

## SETTLEMENT VS. ENVIRONMENTAL DYNAMICS IN A PELAGIC-SPAWNING REEF FISH AT CARIBBEAN PANAMA

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**Abstract.** How are the dynamics of the settlement of pelagic larvae of marine shore organisms into benthic habitats affected by larval production and mortality dynamics, and by environmental (wind and tidal) control of settler delivery? We examined the dynamics of reproduction of the pelagic-spawning fish *Thalassoma bifasciatum* from that perspective at San Blas, Caribbean Panama.

During April–June 1993, ~75% of females spawned each day, with mean output per female per day at about one-third the potential maximum. Output peaked several days before the new and full moon, when tides were high during the afternoon spawning period. Daily fluctuations in output were weakly correlated with light (+), swell (–), and onshore wind (–) on preceding days.

Settler production (determined from otolith back calculations of settlers' fertilization dates) peaked during the wet season (May–November), when winds were light and variable, spawning-period tidal heights were moderate to low, and tidal flows were off-reef at night. These conditions correspond to when most settlement occurs. Settler production was minimal during the dry season (January–March), when onshore trade winds were strong and consistent, and tidal conditions were the reverse of those in the wet season.

Settlement usually occurred in one variably timed pulse per lunar cycle, around the new moon. Variation in monthly settlement strength over 11 yr (1986–1996) was unrelated to onshore wind stress during either settler arrival or settler production. The daily dynamics of settlement were unrelated to the concurrent dynamics of wind or tides, or wind dynamics up to a week before settlement.

Settler production was much less continuous than spawning. Wet season settler-production dynamics were unrelated to tidal dynamics, but (weakly) negatively related to onshore wind stress. Although the dynamics of settler production and settlement were similar, bouts of settler production were about twice as long as bouts of settlement. The average lunar patterns of settler production and observed spawning were similar (weakly bimodal). Settlers produced during different lunar phases differed in the length and variability of their pelagic larval durations (PLDs). Fish with different PLDs all tended to settle around the new moon.

Weakly semilunar spawning may reflect effects of weak tidal influences on egg survivorship, or of environmental constraints on adults' spawning capacity that also limit spawning to well below the potential maximum. Dry season trade winds may produce the seasonal low of settlement by depressing spawning or forcing the onshore transport of eggs and larvae. If settlement is transport-dependent, weak variable winds may have little effect on currents during the wet season, or local geography may limit such effects; tidal dynamics may not affect wet-season settlement dynamics because small (<0.6 m) tides produce weak flows. Alternatively, settlement may not be dependent on transport mechanisms.

Short-term settlement dynamics result from both the dynamics of larval survival (as most larvae have near-mean PLDs) and larvae delaying or advancing settlement to settle around the new moon. Larvae spawned at different lunar phases have different patterns of variation in their PLDs but achieve similar relative settlement success. Larvae with extended PLDs may not suffer low settlement success because the inevitable age-dependent decline in survival has smaller effects on relative settlement success than does large monthly variation in the survivorship of fish spawned during different lunar phases.

**Key words:** Caribbean; environmental dynamics; labrid fish; lunar effects; pelagic spawning; seasonality; settlement dynamics; *Thalassoma*; tidal effects; wind effects.

## INTRODUCTION

In benthic marine organisms whose life cycles include a pelagic larval phase, the intensity of settlement of juveniles into the benthic habitat at the end of their larval lives typically fluctuates considerably across a variety of time scales; daily, lunar phase, monthly, seasonally, and yearly (e.g., for reef and other fishes: Kami and Ikehara 1976, Williams 1983, Eckert 1984, Sale et al. 1984, Doherty and Williams 1988, Fogarty et al. 1991, Fowler et al. 1992, Robertson and Kaufmann 1998). Processes occurring in the pelagic environment that not only affect the growth, survival, and movements of larvae until they become competent to settle, but also influence settlement activity itself all affect the dynamics of larval settlement. Lunar periodism in the settlement of reef fishes, among others, can be partly tidally forced in some situations (e.g., Sponaugle and Cowen 1996), particularly in estuaries (e.g., Boehlert and Mundy 1988, Neira and Potter 1992) or where local topography emphasizes tidal effects on water flow (e.g., Shenker et al. 1993, Thorrold et al. 1993). However, such periodism in settlement also develops independently of tidal regimes (Dufour and Galzin 1993). Local wind regimes can strongly influence settlement dynamics of shore organisms through wind forcing of surface currents that deliver larvae to settlement habitats (Parrish et al. 1981, Hawkins and Hartnoll 1982, Roughgarden et al. 1988, Farrell et al. 1991, Shenker et al. 1993, Thorrold et al. 1993, Herrnkind and Butler 1994, Hutchins and Pearce 1994, Milicich 1994, Caselle and Warner 1996, Sponaugle and Cowen 1996, Kingsford and Finn 1997), as well as through wind effects on larval feeding and development, and hence survivorship (e.g., Lasker 1981, MacKenzie and Leggett 1991, Roy et al. 1992, Leggett and Deblois 1994). Settlement-stage larvae of many shore and reef fishes are large (Leis 1991) and can swim strongly and persistently (Webb and Weihs 1986, Stobutzki and Bellwood 1994). Those capabilities should give such settlers greater independence from the influence of transport mechanisms on settlement than is possible for many small invertebrate larvae, and allow different fish taxa to exert varying degrees of control over where and when they settle (Sweatman 1988, Carr 1991, Booth 1992, Stobutzki and Bellwood 1994). Further, while some reef fishes produce larvae with short, relatively invariable pelagic larval durations (PLDs) (e.g., Thresher and Brothers 1985, Robertson et al. 1988, Wellington and Victor 1989), others have a capacity to extend their pelagic lives after they reach competency and delay settlement (Cowen 1985, Victor 1986c, Sponaugle and Cowen 1994). That capacity could both influence where larvae finally settle (Victor 1984, Cowen 1991) and the timing of settlement (Sponaugle and Cowen 1994). Finally, the dynamics of the production of larvae can also be expected to influence settlement dynamics (e.g., Robertson et al. 1988, Meekan et al.

1993). Thus a large range of factors likely have varying influences on the settlement dynamics of any single species of shore fish, both over time in the same location and at the same time at different locations.

Tropical reef fishes include pelagic spawners, which produce buoyant planktonic eggs, and benthic spawners, whose pelagic larvae hatch from demersal eggs. Most of the information available on the linkage between the dynamics of larval production and settlement among such fishes comes from benthic spawning damselfishes (Pomacentridae: Robertson et al. 1988, 1990, Robertson 1990, Doherty 1991, Meekan et al. 1993). Relationships between the dynamics of spawning and settlement have been examined in only one pelagic-spawning tropical reef fish, the Caribbean labrid *Thalassoma bifasciatum*. Studies of that species by Victor (1986a) in the southwest Caribbean, and Hunt von Herbing and Hunte (1991) in the eastern Caribbean considered links between lunar patterns of spawning and settlement of that species, while Hunt von Herbing and Hunte also examined the relationship between the seasonalities of spawning and settlement. Here we extend on that research by examining how the short-term dynamics of settlement by *T. bifasciatum* are related to (1) the dynamics of spawning activity, (2) the dynamics of the output of fish that survive to settle (settlement production), (3) the capacity of larvae to advance or delay metamorphosis and choose when they settle, (4) variation in settlement success and the length of larval life among fish spawned during different lunar phases, and (5) wind and tidal conditions at both the beginning and end of the larval life.

