

## CHAPTER 13

# The Role of Adult Biology in the Timing of Spawning of Tropical Reef Fishes

D. Ross Robertson  
Smithsonian Tropical Research Institute  
Balboa, Republic of Panama

### I. INTRODUCTION

Most marine fishes, including tropical reef species (Sale, 1980a), have two-phase life cycles that include a planktonic larval stage. The observation of considerable fluctuations in temperate region stocks of marine invertebrates and fishes that have this type of life cycle led to the proposition that their adult population sizes are controlled primarily by variation in the larval supply (e.g., Thorson, 1950). A logical development of this idea, which continues to play a major role in the population biology of such organisms (for reviews see, e.g., Cushing, 1982; Doherty and Williams, 1988a; Roughgarden *et al.*, 1988), is that their temporal patterns of reproduction are tailored to larval requirements and have been selected to maximize larval recruitment and cope with both predictable and unpredictable variation in larval mortality. The hypothesis that larval biology ultimately controls the scheduling of reproduction has dominated analyses not only of seasonal patterns of spawning of temperate marine fishes (e.g., Qasim, 1956; Parrish *et al.*, 1981; Bakun *et al.*, 1982; Lambert and Ware, 1984; Sherman *et al.*, 1984; Checkley *et al.*, 1988), but also of the timing of reproduction of tropical reef fishes on a range of temporal scales (for reviews see Johannes, 1978a; Thresher, 1984; Walsh, 1987; Gladstone and Westoby, 1988).

There is a great variety of patterns of spawning by reef fishes on the daily, lunar and seasonal time scales. Some species have fixed, short diel periods when they spawn, while others spawn throughout much of the day. The timing of discrete diel spawning periods may also vary and track changes in the daily timing of the tides. On the lunar scale, spawning of some local populations may be synchronized, either sporadically or cyclically at lunar, semilunar, and other frequencies. In other cases, reproduction of a population is acyclic

and unsynchronized, although its individual members may have their own cycles of activity. The level of activity varies from individuals spawning only once or twice a month to spawning every day or two. Seasonal spawning patterns among the members of a single reef fish community may range from situations in which an entire local population spawns more or less synchronously once a year, through uni- and bimodal seasonal cycles that vary in their strength and timing, to apparently nonseasonal, year-round activity.

This temporal variation is compounded by variation in where and how species spawn, what types of eggs they produce, and the extent of parental care. Some fishes spawn inside their small permanent feeding areas while others migrate up to tens of kilometers to traditional spawning grounds. When spawning, many species abruptly release a cloud of pelagic eggs high in the water column and pay no further attention to them. In some species, benthic eggs are scattered more or less indiscriminately on the substratum, while in others they are carefully laid in discrete, dense, monolayered clutches in prepared, permanent nests where they are guarded intensively by their parent(s) for several days until they hatch and the larvae disperse.

Although much attention has been focused on the ways in which larval biology may influence the evolution of reproductive patterns of tropical species, we have tended to ignore ways in which adult biology also may do so. While recognizing the central role that larval biology plays in the life histories and reproduction of these organisms, the purpose of this chapter is to consider how adult biology factors may control reproduction on the diel, lunar and seasonal time scales. In it I will review existing larval biology and adult biology hypotheses, evaluate how different hypotheses cope with the available data, and, in some cases, indicate what types of data are lacking. I will point out how adult biology may affect spawning patterns in ways not previously considered, and how adults may sometimes be constrained by their own biological limitations from scheduling reproduction in a manner that is most appropriate for maximizing larval recruitment. In doing so I hope to provide a more balanced perspective of factors that control reproduction in reef fishes and show how adult biology explanations may represent viable alternatives to many larval biology explanations.

## II. DIEL SPAWNING PATTERNS

Almost all the available data are for day-active fishes that spawn during daylight or the crepuscular periods. Analyses of diel spawning patterns have concentrated on predator–prey interactions involving both spawners and their eggs and larvae, although some attention also has been paid to the

energetic requirements of newly hatched larvae, and to the effects of parental care of eggs on parents.

### A. Larval Biology Hypotheses

Existing larval biology hypotheses deal mainly with risks of predation on planktonic propagules as they are released from a reef. Pelagic spawners produce planktonic eggs that disperse immediately after spawning, while eggs of benthic spawners develop on the substratum for a day or more before the planktonic larvae disperse from them. Even though spawning and propagule dispersal are well-separated events in benthic spawners, it has been proposed that diel spawning periods of both pelagic and benthic spawners represent adaptations to larval requirements.

#### 1. *Tidal Influences on Propagule Dispersal*

Johannes (1978a) developed the hypothesis that the tidal regime is the primary factor controlling the diel spawning periodicity of reef fishes. He proposed that dispersal of planktonic propagules away from adult habitat is advantageous and that adults facilitate dispersal and minimize predation on propagules as they leave the reef by spawning at the stage of the tide most appropriate for dispersal, typically the beginning of the ebb tide.

If the tidal regime is a simple one, high tides of a particular relative size consistently occur at the same time of the day. In such a system, restriction of spawning to a particular time of the day could represent a response solely to the tidal regime. Alternatively, spawning during a particular time of the day could be advantageous per se, and fish may spawn at a particular tidal stage only when it occurs during the particular diel period because they are responding to both diel and tidal factors (Robertson, 1983). Time of day per se does appear to be important to some species. Many that live either at localities with almost no tidal influence or in habitats that are not strongly influenced by tidal effects restrict their spawning to a particular time of day but not to a particular tidal stage (see examples in Robertson, 1981; Gladstone and Westoby, 1988; Colin and Clavijo, 1988; Myrberg *et al.*, 1989). Colin and Bell's (1991) observations of intraspecific variation in diel spawning activity of pelagic spawners at a single locality show that although both time of day and the tidal cycle affect spawning patterns, the relative importance of each varies in different habitats. In one habitat with minimal tidal flow a species has a short, fixed, daily spawning period, regardless of the stage of the tide, while in another habitat with strong tidal flows the same species spawns at a fixed tidal stage at a variety of different times during the day.

## ***2. Risks from Mobile Egg-Predators***

There are at least three mechanisms by which the restriction of pelagic spawning to a certain period of the day might reduce losses to mobile egg-predators. Spawning could be restricted (1) to periods when egg-predators are inactive, or (2) to periods when egg-predators, although active, are likely to be satiated by prior feeding. Alternatively, (3) synchronization of spawning could simply oversaturate active egg-predators regardless of their feeding status (Robertson and Hoffman, 1977; Johannes, 1978a; Lobel, 1978; Robertson, 1983; Colin and Clavijo, 1988).

Thresher (1984) criticized this egg-predation hypothesis and claimed that rates of egg predation are too low to be of real significance. Whether any general pattern exists is uncertain. While rates of egg predation are very low at some localities (Colin and Clavijo, 1988), they are known to be high at others (Robertson, 1983; Moyer, 1987). Rates of egg predation also can vary considerably among sites on the same reef (Colin and Bell, 1991) and vary in their impact on different species of spawners at the same site (Colin and Clavijo, 1988).

Many pelagic spawners spawn in the afternoon or around dusk (see Thresher, 1984; Gladstone and Westoby, 1988; Colin and Clavijo, 1988). This diel pattern would be expected if they were restricting spawning to a time when diurnal egg-predators would be expected to be relatively satiated. However, so little is known about diel and tidal patterns of feeding activity of mobile egg-predators (I cannot find any directly relevant published studies) that the various forms of the egg-predation hypothesis cannot be seriously evaluated at present.

## ***3. Initiation of Larval Feeding***

Prompt initiation of feeding is thought to be critical to the survival of newly hatched fish larvae (e.g., Rothschild, 1986). A restricted, fixed daily spawning period could be advantageous if spawning time affects the survivorship of newly hatched larvae by determining the size of their energy reserves and when they begin feeding.

Diel dispersal windows of benthic larvae appear to be quite narrow—in all known cases larvae are released shortly after sunset (Thresher, 1984; Gladstone and Westoby, 1988). Doherty (1983c) proposed that, because benthic eggs that are not ready to hatch during one evening period must wait an additional 24 hours, a failure to hatch during the evening closest to the time when they complete development could result in unhatched but fully developed larvae depleting energy reserves they will need at the start of their planktonic life. Consequently, spawning early in the day may be advantageous

for such species because it maximizes the proportion of larvae that are ready to disperse during the nearest suitable hatching window. This hypothesis could be tested by examining relationships between intraspecific seasonal variation in (1) the duration and timing of diel spawning periods, (2) egg size (which affects development rates), and (3) temperature-mediated egg development times.

