

EARLY LIFE HISTORY TRAITS AND RECRUITMENT PATTERNS OF CARIBBEAN WRASSES (LABRIDAE)

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Abstract. Despite the fact that recruitment can significantly influence the population dynamics of benthic marine populations, relatively little is known about the biological and physical processes controlling recruitment. We selected eight closely related coral reef fishes (wrasses in the family Labridae) to examine the temporal and spatial patterns of juvenile recruitment to the Caribbean island of Barbados. We used a comparative approach to study the relationships among patterns of recruitment, early life history traits, and aspects of the physical environment. For 10 wk during each of three peak recruitment (spring) seasons (1990–1992), we used a biweekly census of recently settled juveniles (8–25 mm standard length, SL) to measure the abundance of six congeners, *Halichoeres bivittatus*, *H. radiatus*, *H. poeyi*, *H. garnoti*, *H. pictus*, and *H. maculipinna*, and two confamilial labrids, *Thalassoma bifasciatum* and *Bodianus rufus*. Analysis of the otoliths of a sample of collected specimens provided estimates of larval durations, postsettlement ages, sizes at settlement, and juvenile growth rates, enabling back-calculation of settlement day for all collected juveniles. We compared temporal patterns of recruitment among species, and spatial patterns of recruitment for the most common species.

Temporal patterns of recruitment were consistent among seasons for most of the labrids examined, although the magnitude of recruitment was less predictable (particularly for *H. poeyi*, *H. maculipinna*, and *B. rufus*). The eight labrids could be divided into two groups based on their early life history traits and within-season temporal patterns of recruitment. *Halichoeres bivittatus*, *H. radiatus*, *H. poeyi*, *H. garnoti*, and *H. pictus* had larval durations that were relatively short and invariant (means of 23–27 d), and all settled at fairly large sizes (9–12 mm SL) during the new moon and first maximum amplitude tide. In contrast, *T. bifasciatum*, *B. rufus*, and *H. maculipinna* had larval durations that were longer or more variable, and all three were able to delay metamorphosis. These three species settled at relatively smaller sizes (8–10 mm SL) during the third-quarter moon and second minimum amplitude tide. We compared temporal patterns of *T. bifasciatum* recruitment between Barbados and Caribbean Panama in an attempt to identify further the proximate environmental cues operating during settlement. Contrasting patterns of *T. bifasciatum* recruitment between the two geographical locations probably result from differences in the relative timing of the lunar and tidal amplitude cycles. Recruitment of labrids to Barbados occurred along the entire west coast of the island. Although some labrids had rather specific habitat requirements (e.g., *B. rufus* associated exclusively with large seaward-facing coral heads such as *Montastrea* spp.), most species were ubiquitous along the west coast. Species-specific juvenile densities did not often vary significantly among sites following major recruitment events, although overall densities were generally lower at a central site. Lower recruitment to that site likely results from reduced rates of larval supply due to prevailing offshore tidal flows.

Thus, temporal and spatial patterns of labrid recruitment to Barbados appear to be more predictable than previously thought for reef fishes. In particular, variation in the tidal amplitude cycle may influence both the timing of settlement and, to a lesser degree, the spatial scale of larval supply. Finally, the interaction of larval biology with such physical processes is evident in the correlation between temporal patterns of recruitment and early life history traits. The functional nature of this relationship clearly warrants further study.

Key words: Barbados; *Bodianus*; Caribbean; coral reef fishes; early life history; *Halichoeres*; larval duration; lunar synchrony; metamorphosis, delay of; tidal synchrony; otoliths; *Thalassoma*; tides.

INTRODUCTION

In recent years, much attention has been directed toward understanding the role of recruitment in structuring marine populations (e.g., reviewed in Doherty

1991, Jones 1991, Olafsson et al. 1994, Booth and Brosnan 1995). Because most benthic marine organisms have complex life cycles in which larvae and adults occupy different environments, the demography of these open populations can be influenced by processes occurring in the benthos after recruitment or by processes occurring in the plankton prior to or during

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TABLE 1. Potential mechanisms creating variation in recruitment.

Scale of variation	Physical	Biological
a) Temporal		
Seasonal (interannual)	Fluctuations in large-scale currents, storm frequency	Reproductive output
Within season		
Episodic	Winds, fronts, eddies, storms, upwelling, relaxation events	Reproductive timing
Biweekly/monthly	Lunar and tidal amplitude cycle	Reproductive timing, length of larval life, delay of metamorphosis, vertical migration, directional swimming
Daily	Diel and tidal cycle	Vertical migration, directional swimming
b) Spatial†		
Geographic	Large-scale current flow Differences in tidal amplitude cycles	Reproductive timing Reproductive source, length of larval life, behavioral responses to current flow cues
Island-wide (among sites)	Local current flow	Habitat selection
Microhabitat (within sites)	Boundary-layer flows	Microhabitat selection (including gregarious settlement)

† Geographic spatial scale is measured over hundreds to thousands of kilometers, island-wide over tens of kilometers, and microhabitat <1 km.

recruitment. "Recruitment" is generally defined as the settlement (transition from a planktonic larvae into a benthically oriented juvenile) and survival of new juveniles to the time of sampling (Richards and Lindeman 1987, Forrester 1990). Although this definition encompasses early postsettlement mortality, when juveniles are sampled very shortly after settlement, "recruitment" becomes functionally equivalent to "settlement."

During the past several decades, demographic paradigms for the regulation of open marine populations have shifted in emphasis between the importance of benthic vs. planktonic processes. The current most widely celebrated view recognizes the importance of both benthic and planktonic processes in structuring marine populations, and suggests that at any point in space and time, benthic populations may be controlled to a greater or lesser degree by density-independent processes influencing the supply and settlement of larvae, or density-dependent processes occurring after recruitment. This concept has been particularly emphasized in the literature on coral reef fishes (Victor 1986a, Warner and Hughes 1988, Forrester 1990, Jones 1990, 1991, Doherty 1991, Hixon and Beets 1993). However, although recruitment dynamics clearly can have an important role in the regulation of benthic marine populations (e.g., for coral reef fishes, Williams 1980, Doherty 1981, 1983, Victor 1983a, 1986a, Doherty and Fowler 1994; as well as a diversity of other species: Cowen 1985, Gaines et al. 1985, Choat et al. 1988, Keough 1988, Roughgarden et al. 1988, Raimondi 1990, Gaines and Bertness 1992, Peterson and Summerson 1992, Cowen and Bodkin 1993, Botsford et al. 1994, Eggleston and Armstrong 1995), relatively little

is known about the physical and biological processes controlling recruitment patterns.

Variation in recruitment on a variety of temporal and spatial scales (reviewed in Doherty 1991, Olafsson et al. 1994) may be influenced by the interaction of physical transport mechanisms and active behavior by adults or larvae (Table 1). Physical mechanisms such as large-scale shifts in prevailing currents can create temporal variation in recruitment among seasons (Cowen 1985, Choat et al. 1988, Farrell et al. 1991, Gaines and Bertness 1992), while within-season recruitment events may be associated with episodic events such as wind stress (Milicich 1994), storms (Reed et al. 1988), wind-induced onshore current flow (Shenker et al. 1993, Thorrold et al. 1994b), fronts or surface slicks (Kingsford and Choat 1986, Wolanski and Hamner 1988, Kingsford et al. 1991), upwelling (Roughgarden et al. 1991) or relaxation events (Wing et al. 1995), or the impingement of mesoscale eddies (Sale 1970, Lobel and Robinson 1986, Boehlert et al. 1992, Lee et al. 1992). On a monthly scale, recruitment may vary with the lunar cycle (reviewed in Doherty 1991, Robertson 1992, Booth and Beretta 1994, Sponaugle and Cowen 1994, 1996a, b) or the tidal amplitude cycle as a result of variable transport during spring or neap tides, including transport by tidally induced internal waves or surface slicks (reviewed in Shanks 1995). Active larval behavior such as vertical migration among water masses (reviewed in Leis 1991, Young 1995) or directional swimming (e.g., Hare and Cowen, *in press*, Leis et al. 1996) probably interacts with these physical mechanisms to control the timing of recruitment.

Aspects of the early life history of benthic marine organisms may also influence the timing of recruitment

(Table 1). For some reef fishes, particularly those with rather invariant larval durations, variation in the magnitude and timing of adult reproduction determines recruitment variability both among and within seasons (Robertson et al. 1988, Meekan et al. 1993, but see Robertson et al. 1993). Early life history attributes such as the length of larval life have obvious impacts on the degree to which larvae are subjected to transport by physical processes (Scheltema 1977, Jackson and Strathman 1981, Cowen 1991, Jenkins and May 1994). The capacity to delay metamorphosis may decouple the temporal relationship between spawning and recruitment for some fishes (Victor 1986a, Sponaugle and Cowen 1994), and enable greater recruitment synchronization to environmental cues (Sponaugle and Cowen 1994). Such developmental flexibility, including variability in larval growth rates (e.g., McCormick 1994) could potentially modify the supply of settlers.

Variation in the spatial patterns of recruitment is probably similarly influenced by physical and behavioral processes (Table 1). Large-scale currents can produce concurrent recruitment events at wide spatial scales (Cowen 1985, Victor 1986a, Doherty 1987, Choat et al. 1988, Pitcher 1988, Farrell et al. 1991), while local differences in tidal currents have the potential to create contrasting patterns of recruitment among distant locations. Because some environmental cycles differ among locations (e.g., the tidal amplitude cycle), environmentally cued spawning or recruitment may differ among sites. Among-site differences in the source of larvae also could lead to variable spatial recruitment. For example, a downstream site may receive a relatively continuous stream of larvae spawned from several upstream sites, whereas an upstream site may receive larvae in pulses correlated with the spawning of that population. In addition, because the duration of the larval period may vary among different populations (Thresher and Brothers 1989, Thresher et al. 1989, Wellington and Victor 1989, 1992), the influence of spawning patterns and physical mechanisms on the supply of larvae may vary among sites. Smaller scale (e.g., within island or region) spatial patterns of recruitment may be controlled by the specifics of local flows; however, if the distribution of various habitats, conspecifics, or predators varies spatially, habitat selection by larvae may contribute to spatial variation in recruitment (e.g., Sweatman 1983, Sale et al. 1984, Eckert 1985, Shulman 1985, Booth 1992). Larvae of sessile invertebrates may actively select microhabitats based on a suite of chemical cues (e.g., Crisp 1974, Pawlik 1992), although physical processes occurring in the boundary layer (e.g., small-scale eddies) also likely passively modify recruitment patterns (e.g., Butman 1987, Eckman et al. 1994).

Clearly, there are many physical and behavioral processes that may function to create the high degree of recruitment variability apparent in benthic marine populations. In general, however, relatively few have been

shown to directly influence the temporal and spatial patterns of recruitment. Because the proximate causes of recruitment variability have been difficult to identify for organisms such as coral reef fishes, there has been little consensus among the theories of ultimate causes of pattern (particularly temporal) in spawning and recruitment (e.g., Johannes 1978, Thresher 1984, Robertson et al. 1990, Robertson 1991). This is due in part to the lack of extensive data on a variety of species (especially closely related species) from diverse locations. Most studies to date have focused on one or two species (but see Robertson 1992) recruiting to a single location. In addition, for many reef fishes studied, larval durations are rather invariant, and temporal patterns of recruitment may simply reflect spawning patterns (Robertson et al. 1988, Meekan et al. 1993). Thus, prior to exploring the ultimate causes of recruitment variability, it is necessary to identify the proximate causes of temporal and spatial patterns of recruitment.

In this study, we selected a group of closely related coral reef fishes to examine the proximate causes of recruitment variability. We examined variability in the temporal and spatial patterns of recruitment for eight species of labrids recruiting to the upstream Caribbean island of Barbados: the slippery dick, *Halichoeres bivittatus* (Bloch); the puddingwife, *H. radiatus* (Linnaeus); the blackear wrasse, *H. poeyi* (Steindachner); the yellowhead wrasse, *H. garnoti* (Valenciennes); the painted wrasse, *H. pictus* (Poey); the clown wrasse, *H. maculipinna* (Muller and Troschel); the bluehead wrasse, *Thalassoma bifasciatum* (Bloch); and the Spanish hogfish, *Bodianus rufus* (Linnaeus). While there may be some seasonality to the spawning of at least one species at Barbados (*T. bifasciatum*; Hunt von Herbing and Hunte 1991), there does not appear to be any lunar synchrony within-season; all eight species are pelagic spawners that spawn daily (Warner and Robertson 1978, Robertson 1981). Because particular patterns of recruitment may be associated with various larval behaviors or early life history characteristics, we conducted a comparative analysis to determine whether certain larval traits (i.e., length of larval life, size at settlement, growth rate) are correlated with specific temporal patterns of recruitment. We also examined within-island variability in spatial patterns of recruitment. We compared these patterns to various environmental characteristics to determine the degree to which recruitment patterns are influenced by active habitat selection or by physical processes controlling larval supply. Finally, to identify which proximate environmental cues might be important in the timing of recruitment, we compared the recruitment patterns of one wrasse (*T. bifasciatum*) to those reported from another geographic location. Environmental cycles (e.g., tidal amplitude cycle) are often different, or offset, among various geographical locations, while lunar cycles are constant; thus, comparisons of temporal recruitment patterns among geographical locations may reveal

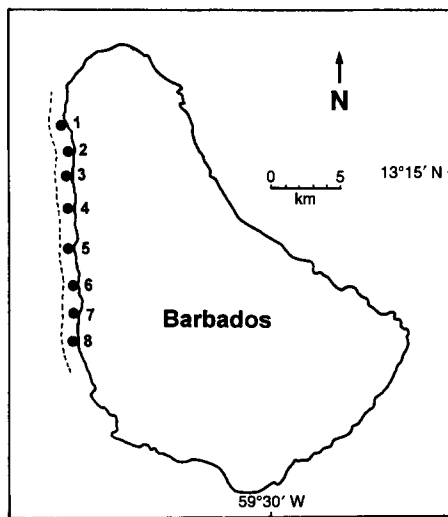


FIG. 1. Map of Barbados, West Indies, with the nearshore census sites (solid circles) located inside the bank reef (dashed line).

which of these two proximate cues are important in the monthly timing of recruitment.