## METHODS

*Study area*

Field work was conducted on reefs adjacent to San Blas Point, on the eastern Caribbean coast of Panama (Fig. 1); the same site as used by Victor (1982, 1983, 1984, 1986a, b) in his study of *T. bifasciatum*. Reef names used here follow Robertson (1987).

*Environmental conditions in the study area*

San Blas experiences two major seasons, a dry season from about mid-December through about mid-April, and a wet season over the rest of the year. Rainfall increases over the course of the wet season, to a peak in October–November (D’Croz and Robertson 1997). The prevailing winds are onshore, northeast trade winds, which blow most consistently and strongly during the dry season (Fig. 1). Winds are lighter and more variable in the wet season (Fig. 1). Average monthly sea surface temperatures at San Blas range from 26.5°C (February–March) to 28.5°C (May–October) (Smithsonian Tropical Research Institute Marine Environmental Science Program website;<sup>5</sup> henceforth STRI and MESP). The maximum tidal range in San

<sup>5</sup> URL = <http://striweb.si.edu/stripage/mesp.html>

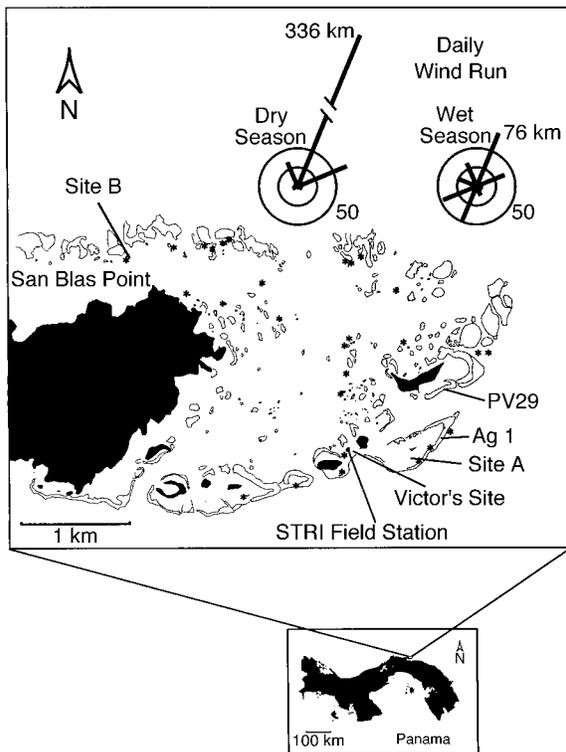


FIG. 1. A map of the study area showing sampling sites and indicating seasonal wind patterns and their orientation to the coastline. Wind roses show mean daily wind run from each octant. Asterisks indicate permanent plots used for monitoring monthly recruitment of *T. bifasciatum*. Sites A and B indicate locations of reefs used for daily collections of settlers. Spawning was monitored in 1993 on reefs Ag1 and PV29.

Blas is 0.6 m (NOAA 1981–1993). The tidal regime follows a complex pattern of seasonal change, with varying mixtures of diurnal and semidiurnal tides, and change in tidal heights, amplitudes, and net on/off-reef tidal flows at different times of the day over the course of the year (NOAA 1981–1993; and see *Results* [Figs. 5 and 8]).

The prevailing major nearshore current in the San Blas area, which is part of a large gyre in the southwest Caribbean (Roberts 1997), flows eastward along the coast of Panama, at an angle of  $\sim 135^\circ$  to the prevailing wind (NOAA 1982). The reef system of San Blas Point is relatively porous to current inflow/outflow, as there are six major channels and numerous small ones scattered around the periphery of that system (Fig. 1). Currents within that reef system are complex and changeable, with reversing flows running in different directions at different locations among those reefs (D. R. Robertson, *personal observations* over 20 or more years). Inflow of oceanic water into the lagoon of that reef system occurs both from the north (ocean) side, and the south. The latter inflow results in part from oceanic flow into the Gulf of San Blas (to the south of San Blas Point [Fig. 1]) through a large (2 km wide,

50 m deep) channel that runs along the eastern edge of that reef system.

Coastal waters in and immediately around the study area are oligotrophic (D’Croz and Robertson 1997). Although terrestrial runoff increases silicate concentrations over the course of the wet season, concentrations of biologically important nutrients (N and P) show no clear pattern of seasonal variation at that site. Abundances of phytoplankton and zooplankton are low throughout the year and the only seasonality they exhibit consists of occasional, brief, small increases in phytoplankton and zooplankton abundance during the wet season. There is no wind-driven seasonal upwelling on the San Blas coast (D’Croz and Robertson 1997).

#### *Environmental data collection*

Tidal data were extracted from digital tide-prediction tables (NOAA 1981–1993) for Mandinga Harbor, <15 km from the study area. Those tables are quite accurate: STRI maintained a continuously recording tide gauge at its field station in our study area from 1990 onwards (source = MESP). Correlations between predicted and observed tidal heights were very high for two randomly chosen periods; at midday every day during 1993, and at every hour during July 1993: Pearson  $r = 0.95$  and  $0.96$ , respectively.

Data on wind speed and direction, sunlight ( $W \cdot m^{-2} \cdot d^{-1}$ ), and water level were recorded continuously and electronically by the Smithsonian Tropical Research Institute’s Marine Environmental Sciences Program (MESP) at the STRI field station on San Blas Point (Fig. 1), from 1992 onwards (source = MESP). Wind data were collected continuously between 1981–1996 at Galeta Island, 100 km west of San Blas Point on the Caribbean coast of Panama (source = MESP). Onshore wind activity at San Blas Point was highly correlated with that at Galeta during 1992–1996: km onshore wind/day (i.e., sum of any of the day’s 24 hourly average speed readings that were from the onshore direction), Pearson  $r = 0.92$  for all seasons,  $0.86$  for the wet season, and  $0.89$  for the dry season; km onshore wind/lunar quarter,  $r = 0.96$  for all seasons,  $0.93$  for the wet season, and  $0.83$  for the dry season. Hence we used Galeta wind data as a proxy for wind at San Blas during 1981–1992.

#### *Natural history of *Thalassoma bifasciatum* in the study area*

The bluehead wrasse, *Thalassoma bifasciatum*, is abundant on coral reefs throughout the Caribbean and surrounding areas. In San Blas it reproduces year round (Warner and Robertson 1978), although it is not known whether there is seasonal variation in either population or per capita output. Although spawning can be observed on any day, Victor’s (1986a) assertion that it is continuous and not lunar cyclic is based on daily monitoring of spawning (by R. R. Warner, *personal communication*) for several short periods (each <2 wk) in

different months and different wet seasons, that, in aggregate, did not sample the entire lunar cycle. Thus a clear understanding of the lunar and tidal patterning of spawning by that species at San Blas is lacking.

Spawning occurs daily during a ~2-h period between 1100–1600, with the timing of peak activity varying from day to day (Warner et al. 1975). To spawn, *T. bifasciatum* migrate to the outer edges of their home reefs, often at their down-current ends, and move up and away from the reef substratum to release their gametes into the water column (Warner et al. 1975).