Colin (1989) suggested that spawning may be timed so that eggs hatch in the morning and larvae have a full daylight period in which to begin feeding. Such a relationship seems unlikely to be of general importance, for two reasons. First, since benthic eggs typically hatch shortly after sunset, their larvae are released during the worst period from the point of view of diurnal feeding. Second, diel hatching periods of pelagic eggs of various species are likely to be broad, since they spawn throughout most of the day (e.g., Robertson, 1983; Colin and Clavijo, 1988; Colin and Bell, 1991) and there can be significant intraspecific variation in development rates of eggs at a constant temperature (e.g., Colin, 1989).

## B. Adult Biology Hypotheses

### 1. *Predation on Spawners*

Hobson (1968, 1974) observed that some predatory fishes are most active in attacking particular types of prey during crepuscular periods, and he developed the idea that aspects of the diel patterns of activity of prey fishes represent risk-minimizing responses to the diel feeding cycles of predatory fishes. This led to the suggestion that, by spawning during the day, pelagic spawners reduce the risk of attack on themselves by crepuscular predators (Robertson and Hoffman, 1977; Johannes, 1978a). However, Thresher (1984) assembled data from a wide variety of sources, which show that crepuscular spawning is very common among pelagic spawners. He suggested that most predatory fishes actually are least active during crepuscular periods, noted that crepuscular spawners indulge in what appear to be more risky types of spawning behavior than do day spawners, and concluded that by spawning at dusk, pelagic spawners could be avoiding high-risk periods. This analysis did not take into account potentially confounding effects of several variables, since it combined data on species in a wide variety of taxa, and from different localities and habitats. However, it is a useful starting point that indicates aspects of the reproductive behavior of prey fishes that should be examined in comprehensive comparative analyses of the activity of entire communities of predatory and prey fishes.

Rates of attempted predation on pelagic spawning fishes are very low in

some areas (Colin and Clavijo, 1988; Colin and Bell, 1991) but can be high in others (Moyer, 1987). Effects of attempted predation range from serious to minimal disruptions of spawning (Colin and Bell, 1991; Robertson, 1983). Large fishes may be relatively immune to predation, and size-mediated variation in predation risks may influence not only the rapidity of spawning and the propensity for spawners to move away from shelter (Thresher, 1984; Colin and Bell, 1991) but also the diel timing of spawning.

The biggest deficiency in any arguments about diel variation in predation risks is that there are *very* few studies of the diel patterns of behavior of predators. Most of the data derive from stomach content analyses (see e.g., Nagelkerken, 1979; Shpigel and Fishelson, 1989, and references therein). Those data and the few observations that have been made of predation indicate that some predators are crepuscular while others feed mainly during the day. It is far from clear whether there are any general diel patterns of predator activity (Sweatman, 1984). Piscivorous fishes sometimes have quite restricted diets (e.g., Nagelkerken, 1979; Shpigel and Fishelson, 1989), and predator-prey interactions that are important to spawning fishes may be quite specific. Future analyses will need to be quite precisely focused to take all of these sources of variability into account.

## 2. *The Duration of the Spawning Act*

In many pelagic spawners a female releases her entire clutch in one act that lasts only a few seconds. In contrast, a female benthic spawner may release eggs individually and take half an hour or so to deposit her entire clutch (e.g., Pressley, 1980; Kohda, 1988; Hunte and Cote, 1989). A consequence of this difference may be that spawning of benthic spawners is more vulnerable to disruption and premature termination than that of pelagic spawners. Risks of disruption of spawning by diurnally active egg-predators could have selected for crepuscular spawning by benthic spawning fishes (Pressley, 1980), many of which spawn around dawn, but not in the evening. Pelagic spawners, on the other hand, spawn at dusk much more often than they do at dawn (Gladstone and Westoby, 1988; Kohda, 1988). This difference could reflect differences in the diel feeding cycles of different types of predators on eggs and on spawners, including asymmetries in the crepuscular activity of those predators (see, e.g., Sweatman, 1984; Nagelkerken, 1979). However, the difference in spawning times also could simply reflect constraints arising from the structure of the spawning act of benthic spawners. While a female pelagic spawner could complete a spawning at dusk even if light levels decline prematurely due to bad weather, a female benthic spawner could have her spawning curtailed by the same event. A similar situation would be very unlikely to occur at dawn.

### 3. *Effects of Cost of Parental Care*

Doherty (1983c) proposed that the timing of spawning of brood-guarding species might represent a response to the cost of parental care. In brooders whose eggs complete development within several days, each additional day a clutch spends in the nest represents a substantial percentage increase in the duration and cost of brood care of that clutch. For day-spawning species whose benthic eggs hatch only during the early evening, it could be advantageous to spawn early in the day so that larvae have the greatest chance of being ready to leave during the first available hatching period. Such a response to the cost of care could account for the preponderance of morning spawning among benthic brooders. Effects of variation in that cost would potentially be most important for tropical species whose eggs develop quickly and at fairly predictable rates at stable high temperatures. Comparison of the diel spawning patterns of temperate and tropical species, or, preferably, of different populations of the same species at different latitudes or different seasons (i.e. under different temperature regimes) could be used to test this hypothesis.

### 4. *Feeding Biology of Spawners*

One area that has been largely neglected is the relationship of diel patterns of spawning to the feeding biology of spawners. Examination of this relationship could be instructive because there may be both benefits and costs to feeding biology from particular patterns of spawning activity. Since reproductive output depends on food intake, diel patterns of spawning could represent adaptive responses that minimize feeding losses. Conover and Kynard (1984) pointed out that, by hydrating its clutch overnight and spawning in the early morning, a diurnally active fish should minimize feeding losses due to the time spent in reproduction, including the period when the body cavity is preempted by the greatly expanded gonads.

The potential influence of feeding costs as a factor selecting for particular diel spawning periods of reef fishes has not been examined. That cost should depend on a variety of factors, including the relative volumes of the clutch and food mass, the amount of time and energy spent on each spawning, the spawning frequency of individuals, the percentage of the day spent feeding, and the distribution of feeding over the day. For example, feeding losses might be expected to have relatively strong effects on herbivorous reef fishes that spend much time migrating substantial distances between feeding and spawning sites (e.g., Myrberg *et al.*, 1989), spawn frequently (Robertson *et al.*, 1990), process relatively large volumes of food during daily feeding periods (e.g., Polunin and Klump, 1989), and spend much time feeding each day and have afternoon peaks of feeding activity (e.g., Robertson, 1984;

Polunin and Klump, 1989). If feeding costs are of general importance, we would expect that herbivorous reef fishes would tend to spawn in the early morning. Herbivorous damselfishes generally do spawn in the morning (Kohda, 1988), whereas herbivorous surgeonfishes generally do not (Robertson, 1983; Myrberg *et al.*, 1989; Colin and Bell, 1991).

The tidal regime also controls diel feeding patterns of many species independently of time of day. Tidal currents provide food for many planktivores. In some benthic feeding species, feeding activity may be restricted regularly by tidally mediated limitations on their access to intertidal feeding habitats. Consequently, in species in which diel patterns of feeding are tidally controlled, particular diel spawning patterns might minimize loss of feeding opportunities, or the development of a clutch in the female (and hence the timing of the spawning period) might be controlled directly by the diel cycle of food intake.

The risk of loss of food to competitors also could influence diel patterns of spawning, and some fishes may restrict spawning to periods when their food competitors are least active. Robertson (1983) was able to relate some of the interspecific variation in spawning times of herbivorous surgeonfishes at a single site to interspecific variation in potential pressure from food competitors. Interspecific variation in spawning times among damselfishes also follows a pattern predicted by this hypothesis, since territorial herbivorous species generally spawn at dawn, when their herbivorous competitors are inactive, while mobile nonterritorial planktivorous species spawn at various times of the day (Kohda, 1988). However, some of the difference Kohda (1988) ascribed to food competition pressures could simply reflect phylogenetic relationships and constraints, since the species he compared belong to a mix of genera and subfamilies.

### C. Conclusions

Although most of the attention directed at factors that select for diel patterns of spawning of reef fishes has focused on the dispersal of planktonic propagules and the feeding activity of predatory fishes on eggs and spawners, so little is known about the feeding patterns of these predators that we cannot realistically assess the absolute or relative importance of either form of predation at this time.

The focus of attention needs to be broadened to include diel patterns of the full range of activities of spawners, particularly those relating to feeding biology, since the timing of spawning may affect the opportunity for adults to engage in other activities. Interspecific variation in diel spawning patterns may also be due to constraints that an extended spawning act might place on

benthic spawners, and to mechanisms that minimize the cost of parental care of benthic eggs.

### III. LUNAR SPAWNING PATTERNS

Lunar and semilunar spawning cycles occur commonly in reef fishes. However, such traditionally emphasized cycles represent only a part of the range of patterns of spawning that occur on this time scale, patterns that include not only cycles at higher frequencies, but also continuous, sporadic, and intermittent acyclic activity. Lunar cycles in the return of juveniles to adult habitat at the end of the planktonic phase also occur in many species (for reviews see Johannes, 1978a; Thresher, 1984; Gladstone and Westoby, 1988; Robertson *et al.*, 1990).

