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Differences in the seasonalities of spawning and recruitment of some small neotropical reef fishes

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Abstract: Seasonal cycles of spawning differ from seasonal cycles of larval recruitment at the same site in eight of nine small species of neotropical reef fishes (eight damselfishes and one blenny). In eight species, spawning is less strongly seasonal than recruitment and in seven species spawning peaks are not synchronized with peaks of recruitment and inferred larval survivorship. These differences between spawning and recruitment cycles could be due to geographic variation in seasonal patterns of spawning or larval survivorship. They could also be due to extrinsic and intrinsic constraints preventing adults from matching their spawning output to a predictable larval survivorship cycle. Seasonal environmental stresses on adults affect the structure of the spawning cycles of some of the study species and limit spawning output during different parts of the larval survivorship cycles of different species. Intrinsic constraints, such as low longevity and a limited capacity to store resources, may effectively prevent adults from delaying reproduction and concentrating reproductive output during the season of peak larval survivorship.

Key words: Coral reef fish; Panama; Seasonality; Spawning and recruitment

Introduction

Seasonal patterns of spawning vary greatly among marine fishes that produce planktonic larvae. In some species, an entire local population may spawn during a single short period each year and females may spawn only once a year. At the other extreme, reproduction occurs throughout the year, with each female spawning numerous times. Tropical reef fishes span the extremes of this range of conditions (Johannes, 1978; Munro, 1983; Shapiro, 1987; Robertson, in press).

Consideration of the selective factors involved in the evolution of spawning seasonality has focused mainly on how patterns of spawning may maximize larval recruitment by accommodating variation in larval survivorship. Adults are thought to restrict their spawning to periods when larval survivorship, which is controlled by oceanographic conditions, is highest. This concept proposes that predictable spawning seasons mirror short, predictable seasons favorable to larvae, while extended spawning seasons represent "bet-hedging" responses (Murphy, 1968; Stearns, 1976) that cope with unpredictable variation in the timing of conditions best for larvae. Ideas such as

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these dominate thinking about the adaptive significance of seasonal spawning patterns of temperate marine fishes and have stimulated considerable research into oceanographic mechanisms that influence larval survivorship (Qasim, 1956; Cushing, 1975; Parrish et al., 1981; Bakun et al., 1982; Iles & Sinclair, 1982; Lambert & Ware, 1984; Sherman et al., 1984; Sinclair & Tremblay, 1984; Checkley et al., 1988). Similar explanations have been used to account for reproductive patterns of tropical reef fishes (Johannes, 1978; Doherty, 1983; Thresher, 1984; Walsh, 1987; Lobel, 1989). However, in contrast to the situation for temperate fishes, there has been very little research aimed at directly assessing what oceanographic mechanisms determine seasonal change in larval survivorship in tropical species. Analyses of tropical systems have been limited to attempts to correlate community-level seasonal patterns of spawning or recruitment with gross seasonal change in various environmental variables (Robertson, in press).

This paper assesses whether patterns of reproduction of nine small neotropical reef fishes (six from the Caribbean and three from the Pacific) support the hypothesis that the seasonal pattern of spawning is tailored to the seasonal regime of larval survivorship. I examine whether average seasonal patterns of spawning match average seasonal patterns of larval survivorship, whether seasonal peaks of spawning coincide with seasonal peaks of larval survivorship, and whether the degree of dispersion of spawning over the year is correlated with the degree of variation in timing of seasonal peaks of larval survivorship.

Study Sites and Their Seasonal Regimes

Data were collected at Punta de San Blas, on the Caribbean coast of the Isthmus of Panama, and at Isla Taboguilla, in the (Pacific) Bay of Panama (see Glynn, 1972; Robertson, 1987; Robertson et al., 1990).