Using analyses of daily growth increments in the sagittal otoliths of recently settled *T. bifasciatum* that he collected at San Blas, Victor (1984) estimated the average Pelagic Larval Duration (PLD) to be 49 d. He also found (Victor 1986a) that settlement intensity fluctuates considerably from month to month, tends to occur in short pulses, and, overall, is concentrated around the new moon.

#### Biological data collection

*Spawning dynamics.*—To estimate the lunar pattern of spawning output by the population of *T. bifasciatum* in our study area we monitored levels of egg production daily for 90 d, 2 April to 30 June 1993. We did this on two adjacent large patch reefs, Porvenir 29 and Aguadargana 1 (PV29 and Ag1 in Fig. 1). Due to their proximity and position at the southeast edge of the San Blas Point reef complex, these reefs experience similar tidal, current, and swell conditions. A 30-m deep channel with a sand bottom isolates the populations of *T. bifasciatum* on those two reefs from each other. We estimated that, while we were monitoring spawning, each of those reefs supported >10 000 individuals of that species.

Because the pelagic eggs of *T. bifasciatum* are small (~0.5-mm diameter) and transparent, and the clutch disperses immediately after spawning, clutch sizes cannot be estimated by direct observation. Because clutch size varies considerably within as well as among different size classes of females (see *Results: Short-term spawning and environmental dynamics*), a combination of the percentage of females observed spawning and their sizes may not provide a reliable indication of a day's egg production by a local population. Consequently we collected random samples of females and used data on the percentage of females spawning and their clutch sizes to estimate daily variation in population egg production.

At ~1030 each day ~200 adults were caught in a lift net baited with crushed sea urchins. The two study reefs were sampled on alternate days, with a haphazardly chosen point within each third of the 350–600 m of the outer edge of each reef being sampled every sixth day. Given that sampling regime and the large populations of *T. bifasciatum* on those reefs, we think that individual fish probably were not resampled very frequently, and would have recovered from any adverse

effects of handling between recaptures. Collected fish were sorted by sex: males have a cone-like genital papilla with a small, round terminal aperture (large males also are differently colored to females and small males [Warner et al. 1975]); females have a transverse genital flap that bulges out when gentle finger pressure is applied to the abdomen. Males were immediately returned to the reef and 50–60 females were taken to the field station ~1 km away and held in a bag net floating in the sea out of direct sunlight. Beginning at 1400 each female in the sample was lightly anaesthetized in a dilute mixture of Quinaldine and Ethanol in seawater and measured (standard length, SL, to the nearest mm). Her belly was then gently squeezed and, if she was ripe, her eggs were expressed into a narrow-tipped, graduated test tube containing distilled water. As soon as the clutch had settled evenly (a few seconds) the volume of the egg mass was measured to the nearest 0.05 mL. If the first few gravid females stripped on a day were not quite ready to spawn (eggs squirt forth readily from ripe females, but ooze out in a gelatinous mass from females that are not quite ready to spawn) the stripping of the remaining females was delayed for another hour. After stripping, females were revived in bag nets for ~2 h then returned to their capture site.

There was a strong linear relationship between clutch size (number of eggs) and clutch volume ( $r^2 = 0.94$ ,  $P < 0.001$ ) among 50 clutches containing 248–4362 eggs that we collected on six different days scattered over our study period. Schultz and Warner (1991) obtained a similar correlation using the same methods with this species. For each ripe clutch that we measured for volume, we estimated clutch size as: clutch size =  $106 + 7150 \times$  clutch volume, with the volume measured in milliliters.

Clutch size varied considerably among females, both within and among size classes (see *Results: Short-term spawning and environmental dynamics*), and each day's sample of fish included females of a range of sizes. Consequently, as a measure of each day's per capita output we used the mean scaled clutch size for all females in that day's sample (including those that failed to spawn), where scaled clutch size for each female = actual clutch size as a percentage of the maximum observed clutch size for females of her body size (see *Results: Fig. 2*).

*Long-term dynamics of settlement.*—As settlement occurs erratically throughout the year (see *Results: Fig. 8*), direct assessment by daily sampling of its long-term dynamics on a large spatial scale (the San Blas Point reef system) was not logistically feasible. To provide such long-term, large-scale data we made monthly censuses of newly settled fish during 1986–1996 in 28 fixed plots scattered over most of the study area (Fig. 1). Each plot was censused 2–5 d prior to each full moon, i.e., <10 d after the average peak of settlement, around the new moon (Victor 1983).

Our assumption that monthly recruitment levels are

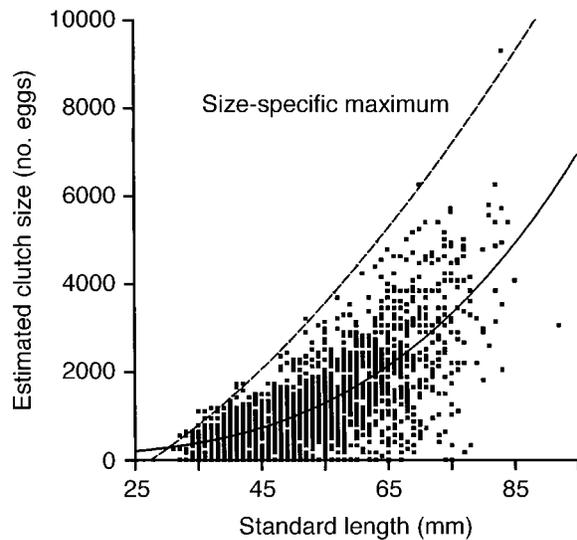


FIG. 2. Estimated sizes of clutches of all females that spawned over 90 d in 1993. The solid line is the best fit power function: clutch size =  $118 + 0.002 \times SL^{3.2}$ ,  $r^2 = 0.51$ ,  $P < 0.01$ ,  $n = 2579$ . The dashed line is the best fit power function for maximum clutch size =  $-1518 + 4.97 \times SL^{1.73}$  ( $n = 15$  highest points for fish 30–82 mm standard length [SL]).

reliable indicators of monthly settlement levels seems reasonable given that (1) monthly recruitment was positively correlated with monthly (i.e., cumulative daily) settlement of *T. bifasciatum* in the study area during 1985–1987 (Robertson 1992), (2) Victor (1986a) found no indications of density-dependent mortality of fish immediately after settlement, (3) Victor (1983) found that settlement dynamics were well preserved in the age structure of the adult population of this species, and (4) Pitcher (1988) and Meekan (1992) determined that short-term settlement dynamics can be accurately reconstructed using collections of recruits made within a few weeks of settlement. Due to differences in the lunar timing of settlement pulses in different months, the relative size of recruitment pulses that occurred earlier in the lunar cycle could have been underestimated (Robertson and Kaufmann 1998). However, because early mortality in this species is high during the first several days after settlement but then tapers off rapidly (Victor 1986a), it seems unlikely that such underestimation would have led to our monthly settlement time series differing to a biologically significant degree from one that daily sampling would have produced. Studies of other reef fishes have found good relations between the supply of settlement-stage larvae and early recruitment (Milicich et al. 1992).

*Short-term dynamics of settlement.*—Daily collections of newly settled fish were made over 30 lunar cycles from two small patch reefs (Fig. 1), site A (63 m<sup>2</sup>) from June through December 1985, and site B (28 m<sup>2</sup>) from January 1986 through December 1987. In addition, collections of recruits-of-the-month were

made at Site A at each full moon from January 1986 through December 1987. All those fish were preserved in 95% ethanol.