Larval biology hypotheses concerning lunar reproductive patterns deal with both the beginning and the end of the planktonic phase. Propagule dispersal hypotheses consider factors that may affect rates of predation on planktonic eggs and larvae as they leave the spawning site. The settlement-linkage hypothesis considers relationships between spawning and the return of pelagic juveniles into adult habitat. Adult biology hypotheses consider not only environmental factors that may directly affect the success of reproductive activities, but also a variety of intrinsic advantages to population synchronization of spawning for both benthic brooding and pelagic spawning species. They also propose that environmental and intrinsic constraints influence the ability of adults to develop population cycles of spawning.

#### A. Larval Biology Hypotheses

##### *1. The Beginning of the Planktonic Phase: Dispersal of Eggs and Larvae*

The propagule dispersal hypotheses propose that success of dispersal of planktonic eggs or larvae is affected by tidal heights and flows or moonlight levels, or that synchronization of spawning is intrinsically advantageous, because of predator oversaturation (for reviews see Johannes, 1978a; Thresher, 1984; Gladstone and Westoby, 1988).

Thresher (1984) reviewed the literature and found that lunar spawning cycles occur more commonly among species that produce benthic eggs than among pelagic spawners. He suggested that this difference is related to propagule dispersal mechanisms: Diel windows during which pelagic eggs can be successfully released are relatively broad and, by adjusting the time of day of release to coincide with appropriate tidal stage, many pelagic spawners can reproduce throughout the month. Benthic eggs, on the other hand, have

much narrower diel dispersal (hatching) windows, and those windows coincide with tides that are appropriate for dispersal only during two short periods each lunar month. A recent, more comprehensive analysis by Gladstone and Westoby (1988) supported Thresher's conclusions. The ability of broad comparative analyses such as these to test hypotheses is limited by potentially confounding effects of many other variables. These include effects of phylogenetic relationships, of differences in sampling effort among taxa, of geographic variation in the tidal regime, and of differences in tidal influences in different habitats at the same site. Such problems can be minimized in analyses of intraspecific variability in spawning patterns in relation to, for example, seasonal and geographic variation in the tidal regime (see, e.g., Conover and Kynard, 1984). These effects also can be reduced if the comparative analysis considers spawning patterns of sets of closely related species living in different habitats at several sites with different tidal regimes.

Robertson *et al.* (1990) performed such an analysis of the reproductive patterns of 17 benthic brooding fishes (15 damselfishes and 2 blennies) at three neotropical sites that have very different, and seasonally variable, tidal regimes. Those fishes exhibit a great variety of lunar spawning patterns, including not only uni- and bimodal lunar cycles of varying strength and lunar timing, but also high-frequency spawning cycles and sporadically synchronized, intermittently variable and continuous spawning. Variation in spawning patterns was examined in relation to sets of predictions from the various dispersal hypotheses. As they are currently framed, those hypotheses assume that larvae of different species have essentially the same requirements for dispersal, and that dispersal mechanisms affect them in the same manner. Lunar hatching patterns of those neotropical fishes followed various predictions of the different propagule dispersal hypotheses, including the tidal control hypothesis, in a small minority of cases. Further, none of the eight species for which data were available consistently conformed to multiple predictions from the tidal control hypothesis. Robertson *et al.* (1990) concluded that, although many damselfishes and blennies from a broad range of habitats have lunar and semilunar spawning cycles, only species that live in habitats from which little or no dispersal may be possible during certain lunar phases consistently exhibit spawning patterns predicted by the tidal control hypothesis. Similar analyses of lunar patterns of spawning of assemblages of pelagic spawning fishes have yet to be made.

## ***2. The End of the Larval Life: Linkage of Spawning and Settlement***

Christy (1978) and Kingsford (1980) proposed that lunar reproductive patterns of some shallow-water invertebrates and fishes may have been selected to maximize the numbers of larvae that are competent to settle during lunar periods that are most favorable for settlement.

Some data support this settlement-linkage hypothesis. Two damselfishes that have lunar spawning and settlement cycles also have relatively uniform-age settlers (Kingsford, 1980; Robertson *et al.*, 1988). Further, at the same Caribbean site as one of those damselfishes, (1) a wrasse whose lunar settlement cycle coincides with that of the damselfish (a peak at new moon) lacks a lunar spawning cycle but has variable-age settlers (Victor, 1986b), and (2) several other damselfishes that have (differently timed) lunar spawning cycles also have settlement peaks around the new moon. This suggests that, at that site at least, there may be a single lunar period that is most favorable for settlement of various species, and that the lunar spawning cycles of some of them could represent a response to the constraint of uniform-age settlers (Robertson *et al.*, 1990). This begs the question why variation in age at settlement might constrain some species and not others.

More equivocal data are available from other localities. In a Japanese damselfish that has a fixed lunar settlement cycle, variation in its spawning (semilunar and acyclic in different years) is contrary to what the settlement-linkage hypothesis would predict. Also, data are beginning to emerge that show that there may be intraspecific geographic variation not only in lunar spawning and settlement patterns, but also in the age at settlement (Doherty and Williams, 1988a; Wellington and Victor, 1989; Robertson *et al.*, 1990). Although such data are not necessarily inconsistent with settlement-linkage, they do reduce its likelihood. There is sufficient variation in lunar spawning patterns among damselfishes, for example (see Robertson *et al.*, 1990), that it should be possible to make a reasonable test of this hypothesis by examining relationships between such variation and variation in settlement patterns and the duration of the planktonic phase in a suite of closely related species at multiple sites.

## B. Adult Biology Hypotheses

### 1. *Moonlight and Nocturnal Activities*

Unimodal lunar spawning cycles could be selected for if moonlight affects the efficiency of some aspect of reproduction. Colin *et al.* (1987) suggested that moonlight could facilitate the long-distance nocturnal spawning migrations of a grouper, while Allen (1972) proposed that moonlight might enhance parental ability in a benthic brooding damselfish. Different groupers spawn at different times of the lunar month (Johannes, 1978a) and a comparison of their diel migration patterns could be used in a simple, preliminary test of the first suggestion. Interspecific variation in lunar spawning patterns of damselfishes at a single site is such that, although some spawn at the time predicted by Allen's hypothesis, many others spawn either when moonlight levels are

lowest or at both extremes of moonlight conditions (Robertson *et al.*, 1990). There are no data available that show whether brooding success is dependent on moonlight conditions in any species.

## 2. *Effects of the Tidal Regime on Adult Activities*

Besides having effects on the success of the dispersal of propagules from certain habitats, the tidal regime also may have direct effects on the spawning ability of adults. Conover and Kynard (1984) proposed that a semilunar cycle in the availability of intertidal spawning habitat could be directly driving the semilunar spawning cycle of a temperate, benthic spawning atherinid. Lunar cycles of spawning of some reef fishes may represent responses to tidal influences on various aspects of adult biology.

The tidal regime must affect the feeding of many reef fishes and produce a variety of lunar cyclic patterns of food intake. Intertidal feeding habitats will be available for differing percentages and times of the day over the course of the lunar month. Tidal currents will bring planktonic food in lunar cyclic patterns. Risks of predation on adults that engage in particular activities in intertidal habitat may also depend on tidally mediated water depth. These effects of the tidal regime are likely to be strongest in species in which propagule dispersal also is most likely to be affected by the tidal regime, that is, nonmigratory benthic spawners that live in laterally extensive intertidal habitats.

## 3. *Intrinsic Advantages to Spawning Synchronization*

Population synchronization of spawning may provide intrinsic advantages to individuals, and synchronization may often be lunar cyclic simply because the lunar cycle provides the strongest, most universally available set of environmental cues.

*a. Synchronization of Aggregating Pelagic Spawners* Many pelagic spawning fishes that live in subtidal habitats and have lunar spawning cycles also migrate to and aggregate at traditional spawning grounds [e.g., some serranids (Shapiro, 1987d; Carter, 1989)]. The association of lunar spawning cycles with migration and aggregation may be related to adult biology constraints.

Colin and Clavijo (1988) observed spawning aggregations of two Caribbean surgeonfishes, one that spawned daily and one that spawned on a lunar cycle. They suggested that this difference is related to differences in the costs of spawning migrations, which appeared to be higher in the lunar cyclic species. Extending this line of reasoning, it can be seen that whether or not lunar synchronization of spawning is likely to facilitate the formation of spawning aggregations may depend not only on the cost of migration but also on the frequency with which individuals spawn and their population density (see,

e.g., Carter, 1989). In an unsynchronized species, the chance that sufficient individuals would arrive at the spawning ground to form an aggregation of some minimum size on any randomly chosen day will be low if individuals spawn infrequently and occur at a low density. With lunar synchronization of activity, an individual of such a species would have a much greater chance of encountering an aggregation whenever it is ready to spawn.