Panama has two obvious seasons. In the dry season, from about mid-December to about mid-April, strong northerly tradewinds predominate and rainfall is low. During the remainder of the year rainfall is high and winds are lighter and more variable. In the Caribbean, dry-season winds blow onshore and produce heavy wave action, strong currents and high sediment movements on coastal reefs. On the Pacific coast, dry-season winds blow offshore and induce a seasonal upwelling of cold nutrient-rich water in Panama Bay, which lowers surface water temperatures to as little as 14 °C (annual maximum = 30 °C), and produces plankton blooms. The Caribbean coast of Panama lacks upwelling and surface water temperatures range from 26 to 30 °C over the year (Panama Canal Company, 1965; Glynn, 1972; Cubit et al., 1989).

Organisms and Methods

ORGANISMS

Spawning and recruitment were monitored in six species of Caribbean pomacentrids: *Abudefduf saxatilis* (Linnaeus), *Microspathodon chrysurus* (Cuvier and Valenciennes), *Stegastes diencaeus* (Jordan and Rutter), *S. dorsopunicans* (Poey), *S. leucostictus* (Müller and Troschel) and *S. partitus* (Poey); one Pacific blenniid: *Ophioblennius steindachneri* (Jordan and Evermann); and two Pacific damselfishes: *S. flavilatus* (Gill) and *S. acapulcoensis* (Fowler).

Adults of the different species range from 5 to 110 g in mean body weigh (D. R. Robertson, unpubl. data). They are sedentary reef fishes that spawn within a few tens of meters of their feeding areas. All are benthic-feeding species except *A. saxatilis*, which feeds on midwater zooplankton.

SPAWNING

All species lay benthic eggs in discrete monolayered clutches that can readily be observed and measured. Eggs are laid in prepared, repeatedly used nests and guarded by the male parent until they hatch 4–5 days after spawning (Robertson et al., 1990). The reef system at Punta de San Blas is broken up into a series of discrete patch reefs that are isolated from one another by areas of sand and seagrasses. Populations of each of the study species on different patch reefs do not interbreed. Spawning output was monitored for 1 yr in one population of *A. saxatilis* (1987), for 3 yr in one population and 1 yr in another of *S. dorsopunicans* (1984–87), for 3 yr in one population and 1 yr in another of *S. leucostictus* (1984–87) and for 3 yr in one population of each Pacific species (1983–85). Spawning output was monitored concurrently for 3 yr (1983–85) in two populations of each of *S. diencaeus*, *S. partitus* and *M. chrysurus*, one population on a reef exposed to dry-season conditions (swell, currents, sediment movements) and one on another reef relatively protected from those conditions. Censusing methods are described in detail by Robertson et al. (1988) and Robertson et al. (1990).

Data on spawning output were obtained from 20–40 nests per population of each species. Rates of egg production ranged from 2 to 15 clutches (102–758 cm^2 of clutch area) per nest per month among the different species. These data are on per capita rates of spawning output; their use as a measure of seasonal change in the local population's output assumes that there is no seasonal change in population density, since population output is a product of per capita output and population density. This assumption seems reasonable, since in the three study species for which data are available, semiannual censuses do not show any indications of predictable seasonal change in population density (D. R. Robertson, unpubl. data). Interannual variation in output of individual species ranged from 1.2 to 1.7 among the Caribbean species, and 1.3 and 2.7 among the Pacific species (D. R. Robertson, unpubl. data).