METHODS

Site description

Barbados is the easternmost island in the Lesser Antilles chain of islands located in the eastern Caribbean. Lying within the belt of northeast trade winds, in the path of the wind-driven Equatorial Current, Barbados is upstream of the other Caribbean islands. Recent data collected offshore suggest that large-scale flow around the island may be topographically steered: as the northwesterly-flowing current impinges upon the southeastern coast of Barbados, it diverges around the island, continuing north and recirculating around a deep ridge well north of the island before continuing downstream (Cowen and Castro 1994). This flow may retain larvae spawned locally, contributing to the maintenance (on ecological time scales) of the high diversity of fishes (Cowen and Castro 1994).

We selected census sites to span most of the western coast of Barbados (Fig. 1). All sites were located on the nearshore reefs, which are distributed between 100 and 400 m offshore and ≈ 600 m inshore of the bank reef (which parallels the west coast). These nearshore reefs consist of high relief spurs of dead coral matrix, outcropping seaward from the continuous reef crest and separated from other spurs by sand or sand-rubble grooves. Reefs are concentrated at small coastal headlands, and extend toward shore, with no regions of seagrass. Sites were 2–2.5 km apart, and each encompassed ≈ 4000 m² of coral and rubble habitat in water depths of 2.5–6.5 m.

Recruitment census

To determine the temporal and spatial patterns of labrid recruitment to Barbados we censused and col-

lected new recruits biweekly (every other week) during the spring of three consecutive years (1990–1992). Spring (March–June) corresponds to the period of generally high larval abundance (Munro et al. 1973, Powles 1975) and peak reef fish recruitment in the Caribbean (Luckhurst and Luckhurst 1977), although the recruitment of *Thalassoma bifasciatum* to Barbados may be higher during summer months (Hunt von Herbing and Hunte 1991). During each census, we counted and collected all recently settled juveniles (8–25 mm standard length, SL) from six randomly selected replicate 5×1 m quadrats; we counted schools (>10 fish) in six 5×5 m quadrats, and collected a subsample (10%) of each school for analysis. For otolith aging purposes we made additional, qualitative collections of several rarer species (*Halichoeres pictus* and *Bodianus rufus*). We used the anesthetic Quinaldine and hand nets during all counts and collections. We preserved collected specimens in 70% ethanol prior to measuring SL, thus our reported SL may be somewhat smaller than the actual sizes at collection, due to shrinkage.

We attempted to measure larval supply directly by the nightly deployment of larval light traps. Although the traps proved successful at collecting the late-stage larvae of a diversity of reef fishes, the abundance of labrids was insufficient for analysis (Sponaugle and Cowen 1996a). However, we were able to use these late-stage larvae to estimate size at settlement. Note that these larvae were similarly preserved in 70% ethanol prior to length measurements.

Otolith analysis

To obtain a measure of larval duration and construct an age-to-length relationship for back-calculating recruitment date, we removed and examined the otoliths from a subsample of juveniles collected during each season. The otoliths of many bony fishes contain concentric marks that are deposited daily, allowing a precise estimate of age at capture (e.g., Brothers et al. 1976, Victor 1982). For reef fishes settling to the benthos, an additional, conspicuous settlement mark is often visible, permitting an estimate of larval duration as well as postsettlement age (Victor 1982). Daily increment deposition has previously been validated for two of the wrasses in this study (Victor 1982); it is reasonable to extrapolate from these for the remaining species. During this analysis, we randomly selected individuals from each 1.0 mm length category (Campana and Jones 1992), and extracted the otoliths using standard techniques (Brothers 1987). Storage of the sagittae and lapilli in medium viscosity immersion oil on microscope slides for 30 d facilitated interpretation. We examined the sagittae with a computer-aided image enhancer (Optical Pattern Recognition System, Bio-sonics Incorporated, Seattle, Washington) that was attached to a Zeiss compound microscope. We viewed the otoliths under transmitted light at $250\times$ (oil immersion) magnification, using an adjustable polarizing

filter placed between the light source and the first stage. We made at least two independent sagittal counts of each sample. For all labrid species except *Bodianus rufus*, a wide discontinuous band was clearly evident between the relatively narrow larval increments and the wider juvenile increments. We interpreted the inner edge of this band to indicate settlement (see Victor 1982), corresponding to the time when settling larvae enter and remain buried under the sand for several days (Victor 1983b; S. Sponaugle, unpublished data); likewise, the outer edge of the band corresponded to the emergence of juveniles onto the reef. Where increments were unclear in this region, we used interpolation based on surrounding increment widths to estimate the number of days fish were buried. For *B. rufus*, no wide band was evident; instead, a sharp transition (interpreted as settlement) existed between the narrow larval increments and the relatively wider juvenile increments. For all species, we added 2 d to the count of presettlement increments to account for the time to hatching (Fritzche 1978, Victor 1982).

Habitat characteristics and resident mature fish populations

Because spatial patterns of recruitment could be influenced by habitat selection by settling larvae or recently settled juveniles, or by differential survival of recruits in different habitats, we selected census sites to minimize site-specific habitat differences. To measure site similarity, we quantified 10 variables at each site: the percentage and diversity of live coral substrate; the percentage of coral rock substrate, coral rubble substrate, sand substrate, algal turf cover, algal turf-sand cover (algal turf visible through heavy sand coating), and sand cover (only sand visible); mean depth; and rugosity. We used a standard point-contact method (Greig-Smith 1964) to record the substrate and cover under, and the water depth above, 20 points along six randomly placed 5-m transects at each site. We considered rugosity to be the degree of variability (standard deviation) in depth among the points.

Spatial patterns of recruitment may also be influenced by conspecific populations (e.g., Sweatman 1983, Booth 1992), as larvae settle into existing populations, or are excluded by (or select not to settle near) predators or dense resident populations (e.g., Shulman 1985). Therefore, we surveyed mature fishes during 1991 and 1992 by counting the number of mature fishes within six randomly placed 5 × 5 m quadrats at each site. For the purposes of this census, we defined "maturity" by size alone (SL > 3 cm). We did not include small, cryptic species such as gobies, blennies, and apogonids in the survey.

STATISTICAL ANALYSIS

Early life history characteristics

We compared otolith-derived measurements of larval duration (non-normally distributed) among species and

TABLE 2. Age-on-length reduced major axes (RMA) regression slopes (± 1 SE) and intercepts (± 1 SE) used to back-calculate settlement date for eight species of labrids recruiting to Barbados.

Species	Year	Slope	Intercept	r^{\dagger}
<i>H. bivittatus</i>	1990	2.61 \pm 0.16	-27.67 \pm 2.82	0.81
	1991	2.56 \pm 0.21	-26.98 \pm 3.31	0.77
	1992	2.24 \pm 0.16	-20.85 \pm 2.74	0.88
<i>H. radiatus</i>	1990	2.62 \pm 0.20	-28.28 \pm 3.17	0.88
	1991	2.65 \pm 0.60	-27.35 \pm 8.64	0.86
	1992	1.99 \pm 0.21	-16.26 \pm 3.57	0.85
<i>H. poeyi</i>	1990	2.54 \pm 0.21	-30.12 \pm 3.62	0.87
<i>H. garnoti</i>	1990	1.83 \pm 0.21	-19.90 \pm 3.88	0.71
	1991	2.10 \pm 0.29	-24.73 \pm 5.19	0.81
	1992	1.99 \pm 0.19	-20.87 \pm 3.24	0.79
<i>H. pictus</i>	1990	1.38 \pm 0.08	-12.11 \pm 1.33	0.96
	1992	1.59 \pm 0.10	-15.10 \pm 1.73	0.89
<i>H. maculipinna</i>	1992	2.46 \pm 0.25	-22.44 \pm 3.70	0.88
<i>T. bifasciatum</i>	1990	2.43 \pm 0.16	-19.07 \pm 2.40	0.90
	1991	2.92 \pm 0.03	-25.85 \pm 4.23	0.70
	1992	2.67 \pm 0.14	-23.49 \pm 2.12	0.93
<i>B. rufus</i>	1991	1.60 \pm 0.16	-14.41 \pm 2.32	0.85
	1992	2.03 \pm 0.12	-20.22 \pm 1.62	0.90

\dagger Pearson product-moment correlation coefficient.

among years using a nonparametric Kruskal-Wallis test, followed by a nonparametric multiple comparison analysis (Dunn 1964, Zar 1984). We used reduced major axes (RMA) procedures to adjust for the inherent variability in the independent variable (length) of the age-on-length linear regressions (Ricker 1973, Laws and Archie 1981). Length-on-age regressions provided an estimate of growth rate (slope) and size at settlement (intercept), and the jackknife method produced estimates of standard error for each statistic (Sokal and Rohlf 1981). We compared growth rates and sizes at settlement among species and years using the T' method for unplanned comparisons (Sokal and Rohlf 1981).

Temporal and spatial patterns of recruitment

Because all age-on-length regressions had generally high Pearson's product-moment correlation coefficients (Table 2), we used separate regressions for each species from each year to estimate the postsettlement age of new recruits of that year. In some instances, where few fish were collected during a particular sampling season, we used the age-to-length regression from another year to estimate ages (i.e., for *Halichoeres poeyi* in 1992, *H. pictus* in 1991, and *H. maculipinna* in 1990 and 1991). For each collection, we weighted the size (age) distribution of collected fish by abundance to provide a more accurate estimate of the relative magnitude of each event. Where species (i.e., *H. bivittatus* and *Thalassoma bifasciatum*) appeared in the 5-m² quadrats (as individuals) and in the 25-m² quadrats (in schools), we tabulated the data from each quadrat type separately.

We tested periodicity in recruitment over the lunar cycle for each species during each year with Rayleigh tests (Batschelet 1981, Zar 1984). Used in the analysis of biological rhythms when cycle periods are predetermined (e.g., lunar or tidal cycle), this test compares

the temporal distribution of recruitment to that of uniform recruitment over the given environmental cycle. Where the distribution of recruitment is non-uniform, circular statistics provide an estimate of peak time (mean vector angle) and dispersion (mean angular deviation) of recruitment (Batschelet 1981). To obtain a general temporal pattern of recruitment, we also pooled the data for each species across all years and repeated the tests.

The biweekly juvenile census also provided data on spatial patterns of recruitment. We calculated the mean density of juveniles at each site for the most common species from each census following a large recruitment event. We tested these densities for site-related differences using the nonparametric Kruskal-Wallis test (due to non-normality of the data), followed where indicated by a nonparametric Tukey-type multiple comparison analysis (Zar 1984). To obtain an overall view of spatial variability in recruitment, we also calculated the mean rank of each site for all these events. We obtained rough estimates of mean juvenile mortality rates through counts made during the second census after a large recruitment event. Although such calculations may underestimate true mortality due to recruitment between sampling periods, we selected windows to minimize these effects. Initial densities were calculated 1 wk after each recruitment peak, and subsequent densities were calculated before the next peak. For each species and each large recruitment event we calculated daily mortality rates (Ricker 1975). For the less common species, we obtained a qualitative measure of site-specific differences in abundance by summing the number of juveniles censused at each site over the three seasons.

Habitat characteristics and resident mature fish populations

We transformed (arcsine square root) habitat measurements where appropriate (Sokal and Rohlf 1981), and then compared these transformed proportions among sites using standard ANOVA and multiple comparison procedures. In five instances (percentage of live coral, diversity of live coral, percentage of sand substrate, percentage of algal turf-sand cover, and percentage of sand cover), transformed variables remained non-normally distributed, so we used nonparametric Kruskal-Wallis tests, followed by nonparametric Tukey-type multiple comparisons (Zar 1984). To provide a relative measure of site similarity, we used principal components analysis (PCA) techniques to group the 10 habitat variables (Tatsuoka 1971). We then regressed juvenile densities (for both common and rarer species) as well as mature fish densities against three separate PCA factors to determine whether habitat descriptors influenced the spatial patterns of recruitment.

To measure the impact of mature fishes on juvenile recruitment patterns, we grouped the counts of resident mature fishes from each site and year into several categories: mean diversity of fishes, mean number of all

fishes, and mean number of labrids per quadrat. Due to low abundances, we did not analyze these data at the level of individual species. We transformed the data where necessary to meet assumptions of normality, and tested among sites and between years with two-way ANOVA and multiple comparison procedures (Zar 1984). We regressed the densities of the most common juveniles against mature fish densities to identify any relationship between mature fishes and new recruits. We also regressed the densities of mature fishes against the three habitat PCA factors to determine whether mature fishes were associated with particular habitat features.

RESULTS

Early life history characteristics and temporal patterns of recruitment to Barbados

The eight species of labrids in this study could be broadly divided into two groups based on several life history traits and their temporal patterns of recruitment. Most of the *Halichoeres* species (*H. bivittatus*, *H. radiatus*, *H. poeyi*, *H. garnoti*, and *H. pictus*) had relatively short, invariant larval durations and exhibited no evidence of delayed metamorphosis. Although recruitment rates varied interannually for several of these species, monthly settlement occurred consistently during the new moon (maximum amplitude tides). The other three labrids, *H. maculipinna*, *T. bifasciatum*, and *B. rufus*, had relatively longer or more variable larval durations, and all three could delay metamorphosis. Settlement by these species occurred during the third-quarter moon and minimum amplitude tides.