The most extreme examples of lunar synchronized spawning aggregations occur among the groupers. In some species, spawning occurs only during a fixed 1- to 2-month period each year, and individuals of a dispersed population migrate tens of kilometers and aggregate and spawn at a traditional spawning ground during a fixed lunar phase (e.g., Colin *et al.*, 1987; Carter, 1989).

*b. Spawning Synchronization of Benthic Brooders* Two adult biology hypotheses propose that there are intrinsic advantages to population synchronization of spawning in species that brood benthic eggs. Those advantages include enhanced effectiveness of brood defense and reduction in mortality of eggs that results from the cost of parental care.

*(i) Synchronized Colonial Spawning* In a number of freshwater fishes and at least one damselfish (Foster, 1989), the effectiveness of defense of benthic eggs by males is increased when nesting is colonial, because of the collective activities of the aggregated males. Lunar cyclic synchronization of spawning should facilitate colony formation in such species.

As expected from the enhanced-defense hypothesis, the degree of development of this synchronized colonial spawning in two cogenetic damselfishes correlates with differences in pressures from egg-predators, which are high in the colonial species and low in the noncolonial one (Foster, 1989). However, the occurrence of this pattern of spawning is not related only to variation in pressure from egg-predators. Highly synchronized colonial spawning, although common among damselfishes, is restricted to planktivorous species that are mobile and normally live in schools, and that temporarily defend territories only when breeding. This spawning pattern is lacking among benthic feeding herbivorous damselfishes whose adults are sedentary and singly defend permanent feeding territories that are dispersed on the substratum. Such species lack the social and ecological potential to form highly aggregated colonies (Robertson *et al.*, 1990).

*(ii) The Cost of Parental Care* Intensive guarding of benthic eggs by parental male fishes, including tropical damselfishes, can be energetically costly, and that cost may induce nest abandonment and filial egg cannibalism by parent males (Robertson *et al.*, 1990). Dominey and Blumer (1984)

proposed that population synchronization of spawning should result in increased parental investment in each clutch, since clutches will be larger and males will be less likely to receive additional eggs if they abandon or eat first-laid clutches. Lunar cycles in brooding activity might reduce egg mortality not only by having effects on parental investment, but also by providing regular, frequent, nonbrooding periods during which males can recuperate from the cost of care (Robertson *et al.*, 1990).

Neotropical damselfishes and blennies show not only different patterns of population synchronization of brooding (sporadic activity, and lunar and higher-frequency cycles), but also unsynchronized cycles of brooding activity in individual nests in some species (Robertson *et al.*, 1990). As expected from the cost-of-care hypothesis, continuous brooding appears to be associated with a negligible cost of care in at least one blenny. However, there are no data that help explain the existence of the variety of patterns of brood cycling in terms of this hypothesis. Different patterns might represent independently evolved, alternative solutions to the same problem (Clutton-Brock and Harvey, 1984), or graded responses to varying intensities of the problem. Population cycles might arise when individual females cannot predict or control brooding activity in unsynchronized nests. Some of the variation also may be due to limitations on the options that different species have. For example, population synchronization of spawning appears to be both less strongly linked to the lunar cycle and more intraspecifically variable in its timing among the schooling planktivorous damselfishes than among the territorial herbivorous species in this family. Two factors may contribute to this difference. First, schooling species may have greater potential to synchronize their activity independently of lunar cues (i.e., by using social cues). Second, variability in spawning output may be produced by unpredictable fluctuations in the planktonic food supply, while a greater constancy in the availability of benthic algae may allow more regular reproductive activity (Robertson *et al.*, 1990). These possibilities remain to be examined in the field.

The cost-of-care hypothesis predicts that lunar cycles of spawning should be more common among benthic brooding species than among nonbrooders that produce pelagic eggs, and such does occur among Caribbean reef fishes (Robertson *et al.*, 1990). Since those brooders and nonbrooders belong to different families, this comparison is limited by potentially confounding phylogenetic effects. However, since both the brooding and pelagic spawning families include both lunar cyclic and acyclic species, it is unlikely that the differences between brooders and nonbrooders are due to evolutionary conservatism in one family or another. There are insufficient data available on benthic spawners that lack parental care to include them in any analysis at this point.

### C. Conclusions

The hypothesis that lunar patterns of spawning are related primarily to the success of dispersal of planktonic propagules away from adult habitat is most strongly supported by data from fishes (particularly benthic spawning species) that live in laterally extensive intertidal habitats, habitats from which dispersal may be severely limited during particular lunar phases. However, the lunar cycle also may control reproductive patterns of species living in this type of habitat by way of effects of the tidal regime on a range of adult activities.

The hypothesis that lunar patterns of spawning represent adaptations that facilitate the entry of juveniles into adult habitat at the end of their pelagic existence is supported by some, but not all, of the few sets of data available.

Adult biology may be a major determinant of lunar spawning patterns of both intertidal and subtidal species. Moonlight might facilitate nocturnal spawning migrations and nocturnal eggcare, although there is no direct evidence for either effect. In many cases the lunar cycle may be most important as a source of environmental cues for spawning synchronization. Lunar spawning cycles may facilitate the formation of spawning aggregations in pelagic spawners that occur at low densities and spawn infrequently. Various patterns of spawning synchronization among benthic brooders, including lunar cyclic activity, may not only facilitate the formation of nesting colonies that increase the effectiveness of nest defense, but also may reduce egg losses due to the costs of parental care. Some of the variation in lunar patterns of spawning among benthic spawners may be related to differences in social system structure and to temporal patterns of food availability.

Hypotheses that invoke adult biology advantages or adult biology constraints appear to be as or more successful than propagule dispersal hypotheses in their ability to account for variation in lunar spawning patterns of reef fishes. Some of the success of adult biology hypotheses may be due to their making less restrictive predictions than the propagule dispersal hypotheses about the structure and lunar timing of cycles of activity. In addition the adult biology hypotheses accommodate interspecific variation that we know exists in adult capabilities and ecology. In the absence of any data that indicate otherwise, the propagule dispersal hypotheses assume that there is great interspecific similarity in requirements and capabilities of those propagules. Thus they may be oversimplified.

## IV. SEASONAL SPAWNING PATTERNS

Most of the discussion of factors that control seasonal spawning patterns of reef fishes has centered on the hypothesis that spawning output tracks the

seasonal cycle of change in larval survivorship. Data are only now becoming available that provide estimates of seasonal change in larval survivorship and enable us to begin to assess its relationship to the spawning pattern. The main existing alternative to the larval survivorship hypothesis proposes that the timing of reproduction ultimately is controlled by the requirements of juvenile fishes in the beginning of their benthic existence. Some thought also has been given to how the reproductive capacity of adults might be controlled by seasonal change in environmental factors that affect them directly.

### A. Larval Biology Hypotheses

#### 1. *Seasonality in the Larval Environment*

Previous analyses of the role of larval biology as a factor controlling seasonal patterns of spawning of reef fishes have been limited to attempts to correlate community-level seasonality of spawning with gross seasonality of environmental variables that are thought to affect the food supply, growth, and dispersal of larvae. These variables include water currents, which might retain larvae near or transport them away from suitable habitat; wind patterns, which may affect not only currents but also the density and stability of food patches; the seasonal cycle of primary production, which might determine the types and average abundance of larval foods; and temperature and day length, which may affect development rates of larvae (Munro *et al.*, 1973; Russell *et al.*, 1977; Johannes, 1978a; Kock, 1982; Doherty, 1983c; Bakun, 1986; Walsh, 1987; Lobel, 1989).

This type of correlative analysis can be extended by examining several predictions from this "gross environmental seasonality" hypothesis. (1) Since the proposed mechanisms of environmental control of larval survivorship are fairly simple, they should affect communities at different sites in the same way and one should see consistency in relationships between environmental seasonality and community-level spawning patterns. (2) Further, closely related species with similar reproductive biology probably have similar larval biology, and, if they live and spawn in the same small area of a reef, they should have quite similar seasonal spawning patterns. (3) The spawning output of individual species should track seasonal gradient(s) of environmental change. (4) Intraspecific latitudinal variation in spawning seasonality should follow consistent patterns of change in relation to environmental change. There are data available that relate to each of these predictions.

*a. Geographic Variation in Community-Level Spawning Seasonality* There are three tropical sites from which sufficient data are available to make a comparative analysis: the Australian Great Barrier Reef, the Caribbean, and Hawaii (Table 1).