RECRUITMENT

Juveniles settle directly into adult habitat. Such recruitment is lunar cyclic in all known cases for the study species (*S. diencaeus*, *S. dorsopunicans*, *S. leucostictus*, *S. partitus* and *A. saxatilis*; Robertson et al., 1988; D.R. Robertson, unpubl. data). Therefore, recruits were censused in permanent plots once each month during a fixed lunar phase (between first 1/4 and full moon). Recruitment was monitored for 6 yr in all Caribbean species except *S. diencaeus*, which was monitored for 9 yr. Recruitment was monitored for 3.5–4.5 yr in the Pacific species (to the end of 1988 in all cases). The total area of habitat censused exceeded 1000 m^2 for each of the Caribbean species and 600 m^2 for the Pacific species. The mean number of settlers censused per species per year ranged from 80 to 775 among the Caribbean species and 50 to 117 among the Pacific species. Average annual numbers of settlers censused were <100 in only two species (*S. diencaeus* and *O. steindachneri*) (D.R. Robertson, unpubl. data). The potential for small sample size to produce error in estimation of the seasonal cycle of recruitment would be greater in species whose recruits are mobile, highly aggregated and patchily distributed, than in species whose recruits are sedentary and scattered fairly uniformly throughout habitat patches. Since only one species (*A. saxatilis*) produced recruits of the former type, and the largest areas censused and the greatest numbers of recruits censused were of this species, small sample sizes do not appear problematic. Interannual variation in total settlement activity ranged from 1.5 to 2.3 among all but one of the Caribbean species (9.3-fold in *S. diencaeus*), and 2.6- to 5.0-fold among the Pacific species (D.R. Robertson, unpubl. data).

I estimated seasonal change in relative larval survivorship using:

$$\left[\frac{\text{percentage of year's recruits that were produced in a month}}{\text{percentage of year's spawning that occurred in same month}}\right].$$

This assumes that the seasonal pattern of recruitment at the study site is representative for larvae that are produced at the study site. To appropriately match recruitment and spawning months for this calculation, the duration of larval life was used. Growth increments in the otoliths of new recruits indicate that larval durations were ≈ 1 month in the damselfishes (Robertson et al., 1988; Wellington & Victor, 1989; Thresher & Brothers, in press; D.R. Robertson, unpubl. data on >15 individuals of each species except *M. chrysurus* ($n = 5$)) and ≈ 2 months in *O. steindachneri* (D.R. Robertson, unpubl. data, $n = 15$).

ANALYSES OF DATA

Two comparisons were made of the seasonal patterns of spawning output and recruitment within each species. First, I used a χ^2 test (the only two-sample circular test whose assumptions could be satisfied; Batschelet, 1981) to compare the average seasonal cycles of spawning and recruitment. These average distributions of activity

were calculated as follows. For spawning output, I used the mean number of cm^2 of eggs per nest per month (averaged over both populations if two were monitored) over all years sampled. For recruitment, the mean number of settlers censused per month (at all sites) over all years was used. For illustrative purposes, both sets of average values were converted to the percentage of the year's activity that occurred each month (Fig. 1). Second, time series analyses were used to determine if there were predictable seasonal peaks in spawning and recruitment of each species. Each multiyear set of data on spawning and recruitment was cross-correlated with the annual cycle (represented by a sine-wave with a period = 12.4 lunar months), using SYSTAT (1988). These serial cross-correlations identified the timing of any regular seasonal maxima and minima of activity (the months with the maximum, significant ($p < 0.05$) positive and negative correlations, respectively). I used the mean vector of each circular distribution (Batschelet, 1981) to estimate the timing of peak activity in each average seasonal pattern of larval survivorship.

I used a combination of the results of the time series analyses and the structure of the larval survivorship cycle to assess the nature of any differences the χ^2 test detected between the average spawning and recruitment cycles. I did not test for differences between the seasonal patterns of spawning and larval survivorship because they are not independent data sets.

I used the mean vector length (Batschelet, 1981) of each average distribution as a measure of the strength of the seasonality of spawning and recruitment, and Czekanowski's index (Bloom, 1981) to measure the degree of similarity of the average cycles of spawning of the different species and also the similarity of their average cycles of recruitment.

To examine intraspecific variation in the strength of seasonality of spawning of populations of three Caribbean species in sheltered and exposed habitats, I compared (a) the relative amounts of spawning of each population in the wet and dry seasons of the 3 yr sampled (G test for independence) and (b) the relative reduction in spawning during each dry-season month in the two populations (Wilcoxon's paired sample test). I also compared the interannual intraspecific variation in the distributions of spawning output in wet and dry seasons by the three Pacific species using a G test.

Other statistical techniques followed Sokal & Rohlf (1981).