New-moon recruits: Halichoeres bivittatus, H. radiatus, H. poeyi, H. garnoti, and H. pictus

Larval durations were similar over all years for the five species of *Halichoeres* (Dunn method: $Q < 3.17$, $P > 0.05$), and were generally short and relatively invariant (Table 3, Fig. 2). Estimated size at settlement was also similar among most of the five *Halichoeres* species (T' method: difference [d] = 0.06–3.85, minimum significant difference [msd] = 2.25–4.95; Table 4), as were early juvenile growth rates (T' method: $d = 0-0.35$, $msd = 0.1-0.4$). However, *H. pictus* tended to settle at a slightly smaller size (T' method: $d = 2.63-3.96$, $msd = 2.40-2.95$) and exhibit higher growth rates than some of the other wrasses (T' method: $d = 0.22-0.36$, $msd = 0.20$). The size of the smallest *H. pictus* collected (11.9 mm, 5–6 d old, postsettlement) tended to be smaller than the smallest *H. poeyi* (14.0 mm, 7–8 d), *H. garnoti* (13.0 mm, 6 d), and *H. radiatus* (12.0 mm, 8 d), but not *H. bivittatus* (11.0–11.4 mm, 5–8 d).

Interannual variability in the recruitment of the five *Halichoeres* species differed among species (Fig. 3). *Halichoeres bivittatus* was consistently one of the most abundant labrids, and recruited regularly each year.

Halichoeres radiatus was less abundant than *H. bivittatus*, but new recruits also were consistently present on the reef each year. The least predictable of all the labrids, *H. poeyi*, was quite rare on the reefs, recruiting in a strong pulse only in 1990. Both *H. garnoti* and *H. pictus* were typically less abundant on the reefs than either *H. bivittatus* or *H. radiatus*, but their temporal patterns of recruitment were consistent among years. *Halichoeres garnoti* tended to recruit in rather small events spread over several days during all three years, while most of the recruitment of *H. pictus* occurred during a single pulse of short duration each year (Fig. 3).

Although there was interannual variability in the size of recruitment events for many species, the timing of these events was generally consistent among years for each species. For these five *Halichoeres* species, monthly patterns of recruitment were similar: pulses occurred during the time of the new moon. Because the lunar and tidal amplitude cycles are closely coupled in Barbados, particularly during our sampling season, pulses of recruitment occurred during maximum amplitude tides associated with the new moon (Table 5, Fig. 4).

Third-quarter moon recruits: Halichoeres maculipinna, Thalassoma bifasciatum, and Bodianus rufus

Larval durations of *Halichoeres maculipinna*, *Thalassoma bifasciatum*, and *Bodianus rufus* tended to be both longer and more variable than larval durations of the first five *Halichoeres* species (new-moon group; Table 3). While mean larval durations of *T. bifasciatum* were significantly longer than durations of all species of *Halichoeres* (Dunn method: $Q = 4.77-9.46$, $P < 0.05$), mean larval durations of *H. maculipinna* tended to be but were not significantly longer than the other *Halichoeres* species (Dunn method: $Q < 3.17$, $P > 0.05$; Table 3). Mean larval durations of *B. rufus* were also consistently longer than *Halichoeres* species, but due to high variability, this tendency was not always significant (Dunn method: $Q = 4.01-6.12$, $P < 0.05$).

Variability in the larval durations of *H. maculipinna*, *T. bifasciatum*, and *B. rufus* (1991) was generally quite high (Table 3). Of all of the labrids, *T. bifasciatum* had the highest variation in larval durations (1991 $CV = 24.3$). Both the high mean larval duration and the higher variability in durations that year were due to the presence of 4 fish (out of 26 dissected) whose otoliths had numerous narrow increments immediately prior to settlement, suggesting a delay of metamorphosis (Victor 1986b, Cowen 1991). Among all the other labrids dissected, only *H. maculipinna* and *B. rufus* exhibited evidence of delay of metamorphosis (6 out of 25 *H. maculipinna* dissected in 1992, and 1 out of 25 *B. rufus* dissected in 1991, resulting in high CV s for each in those years; Fig. 2). These are relatively conservative estimates of the proportion of fish that delayed meta-

TABLE 3. Larval durations† (mean \pm 1 SE) and coefficients of variation (CV) for eight labrids collected from Barbados during three spring seasons (1990–1992).

Species	Year	Larval duration (d)	Range	CV	n
<i>H. bivittatus</i>	1990	23.5 \pm 0.3	20–27	7.4	38
	1991	26.8 \pm 0.6	21–32	10.8	25
	1992	24.5 \pm 0.3	21–29	6.3	31
<i>H. radiatus</i>	1990	25.3 \pm 0.2	23–27	4.7	24
	1991	23.9 \pm 0.4	22–28	6.2	18
	1992	23.4 \pm 0.4	20–28	7.9	24
<i>H. poeyi</i>	1990	25.9 \pm 0.4	22–29	6.1	17
<i>H. garnoti</i>	1990	26.0 \pm 0.5	20–31	8.7	25
	1991	24.8 \pm 0.7	21–30	11.3	17
	1992	23.8 \pm 0.5	21–28	8.7	19
<i>H. pictus</i>	1990	26.7 \pm 0.5	23–30	7.7	18
	1992	26.2 \pm 0.4	23–31	7.3	25
<i>H. maculipinna</i>	1992	27.0 \pm 0.7	23–37	13.4	25
<i>T. bifasciatum</i>	1990	49.0 \pm 1.1	38–64	12.2	32
	1991	53.2 \pm 2.5	41–94	24.3	26
	1992	49.2 \pm 0.8	41–66	10.0	37
<i>B. rufus</i>	1991	40.0 \pm 1.0	32–52	12.2	25
	1992	34.3 \pm 0.3	31–41	4.4	22

† We added 2 d to each count of pre-settlement increments to account for time to hatching.

morphosis because only those with additional, narrower increments on the outer edge of the presettlement region of their otoliths (interpreted as reflecting reduced growth, Victor 1986b, Cowen 1991) were considered to be delayers. Other individuals with longer larval durations may also be delayers without exhibiting these narrower increments (Sponaugle and Cowen 1994).

The sagittae of all of the labrids except *B. rufus* were all rather similar in appearance, with relatively narrow presettlement increments separated from the wider postsettlement increments by a wide discontinuous zone. This zone has previously been interpreted as the period following settlement when the settled larvae are buried under the sand undergoing metamorphosis (Victor 1983b). Because this zone was not evident in the otoliths of *B. rufus*, this wrasse presumably settles directly to the reef, without burrowing in the sand. In fact, several very small specimens of *B. rufus* in various stages of larval to juvenile coloration were collected in the water column near large coral heads, suggesting that metamorphosis is gradual and occurs while these fishes remain above the substrate.

Mean estimated sizes at settlement for *H. maculipinna*, *T. bifasciatum*, and *B. rufus* were all at the smaller end of the size range (Fig. 5), although *H. maculipinna* and *B. rufus* were not significantly different from each other or the other *Halichoeres* species (T' method: $d = 0.05-3.89$, $msd = 1.70-4.95$; Table 4). *Thalassoma bifasciatum* tended to be smaller at settlement than most of the other labrids and was significantly smaller than *H. bivittatus* (1990, 1991), *H. radiatus* (1990), and *H. poeyi* (T' method: $d = 2.67-4.00$, $msd = 2.45-2.95$). The size of the smallest fish collected of all three species was also smaller than any of the

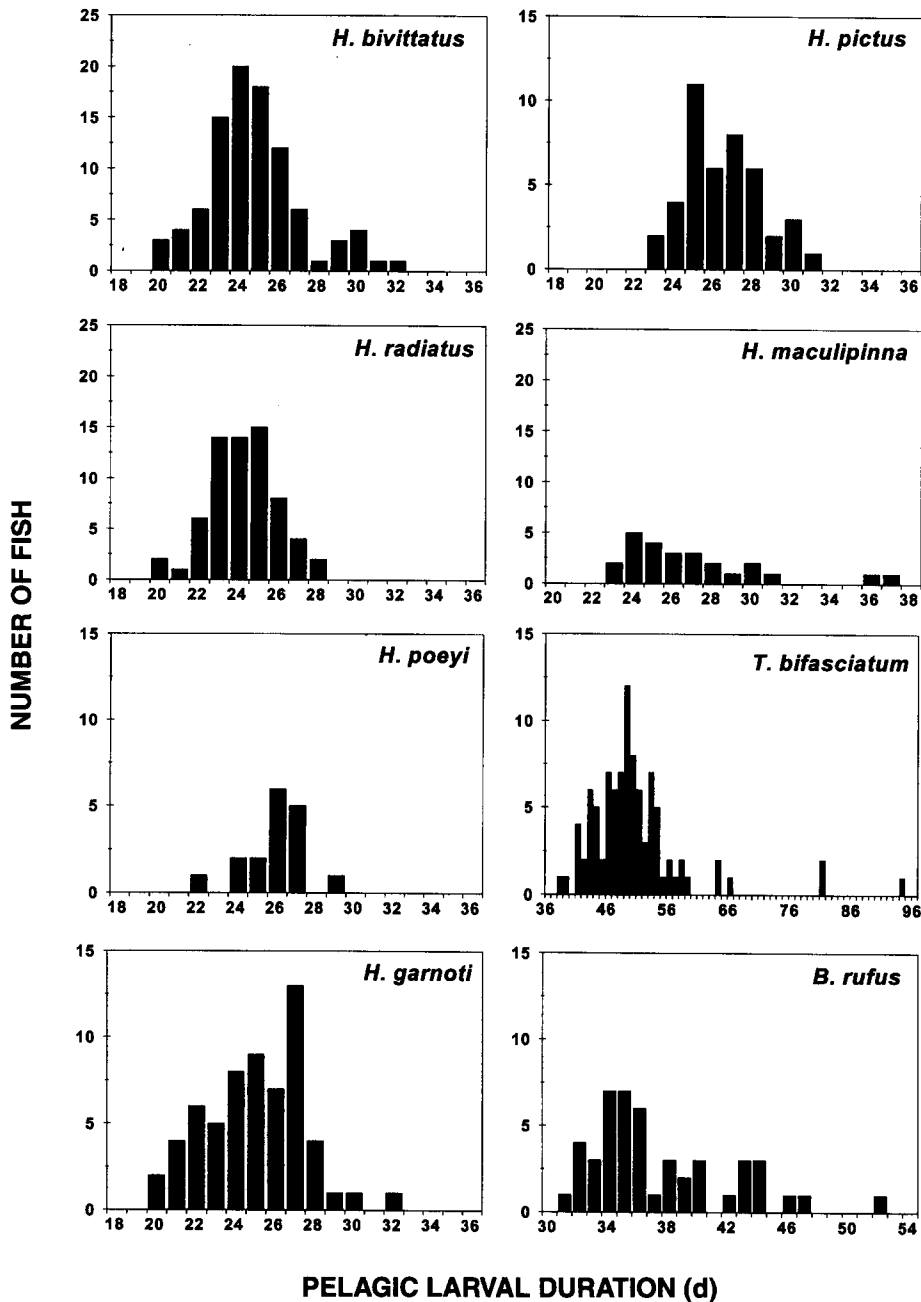


FIG. 2. Frequency of larval durations for eight species of labrids collected at Barbados during three seasons.

other *Halichoeres* species: *H. maculipinna* (10.8–11.0 mm, 3–6 d old, postsettlement), *T. bifasciatum* (10.0 mm, 4–10 d old), and *B. rufus* (9.7 mm, 2 d old). In addition, late-stage larvae of *H. maculipinna* (mean SL = 11.4 mm, SD = 0.73 mm, range = 10.1–12.9 mm, $n = 18$) and *T. bifasciatum* (mean SL = 10.8 mm, SD = 0.18 mm, range = 10.6–11.0 mm, $n = 4$) were smaller than *H. bivittatus* larvae (mean SL = 12.1 mm, SD = 0.71 mm, range = 10.8–13.7 mm, $n = 33$). Note that late-stage larvae were often larger than estimated settlement sizes and the size of the smallest juveniles.

This is probably due to shrinkage during metamorphosis (see *Discussion*). In general, labrids recruiting during the third-quarter moon tended to be smaller at settlement than several other *Halichoeres* species. Furthermore, and in contrast to the new-moon recruits, third-quarter-moon recruits exhibited relatively greater variation in larval duration than in estimated size at settlement (Fig. 5). Following settlement, growth rates for newly settled juvenile *H. maculipinna*, *T. bifasciatum*, and *B. rufus* were similar to one another and to growth rates of the other *Halichoeres* species (*T'* meth-

od: $d = 0-0.35$, $msd = 0.1-0.4$; Table 4), except for *H. pictus*.

Interannual temporal patterns of recruitment varied among *H. maculipinna*, *T. bifasciatum*, and *B. rufus* (Fig. 3). By far one of the most abundant fishes on Barbados reefs, *T. bifasciatum* recruited consistently in pulses of a similar magnitude to *H. bivittatus*. In contrast, *Halichoeres maculipinna* and *B. rufus* juveniles were much less abundant and exhibited greater interannual variability in patterns of recruitment. After poor recruitment seasons in 1990, both species were more abundant in 1991 and 1992. During these years, *H. maculipinna* typically recruited in pulses spread over a number of days, while recruitment of *B. rufus* occurred as relatively short events.

For all three species, *T. bifasciatum*, *B. rufus*, and to a lesser degree *H. maculipinna*, monthly recruitment pulses occurred during the third-quarter moon and minimum amplitude tides (Table 5, Fig. 4). This pattern was consistent among years for both *T. bifasciatum* and *B. rufus* (Table 5, Fig. 3). However, in 1992, recruitment of *H. maculipinna* was not as tightly coupled to the third-quarter moon, but was spread over a broader period of time (Fig. 3).