**Table 1** Community-Level Spawning Seasonality and Environmental Seasonality at Three Tropical Sites

	Site		
	Great Barrier Reef	Hawaii	Jamaica
Latitude	23°S	20°N	18°N
Temperature range	20–28.5°C	22–28°C	25–30°C
Spawning seasonality	Strongly unimodal	Moderately unimodal	Weakly bimodal
	Environmental state during spawning peak(s)		
Temperature	Near maximum	Intermediate	Min & max
Day length	Near maximum	Maximum	Min & max
Prevailing winds	Minimum	Submaximal	Max & min
Hurricanes/cyclones	Maximum	Intermediate	Min & max
Rainfall and runoff	Maximum	Intermediate	Min & max
Dispersive currents	Maximum	Intermediate?	No data
Primary production	Weak peak: <sup>a</sup>	No pattern	Intermediate: <sup>b</sup>

<sup>a</sup> There is a summer peak (due to river runoff) inshore, but no seasonal cycle on offshore reefs.

<sup>b</sup> There may be little interannual consistency in the cycle.

Sources: Russell *et al.*, 1977; Doherty, 1983c; Munro, 1983; Sammarco and Crenshaw, 1984; Walsh, 1987; Furnas and Mitchell, 1987; Doherty and Williams, 1988a; and the U.S. Department of Commerce, 1982a,b, 1989.

Both seasonal patterns of spawning and the extent and nature of seasonal change in various environmental parameters differ among those sites. There is a trend for decreasing strength of spawning seasonality with decreasing latitude (see also Munro, 1983). However, although there are latitudinal changes in some environmental variables (e.g., day length and minimum water temperatures), spawning peaks are not consistently associated with a particular relative or absolute state of any of them (Table 1). Thus, community-level spawning seasonality does not appear to be related in a consistent manner to gross seasonality in any of the environmental factors that are thought to directly or indirectly influence larval survivorship.

This lack of consistency could be due to differences in which factors have most influence on larval survivorship at the different sites. The Hawaiian archipelago is a well-isolated cluster of small islands. Since larvae that move away from the islands may be very unlikely to survive, a premium could be placed on retention of larvae near adult habitats (Johannes, 1978a; Lobel, 1978). Although it has been proposed that spawning peaks in Hawaii when current systems are most likely to retain larvae near the islands, it is unclear

whether such a coincidence does occur (for opposing views see Walsh, 1987; Lobel, 1989). In addition, there are many exceptions to the "ideal" pattern, including among endemic species (data in Walsh, 1987), which might be expected to strongly conform to the predicted pattern.

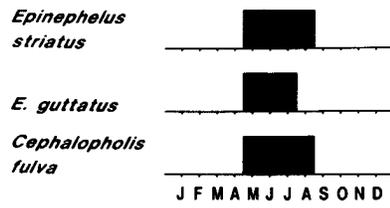
A special-case argument can be used to explain differences between Hawaii and the other two sites, since both of the latter are large reef systems in which larval retention is less likely to be of overriding importance. However, it is not obvious how such a line of reasoning could be applied to differences between the Great Barrier Reef and the Caribbean (see Table 1).

*b. Spawning Seasons of Closely Related Species at the Same Site* The Russell *et al.* (1977) data from the Great Barrier Reef indicate that species in each of at least three families (Apogonidae, Pomacentridae, and Labridae) spawn at opposite seasonal environmental extremes. Similar differences in spawning seasons occur among both labrids and pomacentrids at Hawaii (data in Walsh, 1987). For example, among the herbivorous damselfishes, *Stegastes fasciolatus* has a short spawning season that peaks in late winter (MacDonald, 1981), while *Abudefduf sordidus* spawns at a uniform level from spring through autumn (Stanton, 1985). This diversity of patterns among closely related species at two sites is not predicted by simple environmental seasonality hypotheses.

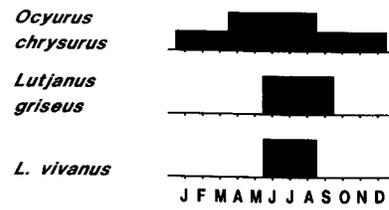
*c. Local Spawning Cycles and Environmental Gradients* Contrary to expectations, seasonal patterns of spawning of many species at different sites do not track environmental gradients. Jamaican fishes include species that appear to be nonseasonal spawners, and others in which the peaks of a bimodal spawning cycle coincide with both extremes of environmental conditions (see Munro, 1983). Further, some Hawaiian fishes, including species in the same family, show either bimodal spawning activity with peaks at both extremes of environmental conditions (Walsh, 1987) or uniform reproduction during all but one period of extreme conditions (Stanton, 1985).

*d. Intraspecific Geographic Variation in Spawning Seasonality* Data on lutjanids and serranids at sites scattered throughout the tropical West Atlantic (Fig. 1) show that simple, consistent patterns of geographic variation in spawning cycles are lacking. First, although three serranids show a pattern of winter spawning at low latitude and spring-summer spawning at high latitude, one other serranid and five lutjanids clearly do not (Fig. 1). Colin and Clavijo (1988) have suggested that a change from winter to summer spawning with increasing latitude arises because these fishes are adapted to spawning at the summer temperatures of the last glacial period, and those temperatures now occur in different seasons at different latitudes. However, there is no obvious reason why lutjanids and serranids at the same series of sites should not show similar patterns of latitudinal variation in spawning seasons (Fig. 1) or why

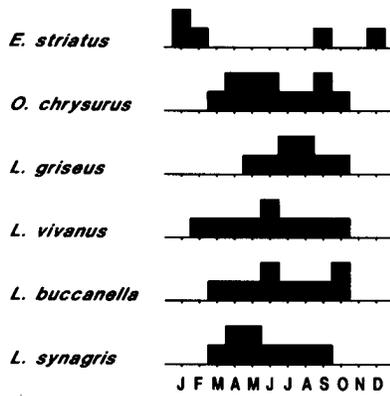
**BERMUDA (LAT. 32 N)**



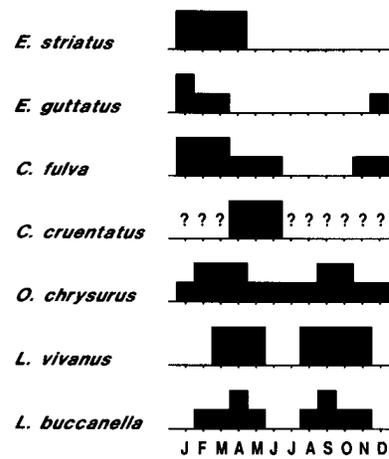
**FLORIDA (LAT. 25 N)**



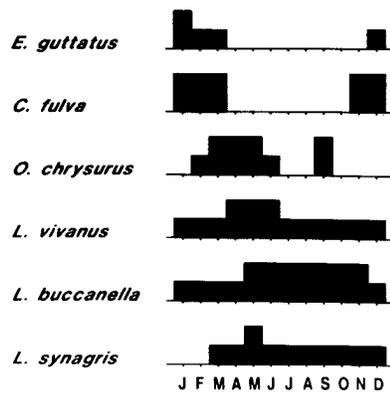
**CUBA (LAT. 22 N)**



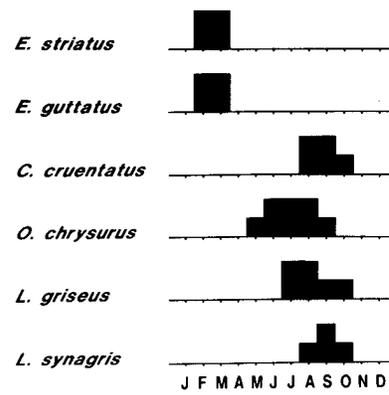
**JAMAICA (LAT. 18 N)**



**PUERTO RICO (LAT. 18 N)**



**VENEZUELA (LAT. 12 N)**



different serranids should show different patterns. For example, the serranid *Cephalopholis cruentatus* spawns in late spring at high and intermediate latitudes (i.e., Bermuda and Jamaica) and in summer at low latitude (Venezuela) [Fig. 1, and *anecdotal* information from Bermuda (B. E. Luckhurst, personal communication, 1989)]. These latitudinal changes in the timing of spawning do not correlate with patterns of change in other variables [e.g., the relative and absolute states of day length and of the annual cycle of primary production (see Burnett-Herkes, 1975; Nagelkerken, 1979)].

Second, the spawning cycles of different serranids and lutjanids vary independently at the different low-latitude sites. While spawning seasons of some species may not differ between two sites, those of others do, and often do in different ways (Fig. 1 and Table 2).

