition and female choice in the Cortez damselfish, *Stegastes rectifraenum*. *Anim. Behav.* **40**: 339-349.
- Jan RQ. 1989. Aspects of reproductive ecology of damselfishes (Pomacentridae, Teleostei), with emphasis on substrate utilisation. Ph.D. thesis, Univ. of York, UK, 244 pp.
- Jan RQ. 1991. Malicious neighbours in leks of sergeant major damselfish, *Abudefduf vaigiensis*. *Bull. Inst. Zool. Acad. Sinica* **30**: 49-53.
- Jan RQ. 1995. What do the sergeant major *Abudefduf vaigiensis* lose from nesting in the territories of Pacific Gregory *Stegastes fasciolatus*? *Zool. Stud.* **34**: 131-135.

- Jan RQ. 1997. Sympatric spawning of the damselfishes *Chromis fumea* and *Pomacentrus coelestis* on the northern coast of Taiwan. *Zool. Stud.* **36**: 26-32.
- Jan RQ, KH Chang. 1991. A monitoring study of the succession on marine sessile macro-organisms five years before and after the operation of a nuclear power plant. In DW Jeffrey, B Madden, eds. Bioindicators and environmental management. London: Academic Press, pp. 21-35.
- Jan RQ, KH Chang. 1993. Substrate partitioning among non-territorial damselfishes during spawning in northern Taiwan. *Bull. Inst. Zool. Acad. Sinica* **32**: 184-193.
- Jan RQ, CF Dai, KH Chang. 1994. Monitoring of hard substrate communities. In KJM Kramer, ed. Biomonitoring of coastal waters and estuaries. Boca Raton, FL: CRC Press, pp. 285-310.
- Jan RQ, RFG Ormond. 1992a. Spawning of damselfishes on the northern coast of Taiwan, with emphasis on spawning site distribution. *Bull. Inst. Zool. Acad. Sinica* **31**: 231-245.
- Jan RQ, RFG Ormond. 1992b. The seasonal spawning of sergeant major damselfish *Abudefduf vaigiensis* in the subtropical waters of Taiwan. *Bull. Inst. Zool. Acad. Sinica* **31**: 290-311.
- Johannes RE. 1978. Reproductive strategies of coastal marine fishes in the tropics. *Environ. Biol. Fishes* **3**: 65-84.
- Jones GP. 1981. Spawning-site choice by female *Pseudolabrus celidotus* (Pisces: Labridae) and its influence on the mating system. *Behav. Ecol. Sociobiol.* **8**: 129-142.
- Jones GP, MD Norman. 1986. Feeding selectivity in relation to territory size in a herbivorous reef fish. *Oecologia (Berlin)* **68**: 549-556.
- Karino K. 1995. Effective timing of male courtship displays for female mate choice in a territorial damselfish *Stegastes nigricans*. *Jpn. J. Ichthyol.* **42**: 173-180.
- Kuwamura T. 1985. Social and reproductive behavior of three mouthbrooding cardinalfishes, *Apogon doederleini*, *A. niger* and *A. notatus*. *Environ. Biol. Fishes* **13**: 17-24.
- Leis JM. 1991. The pelagic stage of reef fishes: the larval biology of coral reef fishes. In PF Sale, ed. The ecology of fishes on coral reefs. San Diego, New York: Academic Press, pp. 183-230.
- Losey GS Jr. 1982. Ecological cues and experience modify interspecific aggression by the damselfish, *Stegastes fasciolatus*. *Behaviour* **80**: 14-37.
- Mapstone BD, AJ Fowler. 1988. Recruitment and structure of assemblages of fish on coral reefs. *TREE* **3**: 72-77.
- McKaye KR. 1979. Competition for breeding sites between the cichlid fishes of Lake Jiloa, Nicaragua. *Ecology* **58**: 291-302.
- McKaye KR. 1984. Behavioural aspects of cichlid reproductive strategies: patterns of territoriality and brood defence in Central American substratum spawners and African mouth brooders. In GW Potts, RJ Wootton, eds. Fish reproduction: strategies and tactics. London: Academic Press, pp. 245-273.
- Miller PJ. 1984. The tokology of gobioid fishes. In GW Potts, RJ Wootton, eds. Fish reproduction: strategies and tactics. London: Academic Press, pp. 119-153.