Mortality rates

For the three most abundant labrids, *H. bivittatus*, *H. radiatus*, and *T. bifasciatum*, initial juvenile densities ≈ 1 wk following a major recruitment peak ranged from 0.6 to 3.8 fishes per quadrat (5 m²; Table 6). Over the next 2 wk, juveniles exhibited daily mortality rates of 1.4 to 13.1%, based on a loss of 0.5–1.9 juveniles per quadrat (Table 6). There was no correlation between these daily mortality rates and initial recruitment densities, thus no evidence of density-dependent mortality during this time period.

Spatial patterns of recruitment to Barbados

Examination of species-specific juvenile densities over the eight sites along the west coast of Barbados revealed a consistent pattern (Fig. 6). Although this trend was significant for only two individual recruitment events (Fig. 6a), in general, recruitment of the three most common wrasses (*H. bivittatus*, *H. radiatus*, and *T. bifasciatum*) tended to be lower in the central region of Barbados (site 6) than at either the northern or southern ends (Fig. 6b). When the other, less abundant labrids were considered together (over all census seasons) for qualitative purposes, a similar pattern was revealed, with most juveniles censused at either end of the island, particularly the northern end, rather than in the center (Fig. 7). Thus, although there was relatively little significance in the spatial pattern of recruitment, there was a consistent tendency for juvenile densities to be reduced at site 6.

Spatial variation in environmental characteristics

To examine whether the observed spatial patterns of recruitment were influenced by habitat selection, we

TABLE 4. Estimated juvenile growth rates and size at settlement (mean ± 1 SE) from reduced major axes (RMA) length-on-age regressions for eight labrids.

Species	Year	Juvenile growth rate (mm/d)	Size at settlement (mm)
<i>H. bivittatus</i>	1990	0.38 \pm 0.02	10.60 \pm 0.45
	1991	0.39 \pm 0.03	10.53 \pm 0.46
	1992	0.45 \pm 0.03	9.30 \pm 0.60
<i>H. radiatus</i>	1990	0.38 \pm 0.03	10.79 \pm 0.42
	1991	0.38 \pm 0.08	10.31 \pm 0.87
	1992	0.50 \pm 0.05	8.15 \pm 0.99
<i>H. poeyi</i>	1990	0.39 \pm 0.03	11.86 \pm 0.49
<i>H. garnoti</i>	1990	0.55 \pm 0.06	10.87 \pm 0.87
	1991	0.48 \pm 0.07	11.75 \pm 0.90
	1992	0.50 \pm 0.05	10.47 \pm 0.66
<i>H. pictus</i>	1990	0.73 \pm 0.04	8.79 \pm 0.48
	1992	0.63 \pm 0.04	9.52 \pm 0.53
<i>H. maculipinna</i>	1992	0.41 \pm 0.04	9.13 \pm 0.58
<i>T. bifasciatum</i>	1990	0.41 \pm 0.03	7.86 \pm 0.50
	1991	0.34 \pm 0.04	8.84 \pm 0.59
	1992	0.37 \pm 0.02	8.79 \pm 0.34
	1992	0.62 \pm 0.06	8.99 \pm 0.63
<i>B. rufus</i>	1991	0.62 \pm 0.06	8.99 \pm 0.63
	1992	0.49 \pm 0.03	9.96 \pm 0.30

analyzed two environmental components: habitat (substrate and cover) characteristics and densities of resident mature fishes. Of the 10 habitat variables considered, 6 varied significantly among sites (Table 7). Because juvenile densities were lower at site 6, we will focus our discussion of particular habitat variables on identifying differences between that site and the others. Overall, site 6 had the highest percentage of live coral, but it was only significantly higher than sites 7 and 3 (Tukey-type: $q = 5.9$, $P < 0.005$). Coral diversity was also higher at site 6 than at sites 7, 3, or 8 (Tukey-type: $q = 4.97-6.83$, $P < 0.05-0.001$). Not surprisingly, site 6 had the lowest percentage of sand cover, but this was only significantly lower than site 3 (Tukey-type: $q = 5.81$, $P < 0.05$). Although not the deepest site, site 6 was significantly deeper than sites 7, 2, and 8 (Tukey: $q = 4.57-4.95$, $P < 0.05$).

Principal components analysis (PCA) of the same habitat variables revealed that sites 3, 7, and 8 could be distinguished from the other sites based on PCA factor 1; factor 2 did not seem to contribute to grouping sites 3, 7, and 8, but may help separate site 1 from the others (Fig. 8). There was less of a distinction among sites based on PCA factor 3 (Fig. 8). PCA factors 1, 2 and 3 explained 36.7%, 28.0%, and 18.6% of the variance, respectively (Table 8).

In general, there was little significant influence of habitat on the spatial patterns of recruitment for most of the labrids, although in a few cases specific habitat requirements may have influenced the distribution of juveniles. The regressions of juvenile densities (means following each major event for the common species, and totals for each of the rarer species) against each PCA factor indicated that there were no significant relationships between juvenile densities and any of the habitat variables ($r^2 = 0.001-0.47$, $P > 0.05$), except

for *H. bivittatus* (1992a) and *B. rufus* (total). Site-specific densities of *H. bivittatus* following the first major recruitment event in 1992 were significantly influenced by PCA factor 1 ($r^2 = 0.70$, $P = 0.01$; Fig. 9), indicating a negative correlation with the percentage and diversity of live coral, and a positive relationship with the percentage of rubble substrate, algal turf and sand cover, and sand cover alone. Juvenile densities of *B. rufus* over all years were significantly influenced by PCA factor 3 ($r^2 = 0.65$, $P = 0.016$; Fig. 9), indicating a positive relationship with mean depth and the percentage of algal turf cover.

Although there were few correlations between juvenile densities and among-site habitat characteristics, on a smaller scale, several within-habitat differences were noted in the distribution of each species. Palest in coloration of all the labrid species considered in this study, *H. bivittatus* juveniles were most commonly found in small groups (but also in large schools following strong recruitment pulses) swimming relatively low in the water column over sand-rubble substrates. Juveniles of *H. radiatus* and *H. poeyi* were almost always solitary and occurred near the sand-coral interface, under large coral overhangs. *H. garnoti* juveniles were fairly widespread, occurring most often as solitary individuals, but also in small, mixed schools near the sand-coral interface. *H. pictus* juveniles were always found in small schools (some mixed), relatively high in the water column near areas of high vertical relief. Newly settled juveniles of *H. maculipinna* and *T. bifasciatum* were similar in their distribution (and roughly, in their coloration), occurring as solitary individuals very low in coral crevices. Over time, *T. bifasciatum* juveniles swam progressively higher in the water column, forming increasingly larger schools. Older *H. maculipinna* juveniles tended to remain more solitary. *B. rufus* juveniles were found exclusively around large coral heads (such as *Montastrea cavernosa*), located at the offshore end of coral spurs. Solitary or small groups remained fairly high in the water column around the coral structure.

There were only a few site-specific differences in the abundance of resident mature fishes, and these differences did not seem to significantly influence the densities of juveniles. Two-way ANOVAs for each variable (mean number and diversity of all fishes, and mean number of labrids censused) indicated a significant influence of site ($F = 2.94-3.90$, $P = 0.001-0.009$, $df = 7, 80$), but not year ($F = 0.001-0.107$, $P = 0.74-0.98$, $df = 1, 80$), with no significant interaction ($F = 0.90-1.02$, $P = 0.43-0.51$, $df = 7, 80$). In general, the mean number and diversity of all mature fishes was

similar across all sites (ANOVA: $F = 1.28-1.93$, $P = 0.09-0.29$, $df = 7, 40$; Fig. 10). The high number of mature fishes at site 2 in 1992 was due to the presence of several very large schools of grunts (Haemulidae). In 1991, the mean number of mature labrids was significantly lower at site 6 than three other sites (Tukey: $q = 4.57-4.95$, $P < 0.05$). However, there were no significant relationships between mature fish counts and any habitat variables ($r^2 = 0.001-0.47$, $P > 0.05$), or between juvenile densities of *H. bivittatus* and *T. bifasciatum* and mature fish densities for a given season ($r^2 = 0.001-0.086$, $P > 0.05$).

DISCUSSION

Temporal recruitment patterns and early life history characteristics

For most of the wrasses in this study, recruitment to Barbados occurs rather predictably during the spring. While the magnitude of recruitment events is somewhat variable, the timing of these events is generally consistent within seasons and among years. Eight species of labrids exhibit two distinct temporal patterns of recruitment, and these appear to be correlated with several early life history traits. The recruitment of five species (*Halichoeres bivittatus*, *H. radiatus*, *H. poeyi*, *H. garnoti*, and *H. pictus*) was closely coupled to the new moon and maximum amplitude tides, while recruitment pulses of three other labrids (*H. maculipinna*, *Thalassoma bifasciatum*, and *Bodianus rufus*) were synchronized to the minimum amplitude tides during the third-quarter moon. Because these recruitment patterns were back-calculated from biweekly collections of juveniles, it is possible that high daily mortality rates of new settlers have obscured real settlement patterns. This effect might be particularly suspect if we obtained a semilunar (biweekly) recruitment pattern. However, we obtained two distinct lunar recruitment patterns for species collected during the same biweekly census. Furthermore, data from a concurrent study on another reef fish (*Stegastes partitus*) confirm that similar back-calculated lunar recruitment patterns exactly matched patterns of larval supply (Sponaugle and Cowen 1996b).

Several early life history traits were correlated with these temporal recruitment patterns. Duration of the larval period tended to be longer and more variable for labrids recruiting during the third-quarter moon. This high variability in larval duration reflects a capacity to delay metamorphosis. While this capacity has been reported previously for *T. bifasciatum* (Victor 1986b), and a temperate labrid (Cowen 1991), this is the first

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Fig. 3. Recruitment by eight species of labrids collected at Barbados during each of three spring recruitment seasons (1990-1992). Lunar phase is indicated by solid (new moon) and open (full moon) circles. Note that y-axes vary for certain species and years.

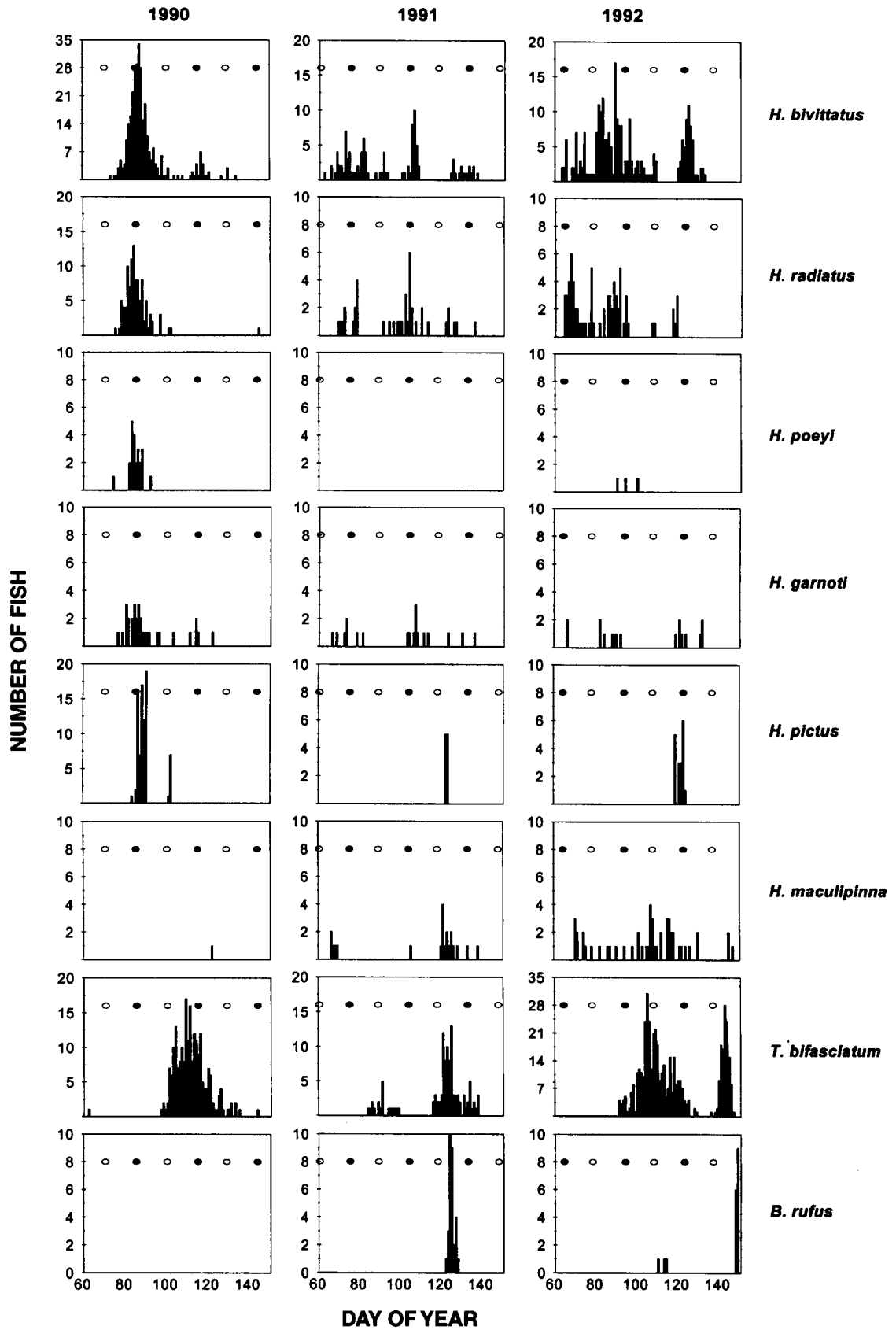


TABLE 5. Rayleigh test statistics for lunar periodicity in settlement of eight labrids for each year that juveniles were collected and for all years summed together. Because the tidal amplitude cycle is closely coupled to the lunar cycle throughout the study period, the timing of settlement relative to the tidal amplitude cycle is similar.