RESULTS

SEASONALITY OF SPAWNING OUTPUT

All species spawned throughout the year and, in all except *S. leucostictus*, minimum activity occurred during the dry season (Fig. 1). There were consistently timed seasonal peaks of spawning in all but two species (Table I, Fig. 1), *M. chrysurus* and *S. flavilatus*. Although *S. flavilatus* had a statistically significant spawning output minimum during dry season (Table I), spawning appears to have been almost nonseasonal in

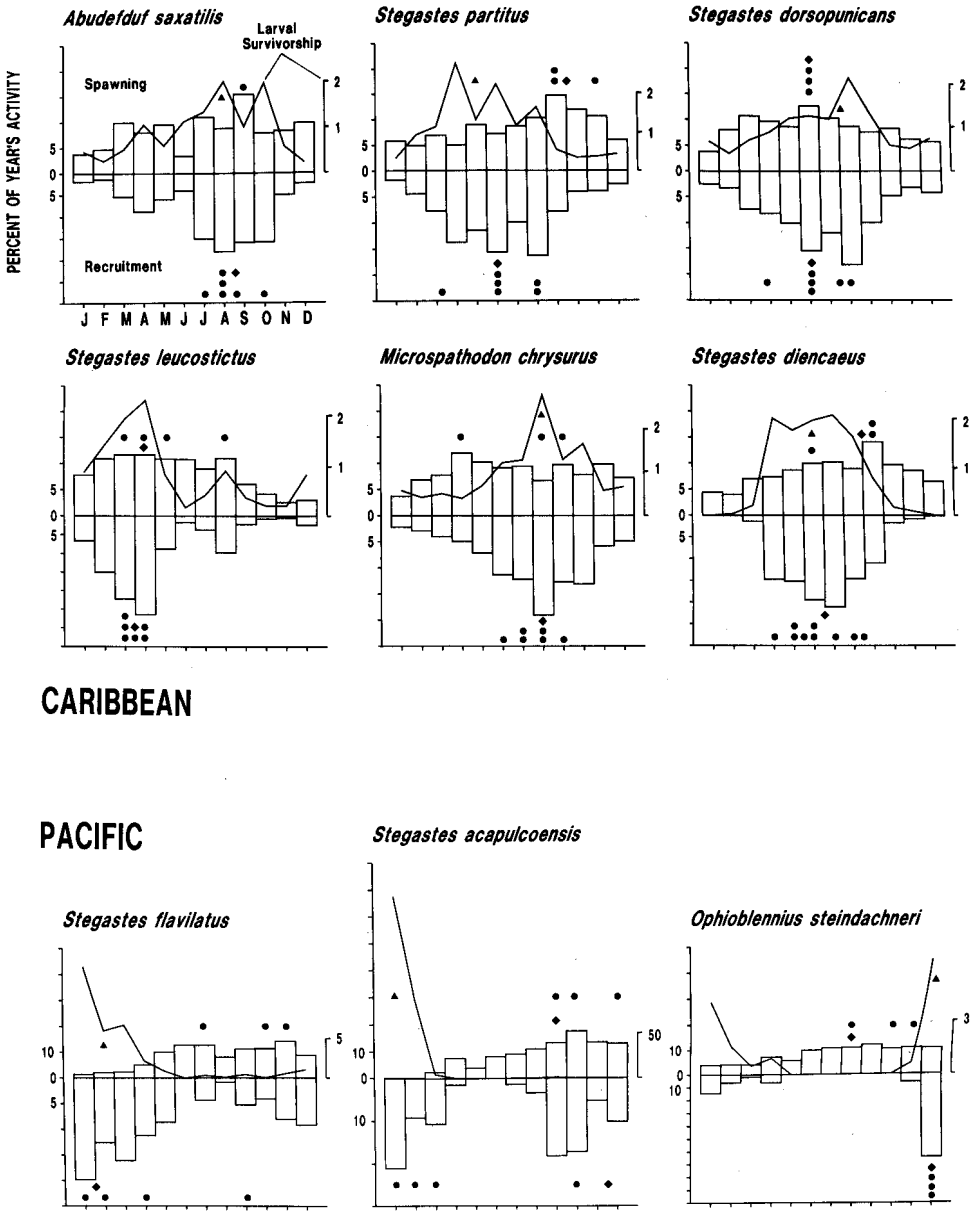

Fig. 1. Average seasonal patterns of spawning, recruitment and relative larval survivorship $\left[\frac{\text{recruitment}}{\text{spawning}}\right]$ of nine species. Recruitment is lagged to correspond to month of production of larvae (e.g., January's recruits are fish that were spawned in January). ●, peak month of spawning or recruitment of each year sampled (position of some symbols between calendar months reflects change in timing of lunar months relative to calendar months). ◆, seasonal peak of spawning or recruitment as detected by time series analysis. ▲, seasonal peak of larval survivorship cycle (mean vector of unimodal circular distribution; not calculated for *S. leucostictus* in which distribution is bimodal).

TABLE I

Test statistics for time series analyses of seasonal patterns of spawning output and recruitment of nine Panamanian reef fishes.

Species	Month with largest significant ($p < 0.05$) correlation value[4]			
	Spawning output		Recruitment	
	Maximum (r)	Minimum (r)	Maximum (r)	Minimum (r)
Caribbean				
A. saxatilis	No data[2]	No data	Aug–Sep (0.49)	Feb (−0.54)
M. chrysurus	NS[3]	NS	Aug (0.53)	Feb (−0.49)
S. diencaeus	Aug–Sep (0.53)	Feb (−0.55)	Jun–Jul (0.46)	Dec (−0.44)
S. dorsopunicans	Jun (0.51)	Dec (−0.58)	Jun (0.46)	Dec–Jan (−0.40)
S. leucostictus	Apr (0.77)	Oct (−0.67)	Apr–May (0.46)	Nov (−0.43)
S. partitus	Sep–Oct (0.66)	Mar (−0.61)	Jun (0.49)	Dec (−0.49)
Pacific				
O. steindachneri	Aug (0.51)	Feb (−0.66)	Dec (0.40)	NS
S. acapulcoensis	Sep (0.64)	Mar (−0.74)	Nov–Dec (0.33)	NS
S. flavilatus	NS	Jan (−0.40)	Jan–Feb (0.46)	Jul (−0.41)

[1] Cross-correlations of activity with annual cycle (see Methods). [2] No multiyear data set. [3] No significant value. [4] Lagged, month indicated is month in which recruits were spawned.