Third, there are indications of mesoscale geographic variation in seasonal patterns of spawning of several Caribbean reef fishes. *Scarus iserti* (Scaridae) appears to have summer versus winter/spring spawning peaks on the north and south coasts of Jamaica (Munro, 1983; Colin and Clavijo, 1988). Two surgeonfishes, *Acanthurus bahianus* and *A. coeruleus*, have different seasonal spawning patterns at two sites off the south coast of Jamaica—a restricted, strongly unimodal pattern inshore, and a more extended, weakly bimodal pattern 100 km offshore (data in Munro, 1983).

These patterns of intraspecific geographic variation in spawning seasons are very difficult to reconcile with larval biology hypotheses that invoke simple, gross seasonal changes in one or another variable in the larval environment. If spawning patterns are responses to larval requirements then changes in the larval environment must be subtle and complex and follow independently varying, species-specific patterns at different sites within the Caribbean.

## 2. *Matching of Seasonal Patterns of Spawning and Recruitment at the Same Site*

Correlative analyses such as the preceding offer limited insight into factors that control spawning seasonality because they do not incorporate information on seasonal patterns of larval survivorship. Direct measurements of larval survivorship have not been made for any tropical species, and at this stage we are limited to measuring spawning output and larval recruitment at the same site and using changes in the ratio of recruitment to spawning effort to

---

**Figure 1** Spawning seasons of lutjanids and serranids at six sites in the tropical West Atlantic. Sources: references in Grimes (1987) and Shapiro (1987d); also Munro (1983), Starck (1971), Colin *et al.* (1987), Bardach *et al.* (1958), Alcalá (1987), Mendez (1989), Perez-Villanoel (1982), Y. Sadovy (personal communication, 1989) for Puerto Rico, and R. Claro (personal communication, 1989) for southwest Cuba. Note: "Venezuela" also includes the Netherlands Antilles.

**Table 2** Similarity of Spawning Seasons of Lutjanids and Serranids at Different Sites in the Caribbean (see also Fig. 1)

	Cuba/Jamaica	Cuba/Puerto Rico	Cuba/Venezuela	Puerto Rico/Jamaica	Jamaica/Venezuela
<b>Lutjanidae</b>					
<i>Ocyurus chrysurus</i>	Similar, J longer	≈ Same	Bi-/unimodal and timing difference	≈ Same, J longer	Bi-/unimodal and timing difference
<i>Lutjanus griseus</i>	ND <sup>a</sup>	ND	≈ Same	ND	ND
<i>L. buccanella</i>	Timing difference	Bi-/unimodal and longer	ND	Uni-/bimodal and timing difference	ND
<i>L. vivanus</i>	Uni-/bimodal and timing difference	≈ Same, PR longer	ND	Uni-/bimodal, PR longer	ND
<i>L. synagris</i>	ND	≈ Same, PR longer	Timing difference, C longer	ND	ND
<b>Serranidae</b>					
<i>Epinephelus striatus</i>	Similar	ND	≈ Same	ND	≈ Same
<i>E. guttatus</i>	ND	ND	ND	≈ Same	Similar
<i>Cephalopholis fulva</i>	ND	ND	ND	Similar	ND
<i>C. cruentatus</i>	ND	ND	ND	ND	Timing difference

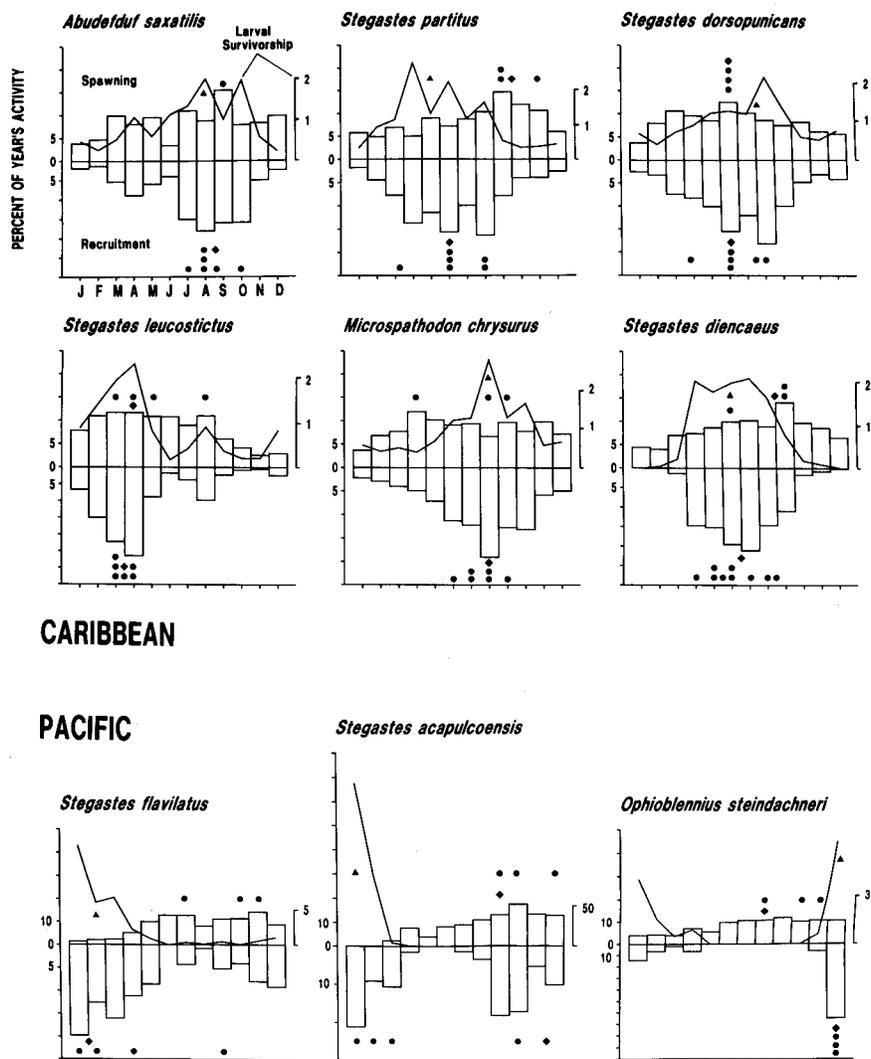
<sup>a</sup> ND = No data.

estimate how relative larval survivorship changes over the year. This method assumes that the recruitment pattern observed at the study site is representative of that experienced by the larvae that were produced there. Seasonal patterns of larval survivorship can be estimated in this way for 12 species from four sites in the Caribbean and the East and West Pacific.

*a. Neotropical Fishes* Robertson (1990) examined spawning and larval recruitment of nine neotropical fishes (eight damselfishes and one blenny) from the Caribbean and Pacific coasts of Panama. The average seasonal patterns of spawning and settlement did not match in any of those species. The seasonality of settlement was stronger than that of spawning in most cases, and/or peaks of spawning and settlement were out of synchrony. The seasonal pattern of spawning differed from the seasonal pattern of larval survivorship in all but one of the nine species (*A. saxatilis*; Fig. 2).

*b. Western Pacific Fishes* Gladstone and Westoby (1988) measured seasonal changes in both spawning effort and recruitment of a small pufferfish, *Canthigaster valentini*, on the northern part of the Australian Great Barrier Reef. Spawning and settlement occur year-round, but both are reduced during the cool half of the year. Their data indicate that since the reduction in spawning is disproportionately greater than the decrease in settlement during the cool season, larval survivorship may be highest during that season (Table 3). That is, spawning effort may be lowest during the period of highest larval survivorship. Gladstone and Westoby (1988) suggested that cool-season spawning may be a bet-hedging strategy to cope with occasional catastrophic losses in recruitment due to warm-season cyclones.

Doherty (1980, 1983c) studied two damselfishes, *Pomacentrus wardi* and *P. chrysurus* (= *P. flavicauda*), at One Tree Island at the southern limit of the Great Barrier Reef. Both of those species showed consistent seasonal patterns of spawning over a 5-year period. Since the study population of *P. wardi* spawns for 2.5 months (October to December), and the larval duration of this species is  $\approx 20$  days (Brothers *et al.*, 1983; Thresher *et al.*, 1989), most larvae produced by that population settle in November and December. However, the great bulk of each year's settlement of *P. wardi* in the vicinity of One Tree Island occurs in one short episode each year, and those episodes have occurred in January or February of each of the five years for which data are available (Russell *et al.*, 1977; D. M. Williams, 1979; Doherty, 1980; Pitcher, 1988a). Thus the consistent spawning season of the study population of *P. wardi* is distinctly asynchronous with the strong, consistent seasonal peak of settlement. Most *P. wardi* that settle at that site must be produced by other populations of adults that have either differently timed or more extended spawning seasons. *Pomacentrus chrysurus*, on the other hand (which has a similar larval duration to *P. wardi*; see Thresher *et al.*, 1989, where *P. chrysurus* = *P. rhodono-*



**Figure 2** Seasonal patterns of spawning, larval recruitment, and relative larval survivorship of nine neotropical fishes. Histograms show the mean percentage of the year's spawning and recruitment that occur in each month. The recruitment pattern is appropriately lagged (e.g., January's recruits are larvae that were spawned in January). Relative larval survivorship is the recruitment %/spawning % for each month. Diamonds indicate average timing of annual peaks (where present) of spawning and recruitment. Triangles indicate peak of larval survivorship cycle (not calculated for *S. leucostictus* because the distribution is bimodal). Circles indicate the peak spawning or recruitment month of each year sampled. (Reprinted with permission from D. R. Robertson, 1990. Differences in the seasonalities of spawning and recruitment of some small neotropical reef fishes. *J. Exp. Mar. Biol. Ecol.* **144**, 49–62.)