It is possible that the small spatial scale of our (and Victor's [1986a]) settlement sampling could have resulted in a high level of noise in the settlement signal. However, the high concordance of daily settlement dynamics of *T. bifasciatum* that Victor (1984) found over several months among a set of small sites scattered over a large area around San Blas Point argues against that possibility. For this reason, and for reasons given above concerning the utility of monthly recruitment censuses, we think that our method provided a reasonably accurate picture of the lunar-scale dynamics of settlement onto the San Blas Point reef system.

*Otolith analyses.*—We used otolith growth increments to estimate the timing of the major transitions (settlement and spawning dates) in the larval lives of all 776 fish we collected between 1985–1987. *T. bifasciatum* develops a growth anomaly (settlement mark) in its otoliths during the first 4–5 d after settlement (Victor 1984). Counts of daily growth increments laid down before and after the inner edge of that mark were used to estimate the settlement date, the PLD (cf. Victor 1984, 1986a), and fertilization date of each fish. S. Swearer analyzed the sagittae of fish collected daily between 1985–1987, and E. Brothers analyzed the lapillae of fish obtained in the monthly collections during 1986–1987. Subsequently, they both made “blind” analyses of the otoliths of 20 fish with varying PLDs that had been analyzed previously by the other person. While there was no consistent difference in the number of post-settlement-mark increments counted by both observers, Swearer consistently obtained about five more pre-settlement increments than did Brothers. This we attribute to them having analyzed otoliths under different magnification, and interpreting them differently. When Swearer made recounts following the protocol used by Brothers, Swearer's pre-settlement counts were not consistently different to those of Brothers. Further, Brothers obtained the same counts when he analyzed sagittae and lapillae from the same individual fish ( $n = 20$ ). Hence we adjusted all pre-settlement-mark counts obtained by Swearer by subtracting five counts from each.

While most studies have used sagittae in their analyses of the PLD of *T. bifasciatum* and other wrasses (e.g., Victor 1983, 1984, 1986a, b, c, Schultz and Cowen 1994, Caselle and Warner 1996, Sponaugle and Cowen 1997), that is not universal (Victor 1986c, Masterson et al. 1997). What the implications of differences in lapillal and sagittal increment counts are and whether sagittae or lapillae provide better estimates of PLDs has not been determined in that or any other species of labrid. Although the sagittae may develop shortly prior to lapillae, both otoliths typically are present in hatchling larvae of reef fishes (Brothers 1984). Secor et al. (1992) note that distinguishing daily and sub-

daily features can be difficult in faster growing otoliths, and sagittae are considerably larger in *T. bifasciatum* and contain sub-daily features (Victor 1986c). Lapillae have been successfully used to estimate PLDs in other reef fishes (Colin et al. 1997). Hence, at present we see no reason to expect that sagittae would necessarily allow more accurate estimation of the PLD than lapillae would in *T. bifasciatum*.

To obtain an estimate of the PLD of each fish we added 2 d to the number of pre-settlement-mark increments, to take into account the delay between spawning and the beginning of increment formation (cf. Victor 1983). Increments in and after the settlement mark were counted as post-settlement increments (cf. Victor 1986a, Masterson et al. 1997, Sponaugle and Cowen 1997).

We estimated the dynamics of the output (i.e., spawning) of fish that survived to settle (settler production) during 1985–1987 using a combination of their PLDs and their settlement dates.

#### Data analyses

*Spawning dynamics vs. wind and tide dynamics.*—In pelagic spawning reef fishes (including *T. bifasciatum* at Barbados [Hunt von Herbing and Hunte, 1991]) spawning activity often is lunar cyclic and peaks when high tides and the daily spawning period coincide (Robertson 1983, Thresher 1984). Hence we examined the relationship between the daily level of spawning activity by *T. bifasciatum* at San Blas and tidal height at 1300, about the middle of the daily spawning period. To test for associations between short-term fluctuations in spawning activity and weather and sea conditions, we examined relationships between spawning output and swell action, sunlight, and onshore wind stress, where onshore wind stress = (wind stress from the NW–E octants) – (wind stress from the SE–W octants) (see Fig. 1). As the effect of wind on surface water flow is related to the square of wind speed (Bowden 1983), we used  $(\text{km wind/d})^2$  as our measure of wind stress. We used the mean daily residual from the water level time series collected at the Smithsonian Tropical Research Institute (STRI) field station as our index of swell.

*Monthly settlement dynamics vs. wind dynamics.*—To assess whether monthly settlement strength was related to wind conditions we tested for correlations between the level of settlement and onshore wind stress (averaged over the month) in two ways: (1) using different lags; zero lag to assess wind effects on settlement itself and –1 lag to assess whether wind affected settlement success by affecting the production of larvae or their early survivorship and (2) using wind stress for the entire lunar cycle and for each lunar quarter; because settlement occurs in short pulses concentrated around the new moon, average wind conditions during the entire lunar cycle may be less relevant than wind conditions during a particular quarter. For these anal-

yses the lunar cycle commenced three days before the full moon, because the full moon quarter spanned 3 d either side of the full moon, and recruits of the month were censused several days before the full moon.

*Daily dynamics of settlement and settler production vs. those of winds and tides.*—Settlement of reef fishes occurs mainly at night (Victor 1983, Robertson et al. 1988, Shenker et al. 1993, Dufour and Galzin 1993) and, at some sites at least, on flooding tides (Shenker et al. 1993, Thorrold et al. 1993). Hence we examined the relationship between the level of settlement and several measures of nocturnal tidal activity: (1) the number of hours of flood tide per night (cf. Shenker et al. 1993), (2) tidal amplitude (maximum height – minimum height; cf. Sponaugle and Cowen 1997), and (3) net tidal flow each night (flood tide flow – ebb tide flow). We compared variation in settler production to tidal heights at 1300, because spawning output fluctuates in relation to that height (see *Results: Short-term spawning and environmental dynamics*). We examined the relationship between settlement (and settler production) and wind using both onshore-wind stress (i.e., prevailing-wind stress), and stress from each compass octant.

*Types of analyses.*—To analyze relationships between the dynamics of environmental variables (winds and tides) and those of spawning, settlement, and settler production we used both time series analysis (the computer package SYSTAT [Wilkinson 1990]) and circular statistics (Batschelet 1981). Other statistical techniques followed Sokal and Rohlf (1981) and Schultz (1985).

To examine the relationship between monthly wind dynamics and monthly settlement dynamics during 1986–1996 we used cross-correlations between both the raw time series and the seasonally adjusted time series, using the smoothed mean monthly values as the seasonal index. We also used cross correlations to examine relations between the short-term dynamics of spawning and settler production vs. winds and tides, using both raw data and data that had been first differenced to remove effects of both short-term and seasonal autocorrelations (Wilkinson 1990).

Poor settlement during any month could result from either a lack of competent larvae (due to low spawning activity or poor larval survivorship), or to competent larvae being present in abundance but failing to settle. To accommodate the former possibility we made three analyses of relationships between environmental factors and settlement/settler-production: (1) the entire time series, (2) the wet season only (the season of peak activity), and (3) the high-activity months (those in which at least 14 settlers were produced or settled).