Species	Year	<i>n</i>	<i>Z</i> †	Lunar settlement day‡	<i>s</i> §
<i>H. bivittatus</i>	1990	314	111.1***	2.5	4.2
	1991	100	21.2***	1.1	4.9
	1992	242	11.1***	0.0	5.9
	All years	656	118.2***	1.8	5.0
<i>H. radiatus</i>	1990	104	38.6***	29.3	4.2
	1991	40	11.2***	29.1	4.6
	1992	72	7.3***	29.3	5.5
	All years	216	53.5***	29.3	4.7
<i>H. poeyi</i>	1990	23	14.3***	0.6	3.1
	1992	3	1.4NS		
	All years	26	15.6***	0.7	3.2
<i>H. garnoti</i>	1990	29	8.2***	0.3	4.6
	1991	19	5.9**	2.0	4.4
	1992	17	2.9NS		
	All years	65	16.4***	0.9	4.8
<i>H. pictus</i>	1990	82	46.3***	4.1	3.3
	1991	10	9.9***	19.5	0.5
	1992	18	15.2***	28.7	1.9
	All years	110	34.8***	2.9	4.4
<i>H. maculipinna</i>	1990	1	1.0NS		
	1991	21	8.8***	21.5	3.9
	1992	52	1.7NS		
	All years	74	5.2**	19.5	5.7
<i>T. bifasciatum</i>	1990	207	25.3***	25.3	5.4
	1991	111	29.7***	20.1	4.6
	1992	478	51.8***	18.1	5.4
	All years	796	68.2***	20.1	5.6
<i>B. rufus</i>	1991	30	27.5***	21.8	1.4
	1992	18	12.9***	25.7	2.6
	All years	48	34.3***	23.1	2.6

† *Z* = Rayleigh test statistic; ** *P* < 0.01, *** *P* < 0.001, NS, *P* > 0.05.

‡ Lunar settlement day was calculated from mean vector angle.

§ *s* = mean angular deviation (days; Batschelet 1981, Zar 1984); day 1 = new moon.

report of delayed metamorphosis by *H. maculipinna* and *B. rufus*. For all species, mean larval durations were comparable to those reported previously for labrids from Panama (*Halichoeres* spp. 24.1–25.9 d, *T. bifasciatum* 49.3 d, *B. rufus* 41.6 d; Victor 1986c) and Bermuda (*Halichoeres* spp. 22–30.5 d, *T. bifasciatum* 55 d, *B. rufus* 32 d; Schultz and Cowen 1994).

Labrids recruiting during the third-quarter moon also tended to be smaller at settlement than the other *Halichoeres* species. The only previously reported sizes at settlement are for *T. bifasciatum* and *H. poeyi* (each ≈12 mm, Victor 1991; *T. bifasciatum* mean length of 11.5 mm, Robertson 1992). Although our estimated settlement sizes are similar for *H. poeyi*, *T. bifasciatum* appears to settle to Barbados at much smaller sizes (7.9–8.8 mm). Our estimated sizes at settlement are also smaller than the sizes of three labrids collected in light traps during the same period. Based on observations of *H. maculipinna* and several other labroid species, we hypothesize that during metamorphosis, some shrinkage occurs and juveniles emerge at a small-

er standard length than the presettlement larvae (S. Sponaugle and R. K. Cowen, unpublished data). However, it is also possible that growth is simply curvilinear during metamorphosis, so that the linear model used to estimate size at settlement results in a smaller estimate of size.

Considering that *T. bifasciatum* spends a significantly longer time in the plankton prior to settlement, yet settles at a smaller size than many of the other labrids, and assuming that size at hatching is similar for all species, mean larval growth rates must be substantially less for *T. bifasciatum* than for the other labrids. Similarly, *B. rufus* probably has an intermediate larval growth rate, with several *Halichoeres* species exhibiting the highest larval growth rates. Following settlement, however, most juvenile labrids grew at similar rates (Table 4), which were slightly to substantially higher than growth rates previously published for *H. bivittatus*, *H. poeyi*, and *T. bifasciatum* (≈0.30 mm/d; Victor 1991). Clearly, there is a decoupling of growth between the larval and juvenile phases of the life cycle.

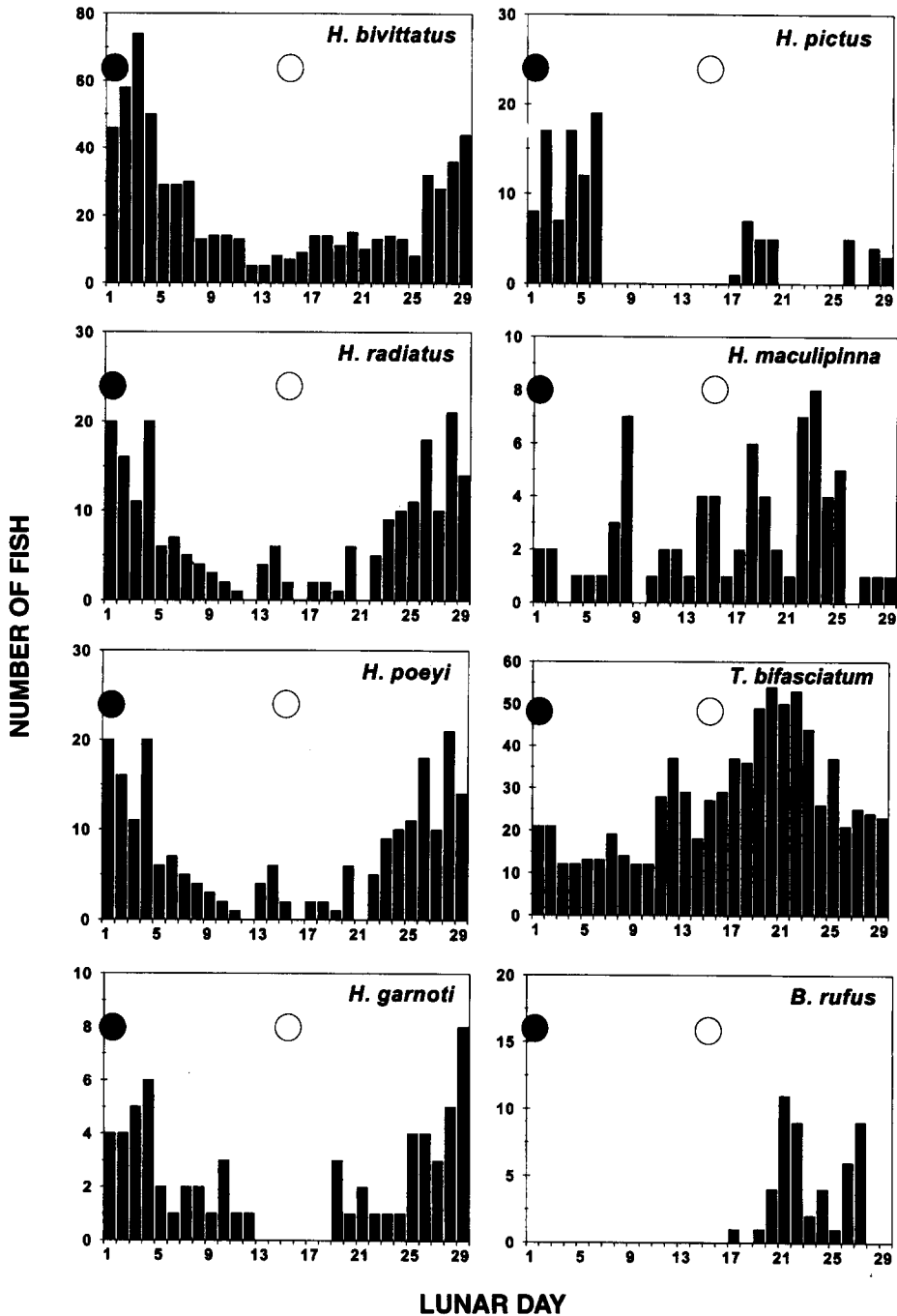


FIG. 4. Distribution of recruitment over the lunar cycle for eight species of labrids collected at Barbados over three spring recruitment seasons combined (1990–1992; total of 10 lunar cycles). Lunar phase is indicated by solid (new moon) and open (full moon) circles.

Processes operating in the pelagic environment appear to select for a range of larval growth rates, whereas reef-based constraints appear to select for more equivalent rates of growth. The relationship between larval life history strategies, recruitment patterns, and juvenile life history traits is probably complex, but its elucidation is critical to a complete understanding of the

population dynamics of organisms with complex life cycles.

Thus, the labrids in this study with relatively short, invariant larval durations (*H. bivittatus*, *H. radiatus*, *H. poeyi*, *H. garnoti*, and *H. pictus*) recruited to Barbados during the new moon and maximum amplitude tides, while those with generally longer or more vari-

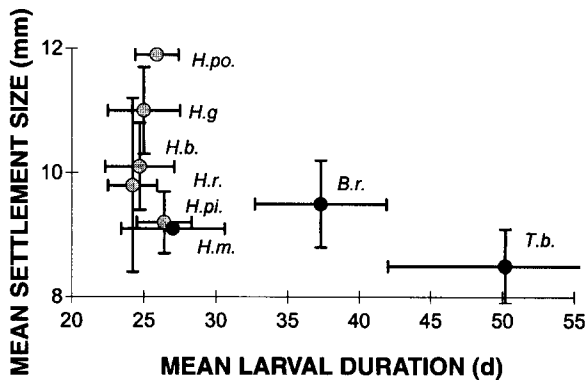


FIG. 5. Mean estimated settlement size vs. mean larval duration for eight labrids with relatively invariant larval durations (*Halichoeres poeyi*, *H. garnoti*, *H. bivittatus*, *H. radiatus*, and *H. pictus*; shaded circles) and for those with more variable larval durations (*H. maculipinna*, *T. bifasciatum*, and *B. rufus*; solid circles). Error bars indicate ± 1 SD. Note that error bars are not available for *H. poeyi* and *H. maculipinna*, since data from only one year were used to estimate size at settlement.

able larval durations, with a demonstrated capacity to delay metamorphosis (*T. bifasciatum*, *H. maculipinna*, and *B. rufus*), recruited during the third-quarter moon and minimum amplitude tides. In addition, several of these later species (*T. bifasciatum* and *B. rufus*) may have slower larval growth rates, and may tend to be relatively small at settlement. Consideration of growth rates and settlement sizes places *H. pictus* slightly outside the two groups because after a rather short, invariant period in the plankton, *H. pictus* appears to settle at a smaller size, and then exhibit faster juvenile growth rates than the others. Interestingly, the temporal pattern of settlement exhibited by *H. pictus* is also slightly offset from (3–4 d after) the new moon.

At this time, the significance of the correlation between early life history traits and recruitment patterns is unclear. Why should a longer larval duration, a capacity to delay metamorphosis, and a possibly smaller size at settlement lead to recruitment timed to the third-quarter moon and minimum amplitude tides? Prior to examining this issue, we need to explore the causes and potential advantages of synchronized recruitment. The comparison of recruitment patterns among these closely related labrids may clarify or eliminate several of the alternatives.

Synchronized recruitment may be a result of either active (behavioral) or passive (physical) processes acting on the early egg and larval stages, the late-stage larvae, or on the new recruits. Several investigators have proposed that recruitment synchrony results from synchronous spawning, which occurs to enhance transport, survival, or growth of the eggs and larvae (Johannes 1978, Thresher 1984, Gladstone and Westoby 1988; see review in Robertson 1991), or survival of the adults (Robertson et al. 1990). Temporal coupling between spawning and recruitment is more likely for species with short, invariant larval durations, such as pomacentrids (e.g., Robertson et al. 1988, Meekan et al. 1993) and is less likely for the labrids in this study because spawning is asynchronous (daily, year-round; Warner and Robertson 1978, Robertson 1981), and larval durations of several species are relatively long and variable. At present, there are no reported data on monthly variation in labrid fecundity; until such data are available, we will assume that cyclic patterns of fecundity do not contribute significantly to patterns of reproduction. While the frequency of spawning may vary seasonally (Hunt von Herbing and Hunte 1991), and fertilization success may be reduced in rough seas

TABLE 6. Mean densities and mortality estimates (± 1 SD) following large recruitment pulses for three common species of labrids recruiting to Barbados during three spring seasons. Means were calculated for each site separately; means for all sites are presented.

Year	Initial density (no. fish/ quadrat)†	No. days after peak‡	Final density (no. fish/ quadrat)†	No. days after peak‡	Mean decrease (no. fish/ quadrat)	Daily mortality (%)§
<i>H. bivittatus</i>						
1990	3.8 \pm 2.2	7	1.9 \pm 1.0	20	1.9 \pm 2.5	5.3
1991	0.6 \pm 0.6	6	0.1 \pm 0.2	23	0.5 \pm 0.6	11.3
1992a	2.1 \pm 2.0	7	0.8 \pm 0.9	22	1.2 \pm 1.4	5.9
1992b	1.2 \pm 1.0	7	0.1 \pm 0.2	23	1.1 \pm 0.9	13.1
<i>H. radiatus</i>						
1990	1.3 \pm 0.7	10	0.7 \pm 0.4	23	0.7 \pm 0.6	5.0
<i>T. bifasciatum</i>						
1990	3.0 \pm 1.1	17	1.6 \pm 0.5	38	1.4 \pm 1.5	3.0
1992	3.7 \pm 1.7	8	2.9 \pm 1.5	25	0.8 \pm 1.3	1.4

† Initial densities were calculated from the first census following the event; final densities were calculated from the second census following the event (number censused/5-m² quadrat).