**Table 3** Life History Parameters of *Canthigaster valentini*<sup>a</sup>


---

<u>Average adult female</u>
Weight: 8.6 g
Survivorship: < 6 months
Estimated annual spawning output: 72,000 eggs ( $\approx$ 1.5 times body weight)
<u>Larval life: Mean duration of 92 days (range 64–113 days)</u>
<hr/>
<u>Seasonal changes in activity</u>
Seasons: Cool—sea temperatures < 24–26°C; Warm—27–28.5°C
Female mortality rate: cool > warm
Female growth rate: cool = warm $\times$ 0.25
Spawning output: cool = warm $\times$ 0.40 <sup>b</sup>
Larval recruitment: cool = warm $\times$ 0.78 to 0.88 <sup>c</sup>
Relative larval survivorship <sup>d</sup> : cool = warm $\times$ 1.9 to 2.2 <sup>c</sup>

---

<sup>a</sup> Data or calculations are based on data from Gladstone (1985, 1991), Gladstone and Westoby (1988), and Stroud *et al.* (1989).

<sup>b</sup> Since no consistent patterns of seasonal change in adult density are evident (W. Gladstone, personal communication), I used seasonal change in per capita output.

<sup>c</sup> Range is for values based on the season during which larvae arrive and the season during which larvae are produced (assuming a larval life of 3 months).

<sup>d</sup> Recruitment/spawning output.

*tatus*), does not show any apparent discrepancy between its seasonal patterns of spawning and settlement (data in Doherty, 1980).

Thus the data from 12 species at four sites indicate that spawning may not be well matched to the seasonal pattern of larval survivorship in most cases. The degree of mismatching ranges from slight between-season differences to a strong within-season discrepancy in a species (*P. wardi*) in which both the spawning and settlement seasons are short.

Since the larvae of reef fishes typically spend weeks in the plankton (e.g., Victor, 1986a; Wellington and Victor, 1989) it is possible that most individuals settle well away from their source, and that local mismatching of spawning and recruitment could be due to geographic variation in either spawning patterns or larval survivorship patterns. Sufficient microgeographic variation in spawning patterns does appear to exist in some species (see Section IV, A, 1, d) to warrant serious consideration of spatial variation in spawning as a potential causal factor. MacDonald (1985) found local seasonal mismatching of reproduction and recruitment of a Hawaiian lobster at various sites in the Hawaiian archipelago and showed how spatial variation in seasonal recruitment patterns was correlated with variation in currents that could transport pelagic juveniles. Thus, local mismatching in this case could reflect spatial variation in the seasonal cycle of pelagic-phase survivorship. However, since this lobster's pelagic phase is long and variable (6 to 11 months), dissimilarity

in spawning and recruitment cycles could be due to variation in the duration of that phase.

There are no data available on intraspecific geographic variation in seasonal recruitment patterns in reef fishes. In addition, there are too few data to show whether variation in larval durations of many species could be sufficient to account for local mismatching of spawning and settlement. The larval life of damselfishes, among others, appears sufficiently short [a few weeks (Thresher *et al.*, 1989; Wellington and Victor, 1989)] that seasonal variation in larval duration is unlikely to be involved in the mismatches described here (Robertson, 1990). The larval duration of *C. valentini* is, however, longer and more variable than in damselfishes (Table 3), and variation in that duration could have been involved in its spawning/recruitment mismatch.

Plausible explanations can be constructed that take into account what we know about larval durations and the dispersive potential of water currents and that attribute local differences between spawning and recruitment to geographic variation in spawning and larval survivorship cycles. However, based on what we know about complexity and the retentive potential of currents and the ability of fish larvae to migrate between different currents, equally plausible arguments can be made that many larvae of many species are retained near their source (e.g., Bakun, 1986) and that mismatches between spawning and larval survivorship cycles do occur. Since there are pronounced interspecific differences in larval durations, morphology, and size at recruitment, and in larval distributions across both vertical and horizontal profiles around reefs (see, e.g., Leis, Chapter 8), we should not expect the larvae of all species to be equally susceptible to a set of dispersal mechanisms. Only more intensive studies of variation in spawning and recruitment cycles, and of larval distributions and ecology, will help resolve the question of how much connection there is between local larval sources and sinks and show whether spawning is tracking larval survivorship cycles.

## B. Juvenile Biology Hypotheses

Russell *et al.* (1977), Stanton (1985), and Walsh (1987) suggested that spawning output could be tracking seasonal change in the suitability of the benthic environment (due to changes in food availability, temperature, and the physical stress) for the growth and survival of juvenile fishes after they arrive in a reef.

Analyses of this possibility have been limited to a search for correlations between community-level spawning seasonality and gross environmental seasonality. It has been shown that differences in the within-season timing of recruitment can strongly affect juvenile growth and maturation rates in temperate reef fishes (Jones and Thompson, 1980; Ochi, 1986a). Similar studies

have not been made of seasonal variation in juvenile growth, survival and maturation rates in tropical species. Species that differ in terms of the extent to which their recruitment cycles match the environmental cycle could make useful test organisms in a comparative study of this question.

### C. Adult Biology Hypotheses

#### 1. *Hawaiian and Red Sea Fishes*

MacDonald (1981) examined seasonal patterns of spawning, food acquisition, and fat storage in two Hawaiian damselfishes and proposed that both use fat reserves built up during the period of peak food availability to support later spawning (but see Walsh, 1987, regarding seasonal change in food availability). He also suggested that interspecific differences in the duration of their spawning seasons could reflect differences in the risk of delaying reproduction, since the two species have quite different average longevities. Fishelson *et al.* (1987) also proposed that a Red Sea surgeonfish stores resources during a strong seasonal peak in availability of algal food and uses those reserves to support spawning immediately afterward. However, in neither study was any estimate made of the proportion of a female's reproductive output that could have been derived from the stored reserves. The Fishelson *et al.* (1987) data indicate that reserves may not contribute much to the surgeonfish's output, since they are depleted in the first month of a five-month breeding season, well prior to the peak of spawning.

Stanton (1985) found that reproduction of the Hawaiian damselfish *Abudefduf sordidus* is uniformly high throughout most of the year but ceases in winter. He suggested that this hiatus could be due to this species' nesting activities being particularly vulnerable to disruption by increased wave action in winter. Since Stanton studied this species at a site protected from such wave stress, direct inhibition seems unlikely to be involved in producing the pattern he observed.

#### 2. *Neotropical Fishes*

Robertson (1990) found that environmental stresses acting on the adults of several Caribbean and eastern Pacific fishes influence the strength of seasonality of their spawning cycles. He proposed that a variety of environmental and intrinsic adult biology constraints control the seasonal pattern of spawning and indirectly determine the extent to which adults match the flux of their spawning output to the seasonal cycle of larval survivorship.

*a. Extrinsic Constraints* In Panama there are two main seasons, one wet and calm and the other dry and windy. Levels of spawning of both Caribbean and

Pacific species during the dry season are negatively correlated with the degree of exposure to physical conditions (rough water, sediment movements, and currents in the Caribbean; low temperatures in the Pacific) in different habitats and different years. Consequently those conditions evidently are stressful for adults and depress their reproductive output. This inhibition of reproduction occurs during different parts of the seasonal larval survivorship cycles of different species. In two of the Pacific species, spawning is minimal but larval survivorship is maximal during the early dry season (Robertson, 1990) (see Fig. 2).

*b. Intrinsic Constraints*

(i) *Risks of delaying reproduction* Although fecundity increases with age in fishes, the value of early spawning may exceed that of delayed spawning in short-lived species because of the risk involved in the delay (Williams, 1966). The magnitude of any risk of a seasonal delay in spawning will depend on both adult longevity and the length of the delay between the peak of spawning potential and the peak of larval survivorship. The potential importance of this constraint varies among the neotropical species and may be quite high in some [e.g., a delay of  $\approx 9$  months in a species whose adults have a half-life of  $\approx 1$  year (Robertson, 1990)].