M. chrysurus since neither a consistent maximum nor a consistent minimum in its spawning were detected.

Spawning output of several Pacific and Caribbean species during the dry season was negatively related to the degree of exposure of the study population to dry-season conditions. First, levels of dry season spawning by two of the three Pacific species were lower in years with lower water temperatures (Table II). Variation among the three

TABLE II

Interannual variation in seasonality of spawning by three Pacific fishes.

Species	Nest depth[2]	Percentage of each year's spawning output released during dry season[1]		
		1983	1984	1985
O. steindachneri	1– 2 m	17.5	14.1	16.3
S. acapulcoensis	4– 6 m	8.0	1.1	3.5
S. flavilatus	6–10 m	25.5	4.8	4.5
Minimum water temperatures[3]		23–23.5 °C	18–20.5 °C	14–16.5 °C

[1] G test (using raw data) of independence of distributions of spawning in dry and wet seasons of different years. Horizontal lines join years that were not significantly different ($p > 0.05$). [2] Below low tide (from Robertson et al., in pess). [3] Recorded monthly by maximum/minimum thermometer in area of *S. flavilatus* nests.

species was related to the degree of their exposure to cold water. Dry-season spawning was highest in *O. steindachneri*, which fed and nested just below low tide level. In that habitat, monthly minimum temperatures were consistently 3–5 °C higher than at greater depths, where the two *Stegastes* species nested and fed (D. R. Robertson, unpubl. data). Second, in the Caribbean, relative amounts of spawning output during the dry season were consistently lower in the exposed-habitat population than in the sheltered-habitat population in *S. partitus* and *S. diencaeus*, but not in *M. chrysurus*. In these two *Stegastes* species, seasonality of spawning was stronger (i.e., there was disproportionately less spawning during dry season) in the exposed-habitat population in each of the 3 yr sampled. In *M. chrysurus*, a similar situation occurred in only 2 of 3 yr (Table III). *M. chrysurus* nests are located in higher, more protected sites that are less affected by movement of bottom sediments than are the lower, more openly situated nests of the two *Stegastes* species.