‡ Number of days between peak in recruitment event and midpoint of census period.

§ Calculated from Ricker (1975).

|| Although time after peak is long for *T. bifasciatum* in 1990, this particular event was quite broad and extended up to the day prior to the census (see Fig. 3).

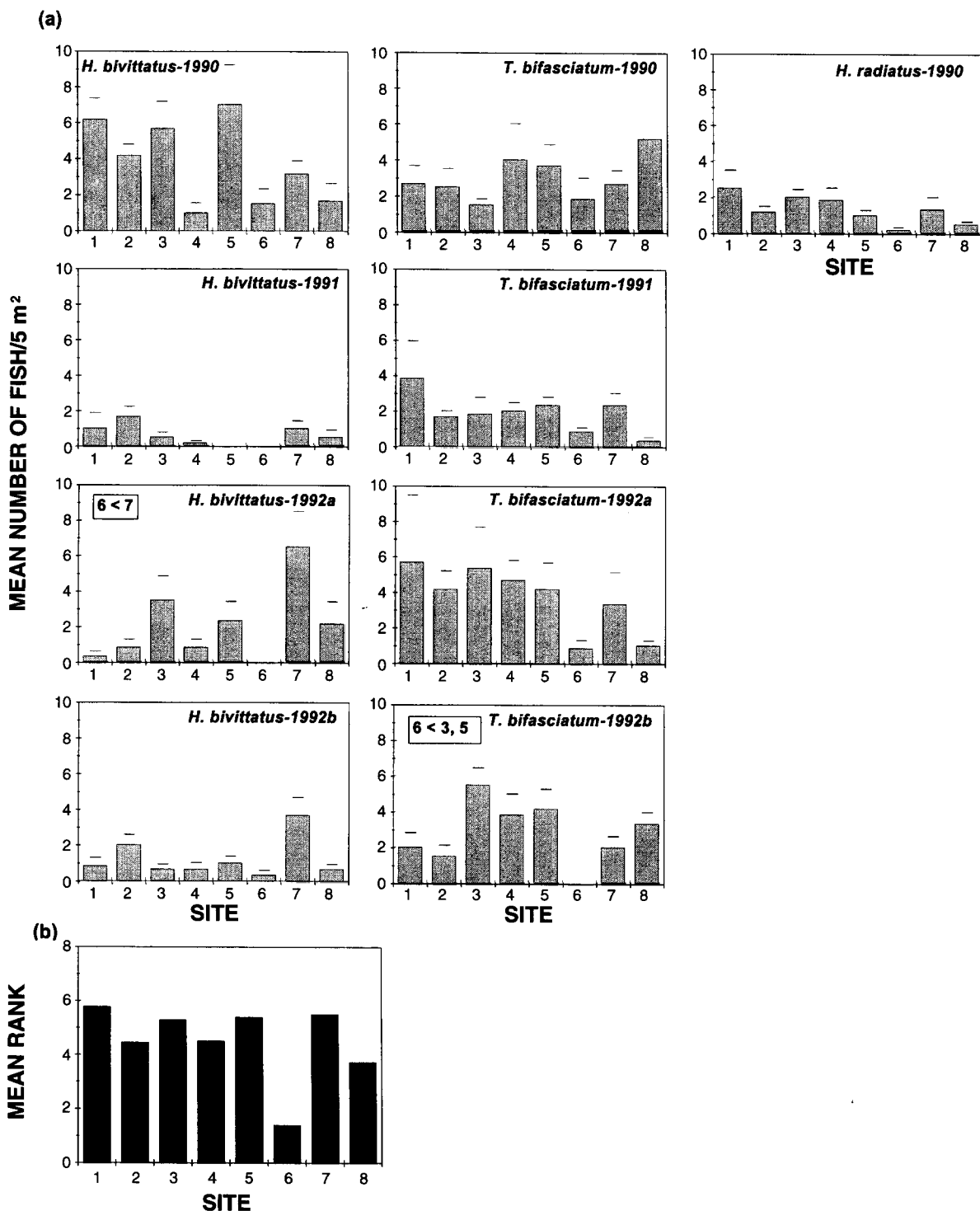


FIG. 6. Site-specific juvenile densities for three common labrids recruiting to Barbados. (a) Mean densities (± 1 SE) following each major recruitment event each year. Significant differences among sites are indicated in the inset (Tukey-type: $q = 4.33-5.37$, $P < 0.05$). (b) Mean rank of each site for all three species and events. See Fig. 1 for site locations.

(Petersen et al. 1992), these factors likely contribute to seasonal rather than monthly cycles of reproduction.

For daily spawners, periodic, synchronous patterns of recruitment suggest that the survival of late-stage

larvae and juveniles may be temporally predictable. For such species, a variable larval duration may enable greater synchronization of recruitment (Sponaugle and Cowen 1994). In a concurrent study, we demonstrated

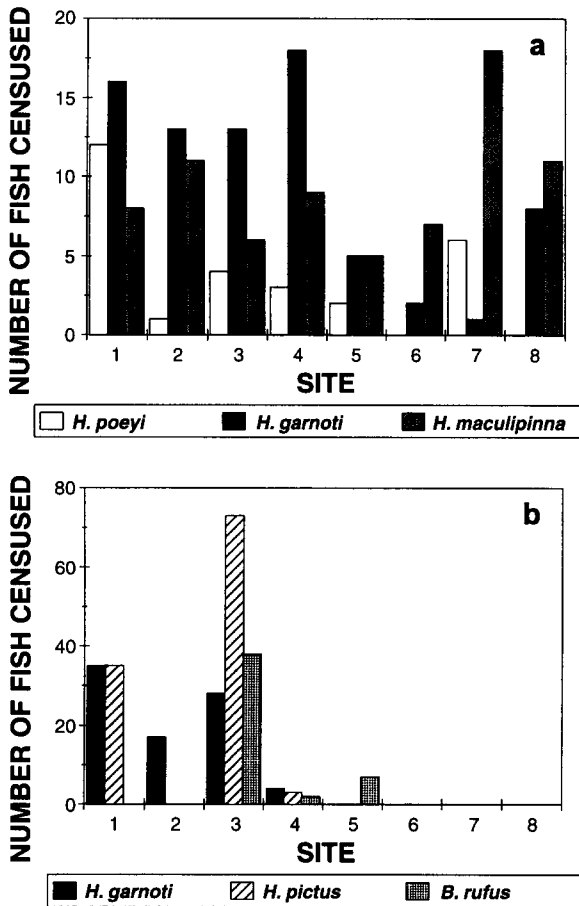


FIG. 7. Site-specific number of juveniles collected during three seasons of biweekly censuses. For qualitative purposes, the total number of juveniles censused was tabulated for the five rarer labrids. Solitary juveniles were censused in 5-m² quadrats (a), and schooling species were censused in 25-m² quadrats (b).

that temporal patterns of recruitment to Barbados reflect variability in the supply of late-stage larvae as measured by light traps (Sponaugle and Cowen 1996b). Thus, the timing of recruitment is not simply the result of differential survival of continuously settling larvae, and probably reflects either predictable processes acting on the pelagic stage, or cued behavior to enhance the growth and survival of new recruits (e.g., Kingsford 1980). For example, pulses of late-stage larvae may form as a result of differential growth and survival rates cued by variable patterns of food availability, mortality, or transport by currents. Similarly, settlement may be behaviorally timed to coincide with cycles of prey availability on the reef, periods of reduced predation on juveniles, or particular flow conditions.

At present, we have no data on food limitation of tropical larvae or new recruits, thus our discussion will focus on the potential effects of predation and transport on the timing of settlement. Recently, piscivorous reef fishes have been shown to reduce the survivorship of recently settled *H. pictus* and *Chromis cyanea* (Po-

macentridae), but not *T. bifasciatum* (Carr and Hixon 1995). Settling larvae may be even more vulnerable to predation; settlement at night, particularly during the darkest nights, has often been suggested to be the result of selection to reduce predation by reef organisms (e.g., Hobson and Chess 1978, Johannes 1978). However, although five of the labrids in our study settle during the new moon, three labrids settle during the third-quarter moon following the full moon, hardly the darkest (nor the brightest) time of the month. Thus, while predation may ultimately drive the timing of recruitment for some species, it is obviously not the sole selective pressure.

Monthly patterns in the supply of late-stage larvae may be due to variable transport during particular times of the tidal cycle. For example, transport of late-stage larvae to reefs may be enhanced when strong onshore flood tides occur at night. Alternatively, late-stage larvae may be able to swim onshore more successfully during other times of the tidal cycle (e.g., when currents are weakest). It is also possible that detection of a suitable settlement site may only occur during particular flow regimes (e.g., offshore flow over the reef).

Because labrids exhibit two distinct patterns in the timing of their recruitment (i.e., during very different stages of the tidal cycle), it is likely that these species vary with respect to their behaviors during approach and settlement. For example, swimming ability is probably linked to a certain degree with size prior to settlement. If labrids actively swim to reefs during settlement, smaller species such as *T. bifasciatum*, *H. maculipinna*, and to a lesser degree *B. rufus* may be relatively slower or weaker swimmers compared to the larger species, and may be more successful at swimming during periods of low current flow (i.e., minimum amplitude tides during the quarter moons). This selective pressure may be balanced by the pressure of visually oriented predators. Because predation is probably reduced on dark, moonless nights (i.e., new moons), recruitment may be most successful during the time of the third-quarter moon (minimum amplitude tides and nights becoming darker). Relatively larger species such as *H. bivittatus*, *H. radiatus*, *H. poeyi*, and *H. garnoti* may be more successful swimming against strong currents, and therefore pulses of recruitment can be more closely coupled to the darkest nights around the new moon. Furthermore, as Carr and Hixon (1995) demonstrate (but in contrast to what size at settlement would suggest), species such as *H. pictus* may be more susceptible to predation than species such as *T. bifasciatum*, thus settlement during the darkest nights may be more important for those species.

Finally, other differences in larval behavior may interact with transport processes and predation pressures to influence the timing of settlement. For example, the depth at which larvae approach reefs may vary among species (Leis et al. 1996), resulting in differences in tidally mediated transport, and possibly in larval vul-

TABLE 7. Habitat characteristics of eight sites along the west coast of Barbados. Site 1 is the northernmost site; site 8 is southernmost (see Fig. 1). Where significant differences occurred among sites, values for each site are presented, with solid underlines connecting sites with no significant differences. There were no significant differences among sites for mean percentage coral rock substrate, rubble substrate, sand substrate, or algal turf cover.

Mean percentage live coral substrate (PLC)								
Site	7	3	8	5	4	1	2	6
PLC	4.2	4.2	<u>10.0</u>	15.0	18.0	19.0	24.0	26.0
Mean diversity live coral (DLC)								
Site	7	3	8	5	2	4	6	1
DLC	2.5	4.2	4.2	<u>6.7</u>	8.4	13.4	13.4	15.0
Mean percentage algal turf and sand cover (ATS)								
Site	4	5	2	3	6	7	8	1
ATS	2.5	8.3	9.2	11.7	11.7	<u>31.7</u>	34.7	48.3
Mean percentage sand cover (SC)								
Site	6	5	8	1	7	2	4	3
SC	1.7	4.2	<u>7.5</u>	8.3	10.8	10.8	15.0	24.2
Mean depth (m)								
Site	7	2	8	5	4	6	3	1
Depth	2.97	<u>3.26</u>	3.42	<u>4.28</u>	<u>4.31</u>	4.49	4.95	5.26
Mean rugosity								
Site	1	8	7	3	4	6	2	5
Rugosity	<u>0.52</u>	0.64	0.66	<u>1.21</u>	1.34	<u>1.40</u>	1.57	1.80

nerability to predators. Differences in larval swimming ability, position in the water column, and susceptibility to predation may account for the two patterns of recruitment by the labrids in this study; however, it remains unclear how other early life history traits, such as the capacity to delay metamorphosis, influence recruitment. The capacity to extend larval life until a suitable settlement site is found may be particularly important for species with long early developmental (i.e., precompetent) periods (Jackson and Strathman 1981, Cowen 1991). In addition, delay of metamorphosis would probably be most advantageous where the successful settlement to the reef is less temporally predictable. For example, depending on local flow conditions, weaker swimmers may not always be able to enter the reef environment. Such a constraint may select for the ability to successfully delay settlement and metamorphosis. In light of this, it is interesting to note that a diversity of other reef fishes and crustaceans recruit to Barbados during the third-quarter moon and neap tides (Sponaugle and Cowen 1996a). In general, the relationship between a number of early life history traits and patterns of subsequent recruitment warrants further investigation (Cowen and Sponaugle, *in press*).

Proximate environmental cues

Proximate cues operating during settlement have typically been difficult to distinguish, largely because environmental cycles (i.e., lunar and tidal amplitude cycles) are often temporally coupled at a single geographic site. Because the lunar cycle is the same everywhere, but the tidal amplitude cycle can shift among

geographical locations, intraspecific comparisons of recruitment patterns among distant locations may potentially isolate the relevant proximate cues operating during settlement. Due to the "open" nature of coral reef fish populations and the dynamics of large-scale current flow in the Caribbean, most fish populations are not likely to be genetically isolated (Mitton et al. 1989, Lacson 1992, Shulman and Bermingham 1995). Therefore, larvae at all locations should use the same cues or suite of cues to time settlement. Geographic differences in the timing of recruitment should only result from offset cycles of these cues. However, to date, few such comparisons have been made.