Cross-correlation analyses assess linear relationships between two variables. However, the dynamics of settlement or settler production might be nonlinearly related to wind stress (cf. Roy et al. 1992), e.g., larvae might be better able to swim to settlement habitats under calm winds than strong winds, regardless of wind

direction. To test for a possible nonlinear relationship between wind and both settlement and settler production we compared the frequency distributions of (1) the occurrence of settlement/settler-production events during time periods with different levels of wind stress and (2) the occurrence of periods with different levels of wind stress regardless of whether settlement (or settler production) occurred.

*Scaling, averaging, and normalizing data.*—Monthly variation in settlement was assessed from monthly censuses of recruits-of-the-month in 28 fixed plots scattered over our study area (Fig. 1). Those plots varied in depth and microhabitat type, and some sites consistently received considerably higher densities of settlers than others. Because we are interested in assessing effects of environmental factors on the temporal patterning of settlement in the study area as a whole, we used the weighted average level of recruitment from the set of plots as our datum for each month. Without such weighting, signals from high-recruitment plots could have dominated the combined-plot time series. We weighted data from each plot equally by scaling each month's recruitment value for that plot relative to the mean of all values from that plot over the entire time series.

The time series of daily settlement in 1985–1987 is based on collections from two small patch reefs that were ~3.3 km apart, on opposite sides of our study area (see Fig. 1); reef A in 1985 and reefs A plus B in 1986–1987. We weighted settlement from the two reefs equally during 1986–1987 (for the same reasons as given above for weighting data from monthly recruitment plots) by adjusting the series from reef B (multiplying all values by 1.88) to equalize the total numbers of fish obtained for each site over that period. We then used the mean of the daily values for the two reefs as the datum for each day during 1986–1987.

We used time series analyses to analyze relationships between settlement (and settler production) and both wind and tide conditions at two temporal scales; daily and lunar-quarterly (using the daily average for the quarter). We also analyzed the wind–settlement relationship at the semilunar level (using the daily average for the new or full moon halves of each lunar cycle). We included the quarterly and semilunar analyses (1) to reduce effects of noise due to both occasional small differences in daily wind conditions at Galeta and San Blas, and the small spatial scale of our settlement sampling, (2) to reduce effects of inevitable small errors in using otolith analyses to estimate the PLD (cf. Rice 1987) and the settlement date, and (3) to accommodate possible short-term lagged or cumulative effects of wind (cf. Shenker et al. 1993, Milicich 1994).

We used circular statistics to analyze the structure of generalized lunar cycles of spawning, settlement, and settler production. Such generalized cycles usually have been assembled by simply pooling data from different cycles (e.g., Victor 1986a, Robertson et al. 1988,

Robertson 1992, Caselle and Warner 1996, Kingsford and Finn 1997, Masterson et al. 1997, Sponaugle and Cowen 1997). Here we analyzed average normalized cycles of activity because they provide a reliable indication of the consistency of any temporal pattern over a series of months regardless of variation in the amounts of settlement in different months. Generalized cycles derived from pooled data are less reliable indicators of such consistency because their structure can be dominated by the structure of a few high-activity cycles, particularly when the sample of months is small.

## RESULTS

### *Short-term spawning and environmental dynamics*

The percentage of sampled females that spawned each day during April–June 1993 varied from 0–100%, with an average of 75% doing so on any day. Although larger females tended to produce larger clutches, clutch sizes varied considerably among females within the same size class (Fig. 2). Average output per female per day varied from 0–48% of the size-specific maximum, and generally was low: the overall average daily level of production by all females was 25% of the size-specific maximum, and 33% by females that actually spawned. There was a very weak positive relationship ( $r = 0.20$ ,  $n = 2579$ ,  $P < 0.01$ ) between the percentage of females that spawned on a day and relative clutch size (clutch size as a percentage of the size-specific maximum); i.e., on days when more females spawned their clutches tended to be slightly larger.

Serial change in daily per capita egg output closely paralleled serial change in the percentage of females that spawned each day (Fig. 3, Pearson  $r = 0.90$ ). However, daily variation in output per female was greater than daily variation in the percentage of females spawning: mean levels of variation (percent deviation from the median) were 36.5% and 21.5%, respectively (Levene's  $t$  test for relative variation [Schultz 1985],  $P < 0.001$ ).

Spawning activity fluctuated in a nonrandom manner over the 3-mo period in 1993 (Fig. 3; Runs test for random variation around the mean: percentage of females spawning,  $P < 0.001$ ; per capita output per female,  $P = 0.018$ ). Although there were no significant autocorrelations at either near-lunar (~30 d) or near-semilunar (~15 d) frequencies (Table 1), the average lunar pattern of spawning (average per lunar day over three lunar cycles) was semilunar (bimodal; Fig. 4): average output per female per day Rayleigh  $Z = 7.0$ ,  $P < 0.001$ , average percentage of females spawning per day (not shown) Rayleigh  $Z = 14.4$ ,  $P < 0.001$ , with peaks of activity (mean angles of the circular distributions) 2.5 d prior to the new and full moons (Fig. 4A). This semilunar pattern was not strong, as there was only about one-fourth to one-third more spawning during the peak lunar quarters than during the offpeak quarters (Fig. 4A).

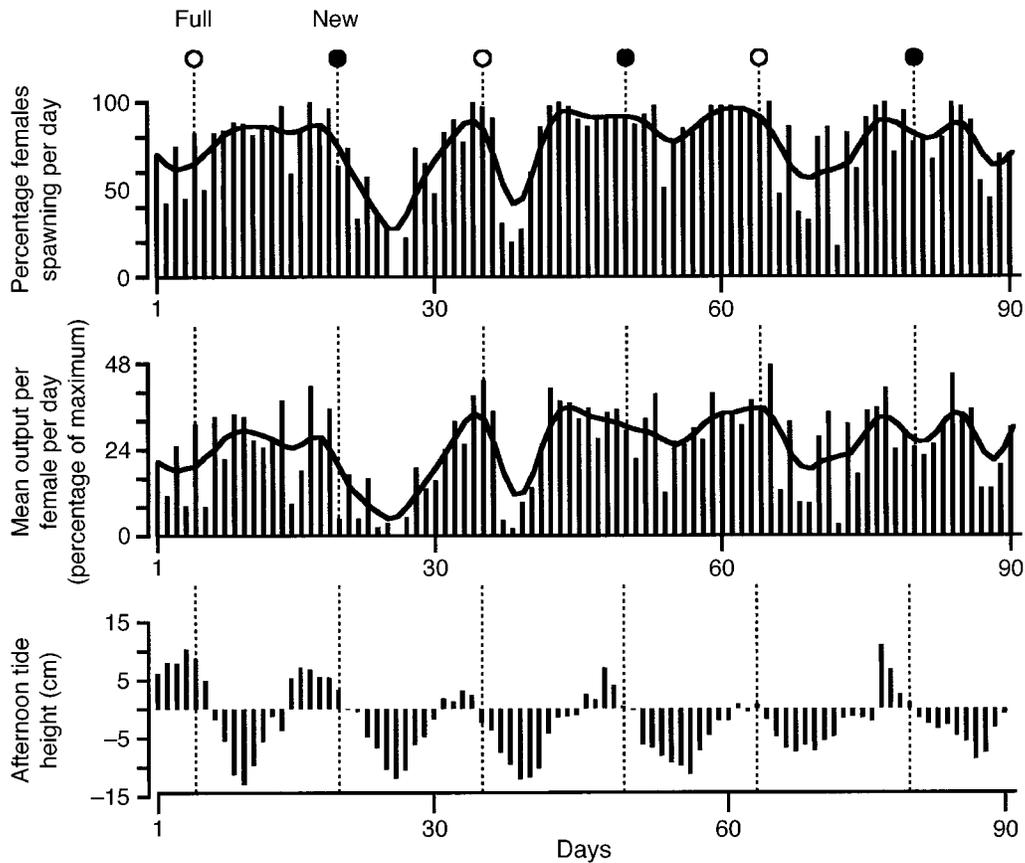


FIG. 3. Time series of daily spawning activity and tidal activity over 90 d in 1993. Upper panel: Percentage of females spawning each day. Middle panel: Mean per capita egg production over 90 d (mean scaled clutch size, where scaled clutch size = clutch size as a percentage of the size-specific maximum). Lower panel: tidal height during the middle of the early afternoon spawning period (1300 h).