- Nakazono A, H Takeya, H Tsukauara. 1985. Studies on the spawning behaviour of *Chromis notata* (Temminck et Schlegel). *Sci. Bull. Fac. Agric. Kyushu Univ.* **34**: 29-37.
- Nelson JS. 1994. Fishes of the world. New York: J Wiley, 600 pp.
- Nursall JR. 1974. Some territorial behavioural attributes of the surgeonfish *Acanthurus lineatus*, at Heron Island, Queensland. *Copeia* **1974**: 905-959.
- Ormond RFG, JM Roberts, RQ Jan. 1996. Behavioural differences in microhabitat use by damselfishes (Pomacentridae): implications for reef fish biodiversity. *J. Exp. Mar. Biol. Ecol.* **202**: 85-95.
- Peterson CW, HC Hess. 1991. The adaptive significance of spawning synchronization in the Caribbean damselfish *Stegastes dorsopunicans* (Poey). *J. Exp. Mar. Biol. Ecol.* **151**: 155-167.
- Pianka ER. 1973. The structure of lizard communities. *Annu. Rev. Ecol. Syst.* **4**: 53-74.
- Planes S, P Romans, R Lecomte-Finiger. 1998. Genetic evidence of closed life-cycles for some coral reef fishes within Taiaro Lagoon (Tuamotu Archipelago, French Polynesia). *Coral Reefs* **17**: 9-14.
- Pottle RA, JM Green. 1979. Territorial behaviour of the north temperate labrid, *Tautoglabrus adspersus*. *Can. J. Zool.* **57**: 2337-2347.
- Pottle RA, JM Green, G Martel. 1981. Dualistic spawning behaviour of the cunner, *Tautoglabrus adspersus* (Pisces: Labridae), in Bonne Bay, Newfoundland. *Can. J. Zool.* **59**: 1582-1585.
- Potts GW. 1984. Parental behaviour in temperate marine teleosts with special reference to the development of nest structures. In GW Potts, RJ Wootton, eds. Fish reproduction: strategies and tactics. London: Academic Press, pp. 223-244.
- Potts GW. 1985. The nest structure of the corkwing wrasse, *Crenilabrus melops* (Labridae: Teleostei). *J. Mar. Biol. Assoc. UK* **65**: 531-546.
- Pressley PH. 1980. Lunar periodicity in the spawning of yellow-tail damselfish, *Microspathodon chrysurus*. *Environ. Biol. Fishes* **5**: 153-159.
- Ridley M. 1978. Paternal care. *Anim. Behav.* **26**: 904-932.
- Roberts CM. 1987. Experimental analysis of resource sharing between herbivorous damselfish and blennies on the Great Barrier Reef. *J. Exp. Mar. Biol. Ecol.* **111**: 61-75.
- Robertson DR. 1983. On the spawning behavior and spawning cycles of eight surgeonfishes (Acanthuridae) from the Indo-Pacific. *Environ. Biol. Fishes* **9**: 193-223.
- Robertson DR. 1991. The role of adult biology in the timing of spawning of tropical reef fishes. In PF Sale, ed. The ecology of fishes on coral reefs. San Diego, New York: Academic Press, pp. 356-386.
- Robertson DR, SD Gaines. 1986. Interference competition structures habitat use in a local assemblage of coral reef surgeonfishes. *Ecology* **67**: 1372-1383.
- Robertson DR, S Hoffman. 1977. The roles of female mate choice and predation in the mating systems of some tropical labroid fishes. *Z. Tierpsychol.* **45**: 298-320.
- Robertson DR, NVC Polunin, K Leighton. 1979. The behavioural ecology of three Indian Ocean surgeonfishes (*Acanthurus lineatus*, *A. leucosternon* and *Zebbrasoma scopas*): their feeding strategies, and social and mating systems. *Environ. Biol. Fishes* **4**: 125-170.
- Sadovy YJ. 1996. Reproduction of reef fishery species. In VC Polunin, CM Roberts, eds. Reef fisheries. London: Chapman & Hall, pp. 15-59.
- Sale PF. 1991. Reef fish communities: open nonequilibrium systems. In PF Sale, ed. The ecology of fishes on coral reefs. San Diego, New York: Academic Press, pp. 564-598.
- Scheltema RS. 1986. On dispersal and planktonic larvae of benthic invertebrates: an eclectic overview and summary of problems. *Bull. Mar. Sci.* **39**: 290-322.