Among labrids, patterns of recruitment that are synchronized to the third-quarter moon and minimum amplitude tides have not previously been reported. Synchronous recruitment cued to different phases of the lunar cycle has been reported for a number of other species from diverse locations. Lunar cycles of recruitment are exhibited by several pomacentrids recruiting to Pacific reefs (Kingsford 1980, Ochi 1985) as well to as reefs off St. Thomas, U.S. Virgin Islands (Booth and Beretta 1994), and Panama (Robertson et al. 1988, Robertson 1992). In fact, many species recruiting to Caribbean Panama have lunar-cyclic recruitment patterns, with pulses occurring around the new moon (in addition to a labrid and several pomacentrids, several acanthurids, and a chaetodontid; Robertson 1992). Synchrony to the third-quarter moon is less frequently encountered, and outside of Barbados, these patterns are usually semilunar (a haemulid at St. Croix, McFarland et al. 1985; and a pomacentrid re-

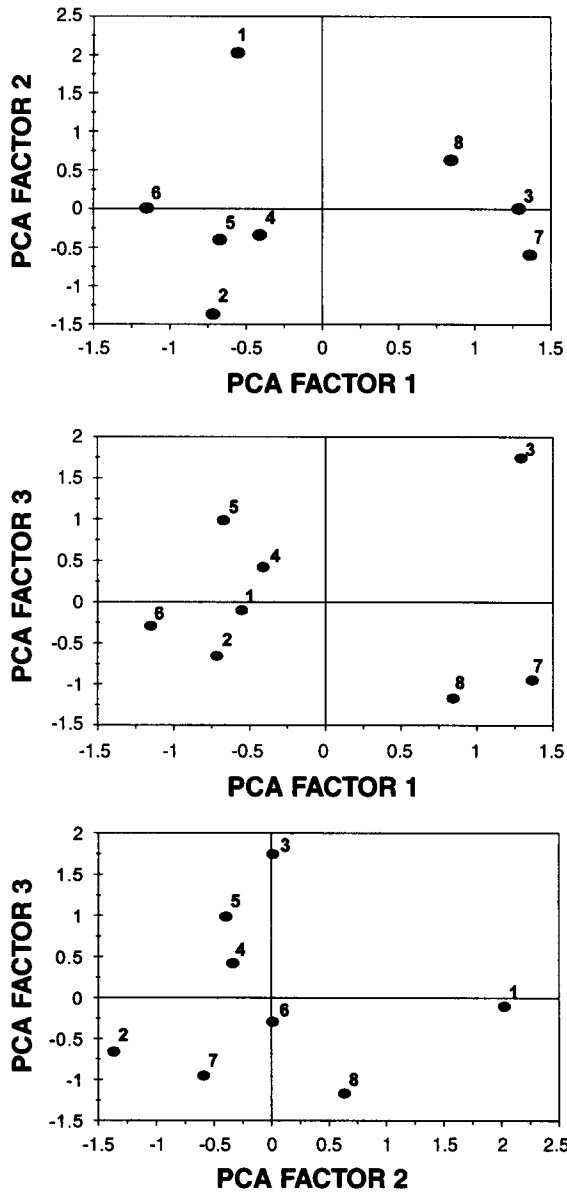


FIG. 8. Principal component analysis (PCA) factors derived from habitat variables measured at each of the eight census sites (indicated by numbers). See Table 8 for factor loadings.

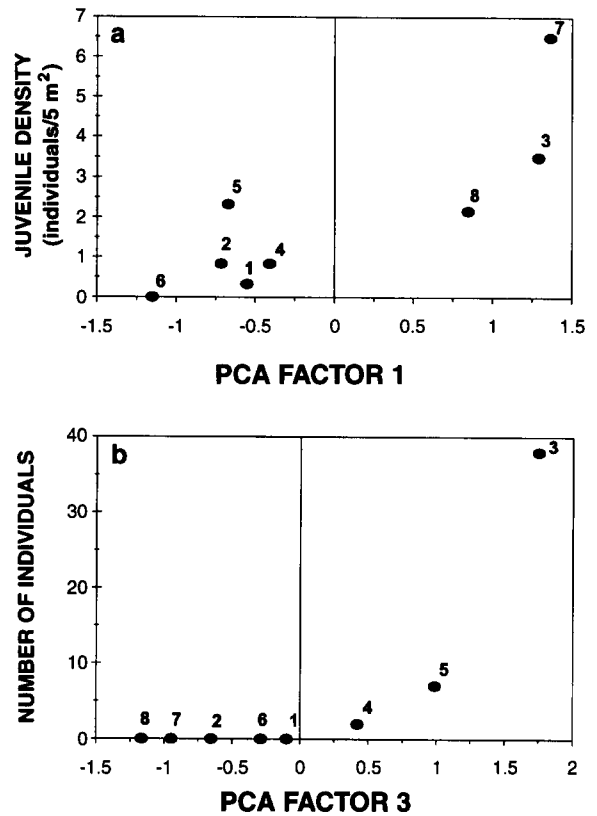


FIG. 9. (a) Densities of *Halichoeres bivittatus* juveniles after a major recruitment pulse in 1990, and (b) total number of *Bodianus rufus* juveniles collected over three seasons, plotted against principal components analysis (PCA) factors 1 and 3, respectively.

cruiting to Panama, Robertson 1992). Recruitment synchrony to the first-quarter moon has been reported for a holocentrid recruiting to Panama (Robertson 1992), and two pomacentrids recruiting to St. Thomas around the time of the full moon (Booth and Beretta 1994). Interestingly, Thorrold et al. (1994a) report that labrid larvae appear in Bahamian channel nets with semilunar frequency, but it is unclear how this periodicity relates to recruitment patterns.

In an attempt to identify the most important proximate cues operating during settlement, we compared temporal patterns of *T. bifasciatum* recruitment to Bar-

TABLE 8. Principal components factor loadings for habitat variables.

Variable	Factor 1	Factor 2	Factor 3
Mean percentage live coral	-0.961	0.007	-0.192
Mean diversity live coral	-0.838	0.348	0.071
Mean percentage rubble	0.686	-0.531	-0.387
Mean percentage algal turf-sand	0.684	0.663	-0.113
Mean percentage sand cover	0.629	-0.128	0.396
Mean rugosity	-0.531	-0.655	0.484
Mean percentage sand substrate	-0.118	-0.687	0.329
Mean percentage coral rock	0.372	0.655	0.486
Mean depth	-0.297	0.628	0.684
Mean percentage algal turf	0.429	-0.459	0.669

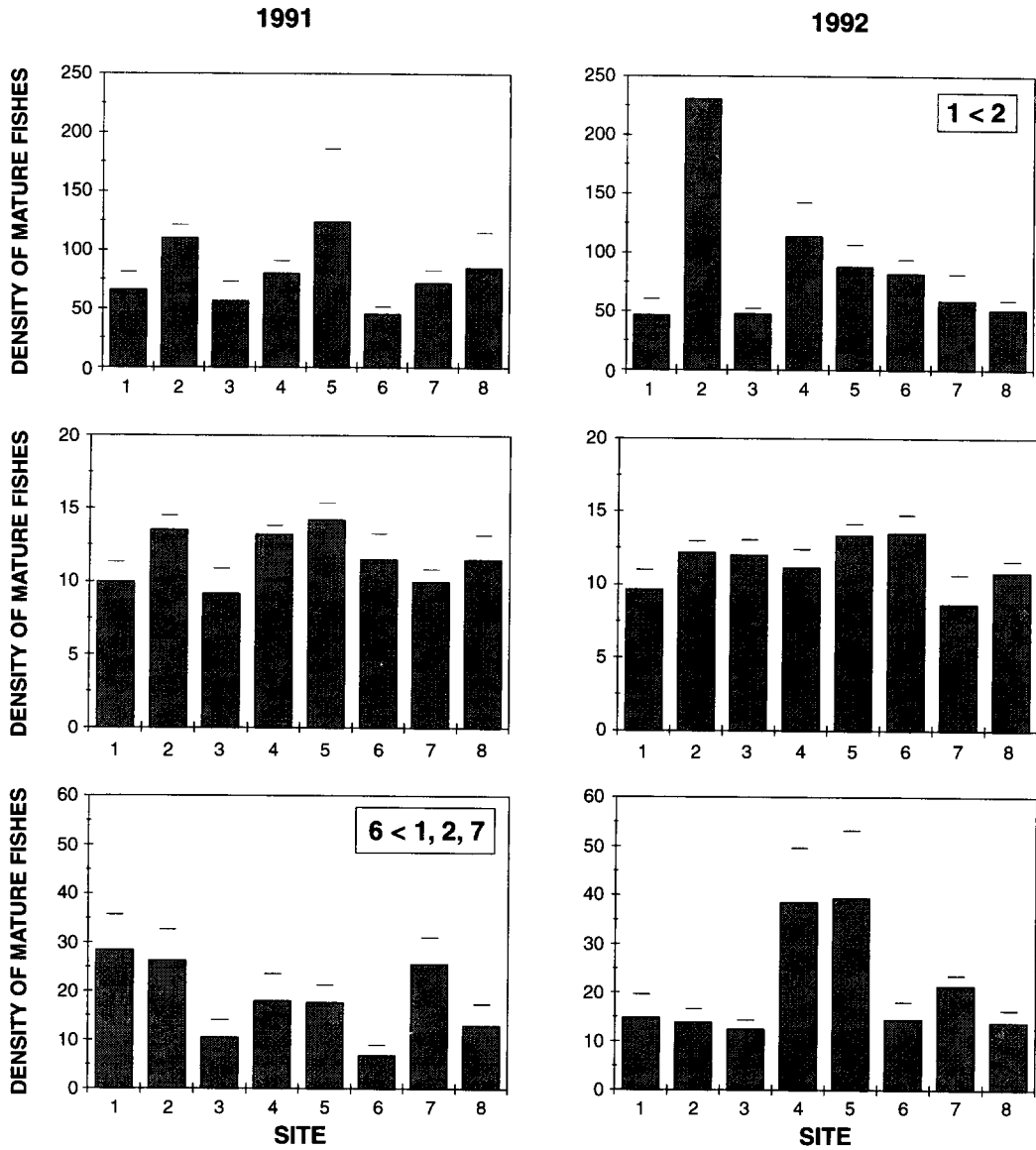


FIG. 10. Mean number and diversity of mature fishes (± 1 SE) and mean number of mature labrids (± 1 SE) censused at each of eight sites at Barbados during two sampling seasons (left column, 1991; right column, 1992). Significant differences among sites are indicated in the inset.

barbados with previously published records from San Blas, Panama (Victor 1986a). Although both locations experience the same lunar phase, there are important geographical differences in the expression of the tidal amplitude cycle. Tides in both locations are mixed, but the semi-diurnal signal is much greater at Barbados relative to the more diurnal signal at Panama. More importantly, the relationship between the synodic and the declination cycle differs between the two locations: tides at Barbados are less influenced by the declination cycle, thus the tidal amplitude cycle (29.4 d) is in phase with the lunar cycle during much of the year, including the study period. The lunar declination cycle has greater influence in Panama, where the tidal

amplitude cycle is 27.3 d (see Barnwell 1976 for further discussion). As a result, the tidal amplitude cycle in Panama is only periodically in phase with the lunar cycle (Fig. 11).

To determine whether *T. bifasciatum* recruitment is synchronized to the lunar or tidal amplitude cycle, we first compressed each data set into a single lunar cycle (as before) and tested with Rayleigh tests (Batschelet 1981, Zar 1984); in a separate analysis, we repeated the tests on each data set reduced into a single tidal amplitude cycle (day 1 being the first day of maximum amplitude tides). Because sampling in Panama was conducted over the entire year, we further subdivided these data into months where maximum amplitude tides

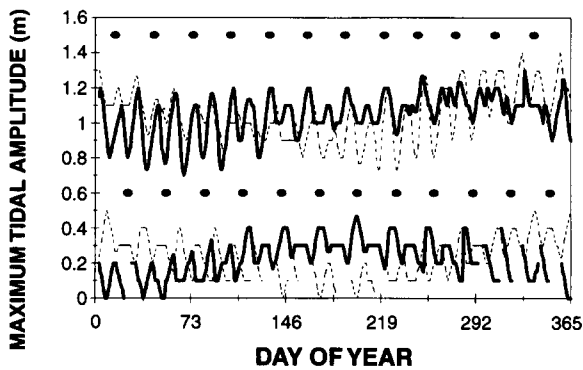


FIG. 11. Annual tidal amplitude record for Barbados (upper curves) and Panama (lower curves), obtained from the British Admiralty and from U.S. Department of Commerce (NOAA) tidal charts, respectively. Lines indicate the 3-d moving average of maximum amplitude tides occurring at night (solid lines) and during the day (dashed lines). New moons are indicated by solid circles.

occurred at night, months when these tides occurred during the day, and transition months when they occurred during both daylight and nighttime (e.g., March, April, September, and October; Fig. 11).

The timing of *T. bifasciatum* recruitment differs between Barbados and Panama. Reanalysis of Victor's (1986a) recruitment data over a lunar cycle indicated that in general, *T. bifasciatum* recruited to Panama in

pulses occurring ≈ 4 –5 d after the new moon (Table 9, Fig. 12). Based on the analysis of recruitment data over a tidal amplitude cycle, the timing of *T. bifasciatum* recruitment also varied between the two locations. Because the tidal amplitude cycle in Barbados was in phase with the lunar cycle during our study, recruitment of *T. bifasciatum* was similarly synchronized to the tidal amplitude cycle, occurring during minimum amplitude tides 21–22 d after the first day of maximum amplitude tides (Table 9, Fig. 12). In Panama, however, most *T. bifasciatum* recruitment occurred 11–12 d after maximum amplitude tides. Overall recruitment of *T. bifasciatum* to Panama was highly correlated with both the tidal amplitude and lunar cycle, although in general, synchronization to the tidal amplitude cycle may be tighter than to the lunar cycle.