TABLE 1. Autocorrelations for daily time series of spawning (Fig. 3), settlement, and settler production (Fig. 8) of *Thalassoma bifasciatum* throughout entire monitoring periods and during high-activity months (HM) only (see *Methods* for details).

A) Spawning, 1993				
Statistic	Maximum autocorrelations at different frequencies			
	Near semilunar (~15 d)		Near lunar (~30 d)	
Percentage of females spawning per day	0.09		0.05	
Mean output per female per day ( <i>n</i> = 3 mo)	0.16		0.06	
B) Settlement and Settler Production				
Period	Maximum autocorrelations at different frequencies			
	Near semilunar (~15 d)		Near lunar (~30 d)	
	All year	HM	All year	HM
Settlement (log[(no. fish/d) + 1])				
1985–1987 ( <i>n</i> = 30 mo [All], 15 mo [HM])	0.06	–0.15	0.11	0.08
1981–1982 ( <i>n</i> = 20 mo [All], 10 mo [HM])	0.08	–0.17	0.25** (25 d)	0.20* (27 d)
Settler Production (log[(no. fish/d) + 1])				
1985–1987 ( <i>n</i> = 30 mo [All], 15 mo [HM])	0.19* (15 d)	0.06	0.02	–0.14

\* =  $P < 0.05$ ; \*\* =  $P < 0.01$ .

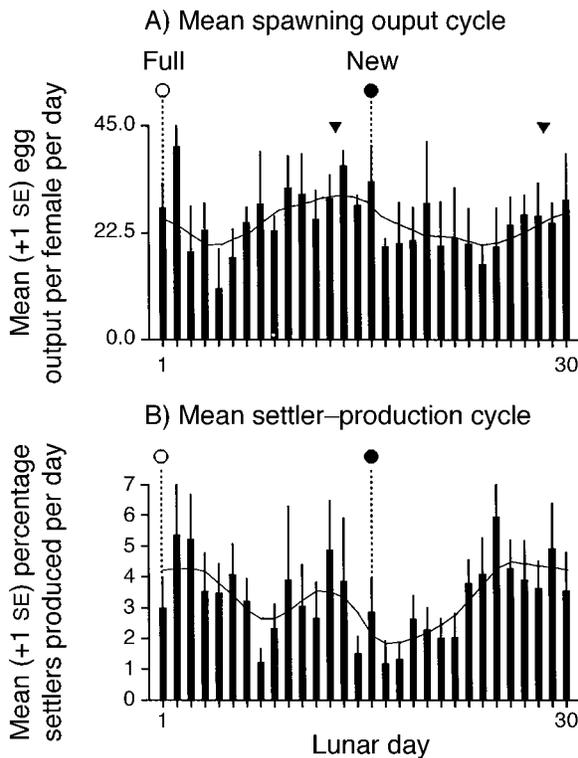


FIG. 4. Mean lunar patterns of spawning and settler production by *T. bifasciatum*. (A) Mean (+1 SE) per capita spawning output (as a percentage of the potential maximum) per day of the lunar cycle ( $n = 3$  cycles in 1993). (B) Mean percentage (+1 SE) of fish spawned on each day of the lunar cycle ( $n = 11$  cycles in 1985–1987 during which at least 30 settlers were produced). Lowess smoothing lines indicate the underlying pattern in each distribution, and triangles indicate the mean angles of the spawning cycle.

There was a very weak positive relationship between spawning activity and tidal height during the early afternoon spawning period: Fig. 3;  $r = 0.29$  for percentage females spawning and 0.21 for output per female (both  $P < 0.05$ ). Superimposed on the medium-term fluctuations in spawning activity was a pattern of erratic, daily variation in output (Fig. 3). The level of spawning activity per day was weakly related to the amounts of both sunlight and swell on the preceding day (for both percentage females spawning and output per female:  $r = 0.26$  for activity vs. solar radiation, and  $r = -0.23$  for activity vs. swell,  $P < 0.05$  in all four cases), but not at other negative lags. Spawning output also was weakly negatively related to onshore-wind stress at lags of  $-1$  d to  $-5$  d (maximum correlation at  $-4$  d:  $r = -0.42$ ,  $P < 0.05$ ).

#### Seasonal change in settlement, settler production and winds and tides

Settlement of *T. bifasciatum* occurred in virtually every month during 1986–1996, but was consistently low during the dry season, and peaked during the wet

season (Figs. 5 and 6). Although annual peaks of settlement were spread throughout two-thirds of the year, most occurred between August and November, about the middle of the wet season (Fig. 5). During the wet season onshore winds were weakest (Figs. 1 and 5, and see also Fig. 8), and nocturnal tidal amplitudes were relatively large, but the resultant nocturnal tidal flows were predominantly ebb flows, i.e., off-reef flows (Fig. 5, and see Fig. 8). Tidal heights during the daily spawning period were at seasonally low-to-intermediate levels in the wet season (Fig. 5, and see Fig. 8).

#### Monthly dynamics of settlement and wind

Monthly levels of settlement fluctuated considerably both within and among years, and over the course of any single wet season (Fig. 6). There were significant, but weak, negative correlations between monthly settlement and onshore wind stress at both 0 and  $-1$  lags throughout the year, and during the dry seasons, but not during the wet seasons (Figs. 6, 7, and Table 2). There were no correlations between seasonally adjusted monthly onshore wind stress and monthly settlement at 0 and  $-1$  lags, either overall, or during either season (Figs. 6, 7, Table 2). Although, for conciseness, the correlation values are not presented here, analyses of relationships between monthly settlement and onshore-wind stress during each lunar quarter produced essentially the same results as those between recruitment and monthly wind stress. Restricting the correlation analyses to 1992–1996, the period when wind data were collected at San Blas itself, also produced the same patterns of results.

Plots of monthly settlement vs. wind stress during the wet seasons do not indicate any nonlinearity in that relationship (Fig. 7): settlement occurred at above and below normal seasonal levels across a considerable range of above and below normal seasonal levels of onshore wind stress. Thus the only relationship evident between wind and long-term monthly settlement dynamics was a weak, inverse, seasonal relationship.

#### Short-term dynamics of settlement

**Lunar patterning.**—Daily settlement fluctuated non-randomly throughout 1981–1982 and 1985–1987 (Fig. 8, Runs tests for variation around the mean: 1981–1982  $Z = -13.3$ ,  $P < 0.001$ ; 1985–1987  $Z = -17.9$ ,  $P < 0.001$ ). Settlement usually occurred in one fairly discrete bout of activity per month, although in about one-fifth of months with appreciable amounts of settlement there were two such bouts (Fig. 8). Settlement was significantly concentrated in one part of the lunar cycle in 22 of 26 high-activity months during 1981–1982 and 1985–1987 (Rayleigh tests:  $P < 0.01$  for unimodal distributions in each of those cases,  $P > 0.05$  in the remainder).