(ii) *Body size and storage capacity* In short-lived species, reproductive effort is expended early and is large in relation to body size (Williams, 1966). A female of a small species can achieve a large absolute reproductive output only by spawning numerous times and releasing in excess of her body weight in eggs each year (DeMartini and Fountain, 1981; Burt *et al.*, 1988). Published information on sizes of the ovaries and clutches of fishes whose females spawn only once or twice a year (e.g., Williams, 1966; Thompson and Munro, 1983a; DeMartini and Fountain, 1981) indicate that storage can allow a female to produce a clutch weighing up to about one-third of her body weight. In two neotropical damselfishes the average female's annual spawning output is equivalent to 3–4.7 times her body weight (unpublished observations). Species such as these would be able to make only minor increases in spawning output during the season of peak larval survivorship by relying on previously stored resources. Thus body size may strongly limit the ability of small fishes to delay reproduction and favor continued spawning during periods of submaximal larval survivorship.

(iii) *Physiology of reproduction* Since fecundity increases with body size, a fish potentially could enhance reproductive output during the season of highest larval survivorship if it reallocated resources from current reproduction into growth during the preceding period when larval survivorship is low. Whether such a reallocation strategy would produce an increase in spawning

during the period of peak larval survivorship sufficient to overcompensate for spawning foregone at other times of the year might depend on whether current levels of egg production are controlled by intrinsic physiological limitations and on the relative costs of growth and reproduction and allometries in those costs.

Per capita rates of egg production can reach about twice a female's body weight during a 2.5-month season in damselfishes (my calculations from data in Doherty, 1980), and six to eight times a female's body weight during a 3.5-month season in other small fishes (Hubbs, 1976). Since both of these rates are considerably higher than those achieved by two of the neotropical damselfishes that Robertson (1990) studied, it seems unlikely that their current flux of output is determined by intrinsic physiological constraints.

Because of differences in the efficiency of conversion of food to growth versus reproduction (Wootton, 1979), growth may be relatively more costly than reproduction. Further, as a result of allometries in metabolic rates, in the rate of growth of reproductive tissue, and in the efficiency of conversion of food (Burt *et al.*, 1988; Pauly, 1986), there may be a decline in the relative rate of reproductive output and an increase in the unit cost of reproduction as body size increases. Even in the absence of any reduction in efficiency with increasing size, an adult that had grown at the expense of prior reproduction would need many more resources for the increase in spawning required of it during the period of peak larval survivorship. Resource limitation on adults during the season of peak larval survivorship could prevent a reallocation strategy from producing increased annual recruitment.

It is possible to see how various combinations of adult biology constraints might have produced the varying degrees of mismatching between the seasonal patterns of spawning and larval survivorship of the neotropical fishes. They are short-lived, small species that have a limited ability to delay reproduction. Their reproductive output is partly controlled by physical environmental stresses, the nature of which differs in the two oceans, and the intensity of which varies in different habitats. Whether their output also could be limited by food availability remains to be determined.

### 3. *Australian Fishes*

Both spawning and recruitment of the pufferfish *Canthigaster valentini* peak during the warm half of the year, although larval survivorship appears to be higher during the cool half. The fact that adult mortality is highest and adult growth and reproduction lowest during the cool season indicates that environmental conditions are unfavorable for adults during that period (Table 3). Delaying reproduction from the warm to the cool period would be very risky, because of low longevity, and the potential to increase output during the cool period could be limited by both small body size and reduced metabolic

potential (Table 3). Thus a mismatch between *C. valentini's* spawning and the larval survivorship cycle could derive from a combination of environmental, longevity, and size constraints.

*Pomacentrus wardi* and *P. chrysurus* (= *P. flavicauda*) are benthic feeding herbivores that Doherty (1980, 1983c) studied in a lagoon. *Pomacentrus chrysurus* is a habitat specialist, and the study habitat is typical for it. *Pomacentrus wardi* is a habitat generalist that occupies a range of other habitats in addition to lagoons (Doherty, 1980, 1983c; Robertson and Lassig, 1980). Differences between the degree of matching of the spawning and settlement seasons of those two species could be a reflection of the extent to which the study habitat is representative for each. Synchrony may have been observed in *P. chrysurus* because the study population was in the habitat in which most individuals of this species occur. Asynchrony may have been observed in *P. wardi* because populations in different types of habitats have different spawning patterns, and only one habitat type was sampled. The One Tree Island lagoon is semienclosed, has limited water exchange with the sea, and experiences physical and biological conditions different than in the remainder of the reef (Russell *et al.*, 1977; Hatcher and Hatcher, 1981). Breeding of both *Pomacentrus* species occurs during the warmest, calmest part of the year (Doherty, 1980). During that period the lagoon could experience a unique pattern of change in environmental variables (e.g., temperature?) that cue or drive the onset and termination of reproduction. For example, there is seasonal bloom of benthic algae (in response to changes in nutrient levels) that is restricted to the lagoon (Hatcher and Hatcher, 1981) and occurs during the onset of *P. wardi's* spawning season.

Although the asynchrony that exists between spawning and recruitment shows that *P. wardi* in the lagoon must have a different spawning season from that of other populations of conspecifics in the region, the significance of this difference is unclear. The few settlers that arrive before the annual settlement peak could result from many populations spawning at the same time as the study population, but few of their larvae surviving to settle. They also could result from high larval survivorship but few populations spawning. Regardless of the precise mechanism, it seems clear that the lagoon population of *P. wardi* is not matching its spawning output to the overall seasonal pattern of larval survivorship since most of that species' successful settlers are spawned at a different time of the year. A simple, testable explanation for this situation is that environmental controls on spawning vary among *P. wardi's* habitats.

#### D. Conclusions

Attempts to relate spawning seasonality to larval survivorship cycles by way of correlations between spawning patterns and gross seasonality in the larval

environment can tell us very little about factors that determine spawning seasonality. The complexity of patterns of inter- and intraspecific geographic variation in spawning seasons and within-site interspecific differences in relationships between spawning and environmental gradients show that, if spawning is tracking change in larval survivorship, then environmental factors that determine larval survivorship must be much more complex, subtle, species-specific in their action and spatially variable than has generally been thought. The simple explanations simply cannot account for the variability that exists.

Data that have recently become available indicate that there are significant differences between local spawning and larval recruitment cycles in many species. These differences could be due to adults employing a bet-hedging strategy of spawning over an extended period to cope with unpredictable spatial variation in the larval survivorship cycle. These differences also could arise because larvae that settle at one site were produced elsewhere and their settlement cycle is a direct reflection of the (different) spawning cycle at their source. If so, the differences in spawning cycles at different sites presumably would be due to adult biology mechanisms since a lack of feedback (i.e., larvae not settling at their source) would prevent selection from tailoring each local population's spawning cycle to a specific local larval survivorship cycle.

The possibility that spawning of tropical reef fishes tracks seasonal regimes of change in environmental conditions for benthic juveniles remains untested. There is evidence for such tracking in temperate reef fishes.

The combined action of a variety of environmental and intrinsic constraints on adults of some species may prevent them from matching their spawning output to the seasonal pattern of larval survivorship. There is no reason to assume that the season that is best for spawning also is best for larval survivorship, and there is evidence to the contrary for some species. The response of many fishes to adult biology constraints may be to spawn continuously, at whatever level environmental conditions permit at the moment, so long as there is some minimal level of return for effort. Relatively benign tropical conditions may permit year-round spawning with little seasonal change or may allow adults of different species to respond to a range of factors that show a variety of seasonal patterns of change. On higher-latitude coral reefs, seasonal environmental constraints on both adults and larvae may increase in strength and produce not only more sharply defined spawning seasons, but also a stronger tendency for those seasons to coincide in a broad range of species. The latitudinal differences in spawning seasons of West Atlantic reef fishes could reflect a latitudinal gradient in the intensity of such constraints.

To assess the relative importance of larval biology, juvenile biology, and adult biology factors as determinants of seasonal patterns of spawning, we need much additional information about the most basic aspects of these fishes'

life histories. How much spatial variation is there in seasonal patterns of spawning and recruitment? What factors affect juvenile growth and maturation? How do environmental factors such as food availability and physical stresses affect adults' ability to reproduce? How do effects of those factors vary seasonally and how do adults partition resources between reproduction, growth, and storage in different seasons? What influence do intrinsic limitations such as low longevity and low storage capacity have on the scheduling of spawning?

If constraints are preventing many small, short-lived reef fishes from releasing their spawning effort during a season of peak larval survivorship, one might expect this to have consequences for their adult populations. There is evidence that adult populations of some reef fishes are determined by larval supply and that these populations are below levels that would be set by resources (reviewed by Doherty and Williams, 1988a). A pattern of consistent partial reproductive "failure" during a season of high larval survivorship could contribute to maintaining the larval supply below levels that would enable adult populations to reach the point where they are controlled by resources.