TABLE III

Habitat variation in strength of spawning seasonality in three Caribbean damselfishes.

Species	Habitat	Amount of spawning/dry-season month as percentage of that in maximum month of same year			Percentage of year's spawning that occurred during dry season[2]					
		Median	n	$T^1(p)$	1983	$G(p)$	1984	$G(p)$	1985	$G(p)$
M. chrysurus	Sheltered	48.5	14		32		36		29	
	Exposed	44.0	14	42.5(NS)	21	88(***)	37	0.2(NS)	25	34(***)
S. diencaeus	Sheltered	48.5	14		38		36		27	
	Exposed	8.5	14	2.0(**)	9	7852(***)	25	30(***)	9	84(***)
S. partitus	Sheltered	40.5	14		26		21		37	
	Exposed	15.5	14	4.0(**)	15	48(***)	9	61(***)	14	181(***)

[1] Wilcoxon's paired sample test; [2] G_{adj} test for independence (using raw data); NS = $p > 0.05$, ** $p < 0.01$, *** $p < 0.001$.

SEASONALITY OF RECRUITMENT

Recruitment occurred throughout the year in all species and each species had a predictable seasonal peak of recruitment activity (Fig. 1). In each species, $\geqslant 2/3$ of the recruits (averaged over all years) were produced during a 2–5-month period and in five species (*O. steindachneri*, *A. saxatilis*, *S. leucostictus*, *S. diencaeus* and *M. chrysurus*) annual recruitment peaks consistently occurred during the same third of the year (Fig. 1).

Average seasonal patterns of spawning output and recruitment were different in each of the nine species (Fig. 1). The nature of those differences varied among the species. Over the entire sample of nine species, the strength of seasonality of recruitment

consistently exceeded that of spawning and the two parameters were not correlated (mean vector lengths: Wilcoxon's paired $T_9 = 1$, $p < 0.001$, and Pearson's $r_9 = 0.02$, NS, respectively). Two species that lacked predictable seasonal peaks of spawning (*M. chrysurus* and *S. flavilatus*) did have predictable seasonal peaks of recruitment. In four of the seven species which had regularly timed seasonal peaks of spawning, the spawning peaks were not synchronous with distinct seasonal peaks of recruitment and preceded the recruitment peaks by from 2–6 months (*O. steindachneri* and *S. acapulcoensis*) to as much as 8–9 months (*S. partitus* and *S. diencaeus*) (Fig. 1).

Spawning patterns of different pairs of species at the same site were more similar to one another than the recruitment patterns of the same pairs of species were. Indices of similarity of spawning patterns of different species pairs are significantly higher than indices of similarity of recruitment patterns (Mann–Whitney $U_{18,18} = 276.5$, $p < 0.001$). While the recruitment patterns of 11 of the 18 species-pairs were significantly different, spawning patterns were significantly different in only two species-pairs (Table IV).

TABLE IV

Interspecific similarity of seasonal spawning patterns and of seasonal recruitment patterns of nine neotropical fishes.