Settlement was concentrated in the half of the lunar cycle centered on the new moon during both 1981–1982 and 1985–1987 (Fig. 9; Rayleigh tests for uni-

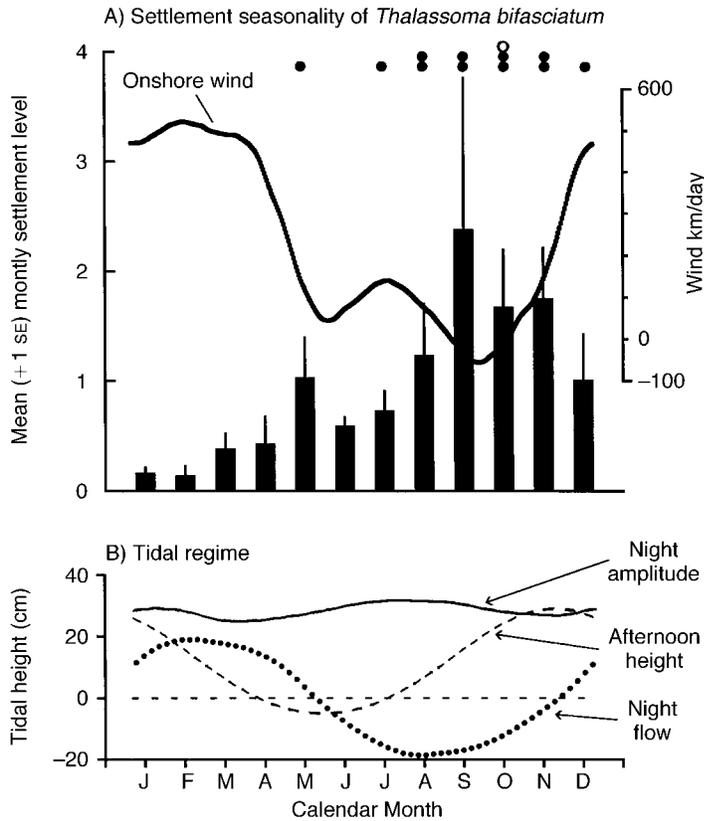


FIG. 5. Seasonal change in settlement of *T. bifasciatum* and prevailing wind and tides at San Blas, Panama. (A) Average seasonal pattern of settlement for 1986–1996, with the long-term (1982–1997) smoothed running mean for onshore wind. Filled symbols indicate timing of each year's best settlement month (open symbol is for 1982, from Victor [1986a]). (B) Seasonal change (30 d running means) in tidal characteristics. Afternoon height = tidal height at 1300 h (when daily spawning occurs); night amplitude = difference between maximum and minimum tidal heights at night; night flow = flood tide flow – ebb tide flow.

modal distributions in Fig. 9, 1981–1982:  $Z = 11.6$ ,  $P < 0.001$ ; 1985–1987:  $Z = 15.5$ ,  $P < 0.001$ ). However, the average lunar patterns of settlement differed somewhat during those two periods (Fig. 9; Kuiper's two sample test,  $P < 0.05$ ): activity was more dispersed over the lunar cycle and peaked 4 d later in that cycle in 1981–1982 than in 1985–1987. A generalized lunar cycle of settlement derived by Victor (1986a: Fig. 2), who pooled data from 1983–1984 with his 1981–1982 data, had a peak (mean angle) intermediate between the peaks for 1981–1982 and 1985–1987 shown in Fig. 9.

Despite the overall concentration of settlement around the new moon, a significant (but weak) autocorrelation at a frequency at  $\sim 30$  d was evident only in the 1981–1982 time series (Table 1). There were no significant autocorrelations at a  $\sim 15$ -d frequency in either time series (Table 1). This lack of consistent near-lunar/semilunar autocorrelations reflects the fact that settlement typically occurred in short pulses at different times relative to the new moon in different months (Fig. 8).

**Tidal patterning.**—The only statistically significant cross-correlations between the dynamics of settlement and nocturnal tidal activity (hours of flood tide, amplitude, or net flow) during either 1985–1987 and 1981–1982 were very weak negative correlations between settlement and both tidal amplitude and hours of flood tide throughout 1985–1987. No correlations

between settlement and tidal conditions were evident during either wet seasons or high-settlement months in either data set (Table 3).

We also assessed whether there was any consistent relationship between settlement and the tidal-amplitude cycle (cf. Sponaugle and Cowen [1997]) by testing the structure of average normalized tidal-amplitude cycles of settlement for 1981–1982, 1985–1987, and both periods combined (Fig. 10). While those analyses show that settlement was concentrated during part of that tidal cycle during each period (1981–1982: Rayleigh  $Z = 13.33$ ,  $P < 0.001$ ; 1985–1987: Rayleigh  $Z = 4.06$ ,  $P < 0.05$ ), the peaks of activity (mean angles) during those two periods were 11 d out of phase. The overall average pattern for both periods was not different from random (Fig. 10: Rayleigh  $Z = 1.49$ ,  $P \gg 0.05$ ).

**Relation to wind dynamics.**—There were significant but weak negative correlations between daily settlement and concurrent (zero lag) onshore wind stress throughout 1985–1987 and 1981–1982, but not during either the wet seasons or high-settlement months in either period (Table 3). There were no significant correlations between the differenced settlement and wind time series, at either zero lag (Table 3), or at lags up to  $-7$  d. No significant correlations were evident between settlement and wind activity during the wet seasons or high-settlement months when we used wind stress per compass octant rather than onshore wind