- Shapiro DY, DA Hensley, RS Appeldoorn. 1988. Pelagic spawning and egg transport in coral-reef fishes: a skeptical overview. *Environ. Biol. Fishes* **22**: 3-14.
- Taborsky M, B Hudde, P Wirtz. 1987. Reproductive behaviour and ecology of *Symphodus (Crenilabrus) ocellatus*, a European wrasse with four types of male behaviour. *Behaviour* **102**: 82-118.
- Thresher RE. 1984. Reproduction in reef fishes. Neptune City, NJ: THF Publ., 399 pp.
- Thresher RE, EB Brothers. 1989. Evidence of intra- and inter-oceanic regional differences in the early life history of reef-associated fishes. *Mar. Ecol. Prog. Ser.* **57**: 187-205.
- Warner RR. 1984. Deferred reproduction as a response to sexual selection in a coral reef fish: a test of the life historical consequences. *Evolution* **38**: 148-162.
- Warner RR. 1985. Alternative mating behaviors in a coral reef fish: a life-history analysis. *Proc. 5th Int'l. Coral Reef Congr.* **4**: 145-150.
- Warner RR. 1987. Female choice of sites versus mates in a coral reef fish, *Thalassoma bifasciatum*. *Anim. Behav.* **35**: 1470-1478.
- Warner RR. 1991. The use of phenotypic plasticity in coral reef fishes as test of theory in evolutionary ecology. In PF Sale, ed. *The ecology of fishes on coral reefs*. San Diego, New York: Academic Press, pp. 387-398.
- Warner RR, SG Hoffman. 1980a. Local population size as a determinant of mating system and sexual composition in two tropical marine fishes (*Thalassoma* spp.). *Evolution* **34**: 508-518.
- Warner RR, SG Hoffman. 1980b. Population density and the economics of territorial defense in a coral reef fish. *Ecology* **61**: 772-780.
- Warner RR, P Lejeune. 1985. Sex change limited by paternal care: a test using four Mediterranean labrid fishes, genus *Symphodus*. *Mar. Biol.* **87**: 89-99.
- Wellington GM, BC Victor. 1988. Variation in components of reproductive success in an undersaturated population of coral-reef damselfish: a field perspective. *Am. Nat.* **131**: 588-601.
- Williams AH. 1978. The ecology of three-spot damselfish: social organization, age, structure, and population stability. *J. Exp. Mar. Biol. Ecol.* **34**: 197-213.

## 資源限制主導珊瑚礁魚類的生殖策略：一個新的假說

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珊瑚礁魚類產卵的方式往往因種而異，其中底棲性卵產卵者和漂浮性卵產卵者無論是在魚種數目上或是在個體數上，都佔有最重要的地位。本文在此提出一個新的假說，以解釋這些底棲性卵產卵者以及漂浮卵產卵者的生殖策略。這個假說是建立在兩個基本假定上：（一）產底棲性卵是珊瑚礁魚類進化的方向。（二）在珊瑚礁環境中，魚類能夠用以構築生殖巢的資源（也就是基質）是有限的。因此資源上的限制是造成採取不同生殖策略的主要因素。根據此一假說可推論：能成功的獲取築巢基質的魚類將產底棲卵，無法獲得合適基質的魚種則仍產漂浮性卵。基於這個假說所推演出來的預測與許多魚類生殖的現狀相符合，因此這個「資源限制說」可用來補充說明目前珊瑚礁中不同的魚種何以會發生有不同的生殖類型。

**關鍵詞：**雀鯛，巢，生殖，產卵，領域性。

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