		Czekanowski's similarity indices[1]					
		Recruitment					
		A.sx.	M.ch.	S.dc.	S.dp.	S.le.	S.pt.
(A) Caribbean							
	A. saxatilis	–	0.86	0.64**	0.78	0.45**	0.72**
	M. chrysurus	0.86	–	0.65**	0.85	0.42**	0.77
Spawning	*S. diencaeus*	0.90	0.89	–	0.75	0.44**	0.78
	S. dorsopunicans	0.84	0.90	0.86	–	0.51**	0.91
	S. leucostictus	0.73*	0.81	0.75	0.84	–	0.58**
	S. partitus	0.86	0.85	0.92	0.80	0.73*	–
		Recruitment					
		O.st.	S.ac.	S.fl.			
(B) Pacific							
	O. steindachneri	–	0.40**	0.45**			
Spawning	*S. acapulcoensis*	0.85	–	0.67**			
	S. flavilatus	0.86	0.82	–			

[1] Higher values denote greater similarity. χ^2 test (Batschelet, 1981) for differences between seasonal patterns of distribution, * $p < 0.05$, ** $p < 0.01$.

SEASONALITY OF SPAWNING VS. LARVAL SURVIVORSHIP

Distinct seasonal variation in larval survivorship was present in all nine species and was strongest among the Pacific species. The seasonal pattern of spawning output

matched that of larval survivorship in only one of the nine species (*A. saxatilis*, Fig. 1). Seasonal peaks of spawning and larval survivorship coincided in one other species (*Stegastes leucostictus*), predictable, though weak spawning peaks occurred 2–9 months before peaks of larval survivorship in five species (*O. steindachneri*, *S. acapulcoensis*, *S. diencaeus*, *S. dorsopunicans* and *S. partitus*), while two species (*M. chysurus* and *S. flavilatus*) that had peaks of larval survivorship lacked distinct peaks of spawning output. In the two Pacific *Stegastes* species, spawning output was minimal during the period of peak larval survivorship (Fig. 1).

Discussion

The differences between spawning cycles and the recruitment and inferred larval survivorship cycles of most of the species sampled do not support the hypothesis that the spawning cycles of these fishes have been selected to maximize larval recruitment by the matching of spawning output to a seasonal cycle of larval survivorship. According to that hypothesis, average annual cycles of spawning and larval survivorship should match and predictable seasonal peaks in larval survivorship should be reflected in predictable, synchronized spawning peaks. During this investigation, spawning cycles differed from recruitment and larval survivorship cycles in terms of both the degree of seasonality and the degree of synchrony of peaks of activity. Although all species had distinct seasonal cycles of recruitment, spawning output was more weakly seasonal than recruitment and the strength of spawning seasonality was not correlated with the strength of recruitment seasonality. Two species that had predictable recruitment peaks lacked predictable seasonal peaks of spawning and spawning output of one of them (*M. chrysurus*) appeared to be almost nonseasonal. Further, a seasonal spawning peak coincided with the seasonal peak of larval survivorship in only two of seven cases. Matching of spawning and larval survivorship cycles appeared to occur in only one species (*A. saxatilis*). This could be due to chance, since spawning of this species was monitored for only 1 yr.

There are a variety of possible reasons for the differences between spawning and recruitment cycles indicated by the data presented here. These include sampling bias, geographic variation in spawning and/or larval survivorship cycles, seasonal variation in the larval duration and the action of adult-biology constraints that control the pattern of spawning output in these species.

Sampling bias is an unlikely explanation for most of the observed differences between spawning and larval survivorship cycles. The sampling periods appear representative. Three species for which longevity data are available (*S. partitus*, *S. diencaeus* and *M. chrysurus*) are short-lived in relation to the observation periods (average adult longevity $\approx$ 1, 2–3 and 3.5 yr, respectively; D. R. Robertson, unpubl. data; McDonald, 1981). However, differences between the cycles of spawning and recruitment of the Pacific species may be less pronounced than Fig. 1 indicates. The south sides of islands

in Panama Bay, such as the study site, experience lower temperatures (i.e., more extreme upwelling conditions) than the north sides (Glynn & Stewart, 1973). Since spawning output in dry season is positively correlated with water temperature, the average level of spawning during that period in Panama Bay may be greater than is indicated from my data, particularly for the two *Stegastes* spp.