Because the moon is in the same phase at both geographical locations yet recruitment patterns differ, tides must play a role either solely, or more likely, in concert with the lunar cycle. A number of crabs possess species-specific hierarchies of rhythms that enable the tracking of several environmental cycles at the time of larval release (Morgan and Christy 1994, Morgan 1995). Phase shifts of these cycles at different locations result in variable temporal patterns of reproduction (Morgan and Christy 1994). Similar responses by reef fishes to the lunar and tidal amplitude cycles may create

TABLE 9. Rayleigh test statistics for tidal amplitude and lunar periodicity in recruitment of *Thalassoma bifasciatum* to Barbados (1990–1992) and Caribbean Panama (1981–1982). See Table 5 for the test statistics for lunar periodicity of recruitment to Barbados.

Time period	<i>n</i>	<i>Z</i> †	Settlement day (tidal or lunar)‡	<i>s</i>
Barbados—tidal				
1990	218	23.0***	25.7	5.4
1991	111	31.0***	21.3	4.6
1992	482	48.7***	20.2	5.5
All years	811	77.2***	21.7	5.5
Panama—tidal§				
Night maximum	102	11.2***	12.5	5.0
Day maximum	257	13.7***	5.3	5.4
Transition	344	88.7***	12.5	4.3
Night and transition	446	97.4***	12.5	4.5
Day and transition	601	53.3***	11.1	5.2
Total	703	63.6***	11.3	5.1
Panama—lunar§				
Night maximum	69	2.1NS		
Day maximum	310	6.1**	13.4	6.2
Transition	307	92.6***	3.5	4.5
Night and transition	376	86.9***	3.5	4.8
Day and transition	617	37.1***	4.7	5.8
Total	686	38.8***	4.6	5.8

† *Z* = Rayleigh test statistic; ** $P < 0.01$, *** $P < 0.001$, NS, $P > 0.05$.

‡ Settlement day was calculated from mean vector angle; *s* = mean angular deviation (days; Batschelet 1981, Zar 1984); day 1 of tidal cycle = first day of maximum amplitude tide; day 1 of lunar cycle = new moon.

§ Data for *T. bifasciatum* recruiting to Panama were reanalyzed from Victor (1986a), and split into months where maximum amplitude tides occurred at night, during the day, or both (transition months).

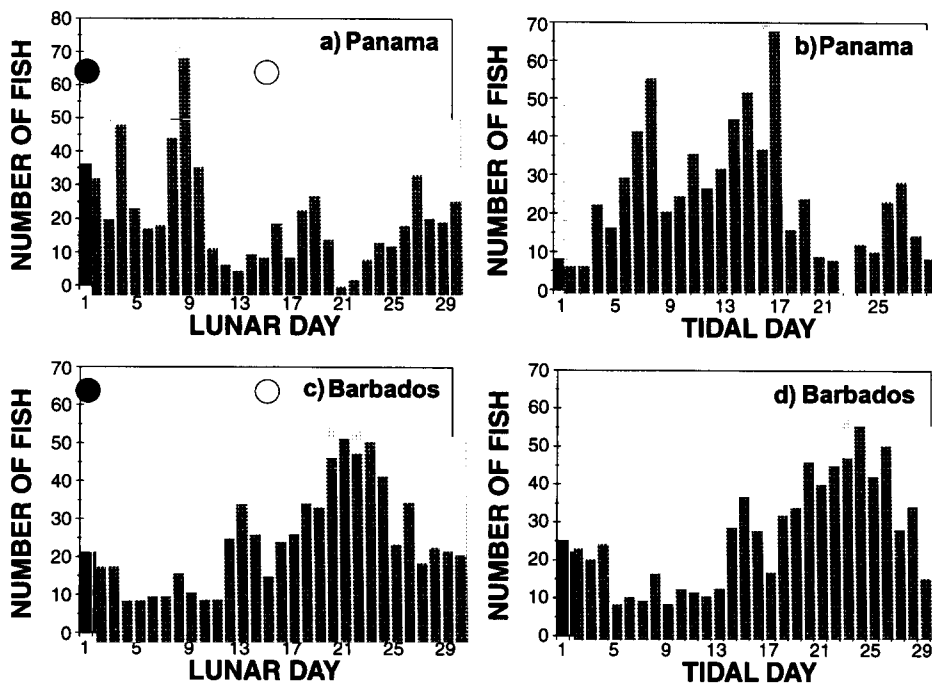


FIG. 12. Distribution of recruitment over (a) the lunar and (b) the tidal cycles for *Thalassoma bifasciatum* at Panama (from reanalysis of data from Victor 1986a), and over (c) the lunar and (d) the tidal cycle for *T. bifasciatum* at Barbados. Lunar phase is indicated by solid (new moon) and open (full moon) circles. Day 1 of each tidal cycle corresponds to the first day of maximum amplitude tides.

complex variation in recruitment patterns at distant geographical locations.

Seasonal shifts in the relation of the tidal amplitude cycle to the lunar cycle may contribute to seasonal variation in recruitment patterns at Panama. Most recruitment of *T. bifasciatum* occurred during months when maximum amplitude tides occurred during night and day (transition months) and months when maximum tidal amplitudes occurred only during the day (Table 9). The timing of recruitment events during the months with daytime maximum tidal amplitudes differed from events during other times of the year: pulses were less distinct and occurred just prior to the first minimum amplitude tide, often near the full moon. In fact, Robertson (1992) suggests that recruitment of *T. bifasciatum* is semilunar cyclic for up to one-third of the months during which significant recruitment occurs. This pattern alone points to the importance of tides in the timing of recruitment pulses.

Although data from Barbados indicate a distinct lunar pattern of recruitment for *T. bifasciatum*, it is possible that these patterns shift seasonally in Barbados as well. Such a shift may have led Hunt von Herbing and Hunte (1991) to conclude that recruitment of *T. bifasciatum* to Barbados is not lunar-cyclic, although it is also possible that the lack of a clear signal may have been due to their sampling of much larger (SL > 30 mm) fishes. Even if patterns of recruitment to Barbados shift seasonally, recruitment patterns in Panama were most distinct during the transition months, and it

is during these months that recruitment patterns of *T. bifasciatum* are in clear contrast to those in Barbados. Nonetheless, Robertson's (1992) point that long time-series (at least year-round) measurements of recruitment are necessary to obtain an accurate perspective on synchrony is valid. In fact, by comparing intra-annual shifts in the timing of recruitment to seasonal shifts in cues such as the tides, further insight may be gained into identifying the proximate cues involved.

In addition to the relationship between the lunar and tidal amplitude cycles, the influence of the tidal cycle on the nearshore environment may differ between Barbados and Panama. The tidal range is greater in Barbados (1.2 m) than in Panama (0.6 m) and may result in stronger tidal flows. Interaction of these flows with the prevailing currents may translate into rather strong alongshore (north-south) currents. Perhaps due to this stronger tidal influence, recruitment during minimum amplitude tides is necessary for fishes that are weaker swimmers. In Panama, lower amplitude tides may have less overall effect on nearshore flow, and recruitment during maximum amplitude tides may be more feasible. However, the influence of tidal amplitude cycle may shift seasonally as well. Strong trade winds during the dry season (mid-December through mid-April) generate heavy wave action and northward-flowing nearshore currents, in contrast to the wet season, where winds and currents are typically lighter (Glynn 1972, Robertson 1990). Such a seasonal change in flow conditions may contribute to the shift in recruitment timing

between the months with daytime maximum amplitude tides (during most of the dry season) and other months. Seasonal shifts in nearshore currents and in the relative phasing of the tidal amplitude cycle may also influence the length and timing of the recruitment season, although these seasons are also likely to be defined by seasonal reproduction and the interaction of larval, juvenile, and adult biology with environmental cycles (Robertson 1991).

Variability in the synchrony of other behaviors suggests that tides are important in other aspects of reef fish biology. In particular, the timing of spawning shifts among sites where the relative influence of tides varies. Several labrids spawn daily during ebb tides in Florida (Thresher 1979) and in Barbados (Hunt von Herbing and Hunte 1991), but not in Panama (Robertson 1981). Similarly, at one site at Enewetak Atoll where tidal flows are minimal, several labroids spawn at a fixed time each day, while at a nearby site where tidal flows are stronger, the timing of reproduction shifts daily while tracking the tidal cycle (Colin and Bell 1991). Our data suggest that tides can influence the timing of recruitment for reef fishes, resulting in geographical variation in recruitment synchrony among locations where the relative strength or timing of tidal currents varies.

Despite the fact that most benthic marine populations are open and genetically mixed, behavioral and other life history traits may vary significantly among populations from widely separated geographic locations. This variation is inherently introduced by local differences in the expression of proximate environmental cues. Careful examination of these traits in the context of variable environmental cues is clearly necessary both in the identification of critical proximate cues as well as in understanding ultimate constraints to adaptation. Further comparisons of behavioral life histories among distant locations may reveal the mechanisms by which open populations adapt to local environmental conditions. While behavioral plasticity is one solution, adaptation to common temporally persistent physical or environmental processes (such as the tidal amplitude cycle) may be more likely. Less predictable, episodic features may lend a certain degree of noise to the system, but are unlikely to underlie behavioral traits.

Spatial pattern of labrid recruitment to Barbados

Recruitment of labrids to Barbados occurred on an island-wide scale: pulses of new recruits arrived concurrently at all sites along the west coast of the island. The overall pattern of lower juvenile densities at a central site along the west coast does not appear to be determined by large-scale habitat selection or by the presence of resident fishes. Estimates of early juvenile mortality for the most abundant labrids indirectly suggest that spatial patterns of recruitment were probably not greatly influenced by differential mortality rates of new recruits. For the most common labrids, juvenile

densities 1 wk after recruitment were lower than the estimated carrying capacity for mature *T. bifasciatum* on several Barbados reefs (0.8–1.2 fishes/m²; Hunt von Herbing and Hunte 1991). In addition, there was no correlation between daily mortality rates and initial juvenile densities, unlike those reported for older *T. bifasciatum* in Barbados (0–60% monthly mortality, positively correlated with fish density; Hunt von Herbing and Hunte 1991). While reported mortality rates are typically highest during the first few days following settlement and taper off with time (Victor 1986a, Sale and Ferrell 1988), it is possible that juvenile *T. bifasciatum* density in Barbados only impacts survivorship at later ages.

Because early juvenile mortality is apparently not density-dependent, and overall labrid recruitment appears to be unrelated to habitat features and densities of mature fishes, spatial patterns of recruitment probably reflect variation in the supply of larvae. Lower overall densities of labrids at the central site (site 6) are likely the result of differential larval supply due to variable nearshore tidal currents. During a concurrent study on nearshore currents and patterns of larval supply at Barbados, we demonstrated that the east–west component of nightly transport by tidal currents is directed offshore at the central site, in contrast to generally onshore transport at the northern and southern ends of the west coast (Sponaugle and Cowen 1996a). Light traps deployed during this time period collected a lower abundance and diversity of larval reef fishes than traps from a northern and southern site (Sponaugle and Cowen 1996a). Thus, offshore flow near the central region of the west coast may result in a lower rate of larval supply to these reefs.

Coupling of behavioral and physical processes can occur on a variety of temporal and spatial scales to influence patterns of larval supply and recruitment. The intersection of these mechanisms must be understood in order to fully define population boundaries, including the identification of sources and sinks of larvae. Due to consistent flow patterns, certain areas may always receive lower numbers of larvae. Additionally, these same flow conditions may result in spatial variation in the reproductive contribution of adults. Behavioral responses to these physical features lend significant complexity to the system and call into question the degree to which particular populations are truly open. Successful tracking of fish or invertebrate larvae in the field has proved quite difficult (e.g., Stoner 1990; G. P. Jones and M. J. Milicich, unpublished data), but remains essential to fully understanding the population dynamics of most benthic marine organisms.

Conclusions

The results of this study demonstrate that both physical and biological processes are important to the population replenishment of coral reef fishes. Spatial variation in physical phenomena such as tidal currents can

lead to consistent spatial differences in the supply of larvae and subsequent distribution of juveniles. The tidal amplitude cycle also appears to be more important than previously thought in the specific timing of recruitment. Temporal patterns of recruitment are probably the result of a balance between tidal amplitude and lunar cues at the time of settlement. However, the correlation between particular early life history traits and temporal patterns of recruitment indicates that biology is also clearly involved. Physiological and behavioral differences during larval life differ among eight closely related fishes, leading to distinct temporal patterns of recruitment.

The transition between a pelagic and benthic existence involves a radical change in both physical environment and the physiological traits necessary for survival in each environment (Thorson 1950). Because most marine organisms have complex life histories, stage-specific adaptation to environmental constraints is probably a common phenomenon. Due to environmental complexity, the range of solutions to these constraints probably varies enormously between the pelagic and benthic realms. A potentially intricate shifting of life history strategies in response to all of these constraints must occur rapidly following settlement. Given the importance of this transition, it is surprising how very little we currently know about any of the processes influencing the stages on either side of the settlement event. Although workers in temperate marine systems have traditionally focused great attention on early life history stages in attempt to better understand stock-recruitment issues (e.g., Sissenwine 1984, Rothchild 1986), until recently, very few studies have examined the relationship between events occurring during larval life and subsequent patterns of recruitment in tropical reef fishes (reviewed in Cowen and Sponaugle, *in press*). In the present study, we attempted to bridge this gap and to examine whether events occurring during one phase of the life cycle are related to patterns evident in a subsequent phase. Our results demonstrate that aspects of larval life, as reflected in several early life history traits, are related to recruitment dynamics. We suggest that further work into the specific linkage between the pelagic larval stage and the juvenile phase has the potential to reveal the processes operating in each environment to control population dynamics. Furthermore, comparative studies among and within diverse groups of organisms that experience a similar phase transition between environments may help isolate general physical processes important to all marine organisms with complex life cycles.

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