Geographic variation in spawning and larval survivorship patterns could account for the intraspecific differences between spawning and larval survivorship cycles. Since the larval life of the study species varies from 1 to 2 months, dispersal of larvae could decouple recruitment from spawning at the same site. The local recruitment pattern could be due to large-scale spatial variation in either spawning or larval survivorship. In the latter case, local spawning could be matching some regional average of a set of different larval survivorship cycles (i.e., spatial bet-hedging). However, spawning patterns of different species at the same site are both similar and weakly seasonal. If recruitment patterns at the Panama study sites are direct reflections of spawning patterns at other sites, the latter would have to be more strongly seasonal and more interspecifically diverse than those observed in this study. Similarly, there would have to be considerable interspecific diversity in larval survivorship cycles if each weakly seasonal spawning pattern is matching some average of a set of spatially variable larval survivorship cycles.

In the analyses of differences between spawning and recruitment described in the results, I assumed that there was no seasonal variation in the larval duration. Although the existence of such variation could account for apparent differences between spawning and recruitment, such seems unlikely, at least for the damselfishes. In all known cases, the larval life of damselfishes is $\approx 3-5$ wk (Robertson et al., 1988; Wellington & Victor, 1989; Thresher & Brothers, in press). In damselfishes with lunar recruitment cycles, larval durations would have to increase 2- or 3-fold to have an effect on the relationship between the spawning and recruitment cycles. Such large variation in larval duration is not known to occur in these tropical species, and in one of the species considered here (*S. partitus*) year round sampling did not detect any such variation (Robertson et al., 1988). The larval duration of *O. steindachneri* is substantially longer than that of the damselfishes, and the environment its larvae inhabit is highly seasonal. Although seasonal variation in larval duration could produce some of the apparent mismatching seen in this species, such variation would have to be very large to account for the extreme mismatching that occurs (Fig. 1).

The three explanations of the differences between spawning and recruitment patterns discussed above all imply that mismatching does not really occur. It is also possible that mismatching does occur and is due to extrinsic and intrinsic constraints preventing adults from matching spawning output to predictable larval survivorship cycles.

Extrinsic constraints include the influence of environmental stress. Adverse dry-season water conditions, the nature of which differs on the two sides of the isthmus, depress spawning of both Caribbean and Pacific species. These environmental stresses affect different species to different degrees, and reduce spawning to different degrees and

during different segments of their larval survivorship cycles. In two Caribbean species (*S. diencaeus* and *S. partitus*), dry-season depression of spawning occurs during off-peak parts of larval survivorship cycles, while in three Pacific species it occurs during part of the seasonal peak of larval survivorship.

Intrinsic constraints that could prevent a strategy of delaying and concentrating output during the seasonal peak of larval survivorship from producing a net increase in annual recruitment include low longevity and a low capacity to store resources for reproduction.

Life expectancy could be low enough in some species for current reproduction to be favored over future reproduction even when the latter offers a higher return per unit effort (Williams, 1966). The potential effect of this constraint would be strongest in *S. partitus*, which has an average adult longevity of 1 yr, and whose spawning peaks ≈ 9 months before larval survivorship, and weakest in a species such as *M. chrysurus*, which has an average adult longevity of 3.5 yr.

Low capacity to store resources may limit the potential for small species, such as those studied here, to increase future spawning output. While fishes seem able to store resources sufficient to produce a clutch that is 20–35% of a female's body weight, the annual egg output of a serial-spawning female of a small species often weighs much more than her own body weight (e.g., Burt et al., 1988). Since, in at least two of the study species, a female produces ≈ 3–5 times her own body weight in eggs per year (Robertson, in press), they can store little of what they expend.

The data presented here offer little direct support for the idea that the seasonal spawning cycles of these tropical species are well tailored to the seasonal patterns of survivorship potential for their larvae. If such tailoring does occur then local spawning and recruitment must not be coupled for the species studied, and there must be substantial geographic variation in spawning and larval survivorship patterns. However, if local spawning and recruitment are essentially coupled it may be that environmental and life history constraints prevent adults from releasing their reproductive output to take best advantage of predictable, seasonal peaks of larval survivorship.

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