Dynamics of settlement of *Thalassoma bifasciatum* vs. wind

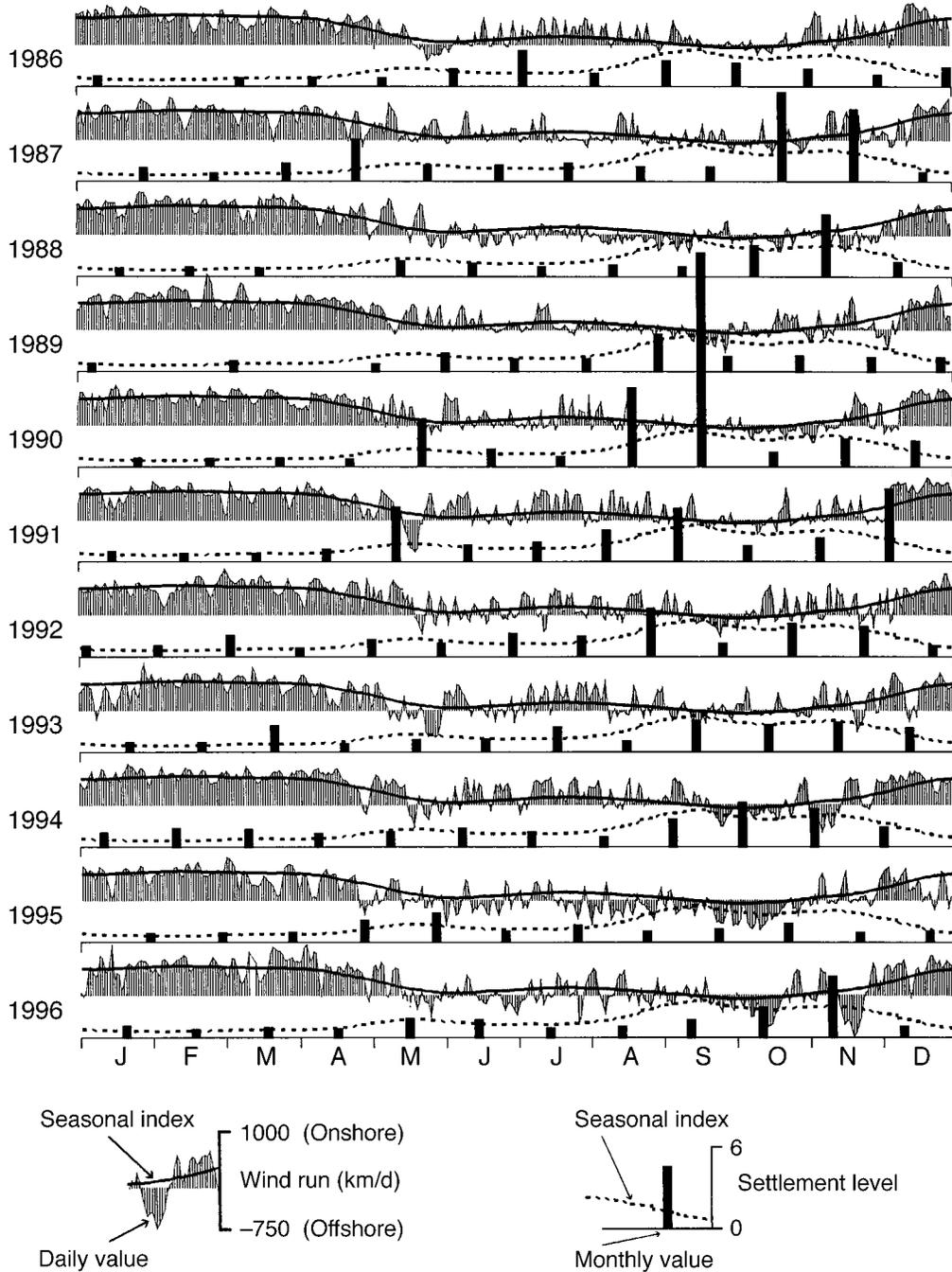


FIG. 6. Time series of monthly settlement of *T. bifasciatum* vs. onshore wind during 1986–1996, at San Blas, Panama. Bars showing settlement levels are placed at the new moon of each lunar cycle, to indicate the approximate timing of settlement. Monthly settlement level = mean scaled level for all plots censused that month.

stress. Cross-correlations between the quarterly and semilunar dynamics of settlement and onshore-wind stress produced essentially the same results as analyses of daily dynamics (Table 3, for brevity only results of quarterly analyses are shown). There were no differences between the frequency distributions of settlement

events per wind-category day (or lunar quarter) and wind-category days (or lunar quarters) during the wet seasons of either 1981–1982 or 1985–1987 (Fig. 11A; Kolmogorov-Smirnov two sample tests for both daily and lunar quarterly activity (latter not shown), all  $P \gg 0.05$ ). Thus, as with long-term monthly settlement dy-

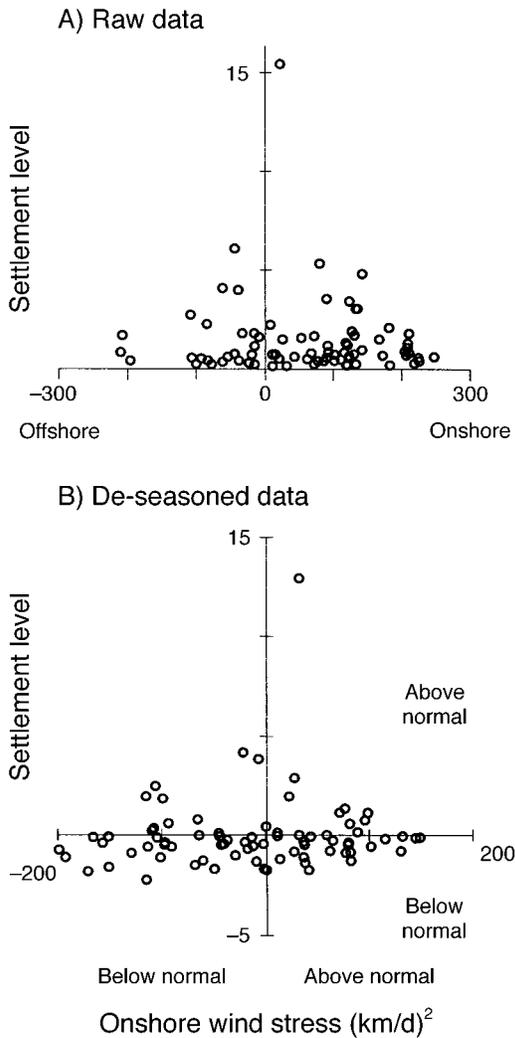


FIG. 7. Relationship between monthly settlement strength of *T. bifasciatum* and concurrent monthly onshore wind stress during the wet seasons of 1986–1996. (A) Raw settlement vs. raw wind stress. (B) Seasonally adjusted settlement vs. seasonally adjusted wind stress (see *Methods* for details). Settlement level = mean scaled level for all plots censused in any month.

namics, the only relationship evident between wind and short-term settlement dynamics was a relatively weak inverse seasonal relationship.

#### Settler-production dynamics

Appreciable levels of output of fish that survived to settle (settler production) occurred in two-thirds of the months during 1985–1987 (Fig. 8). Such production was nonrandomly distributed throughout that period (Runs test for variation around the mean:  $Z = -15.8$ ,  $P < 0.001$ ). It occurred fairly continuously throughout periods ranging from about one-fourth of a lunar cycle to over two lunar cycles (Fig. 8), but was concentrated in one part of the lunar cycle in most months (Fig. 7, Rayleigh test for unimodal distributions,  $P < 0.05$  in 10 of 15 high-activity months,  $P > 0.05$  in the remainder). Autocorrelation functions do not indicate any semilunar or lunar cyclicism in settler production (Table 1; the significant, but very weak, correlation at 15 d in that Table is due to a trend in the time series rather than semilunar cycling). The mean normalized lunar cycle of settler production was weakly, but nonsignificantly, bimodal, with faint peaks of activity several days prior to the new and full moons (Fig. 4B, Rayleigh tests for uni- and bimodality, both  $P > 0.05$ ).

Although settler production typically (14 of 15 cases) was more concentrated in one part of any lunar cycle and less continuous than the spawning we observed in 1993 (Table 4), it was much more continuous and tended to be less temporally concentrated in part of any lunar cycle than settlement itself was: first, periods during which settlers were spawned fairly continuously (i.e., periods during which  $>10$  fish were produced and which had production breaks  $<4$  d) were considerably longer (range 16–79 d, median 35 d,  $n = 10$ ; Fig. 8) than periods during which there were equivalent levels of settlement by those fish (range 10–24 d, median 15 d,  $n = 15$ ; Fig. 8;  $U$  Test,  $P = 0.002$ ). Second, settler production showed a weak (but nonsignificant) tendency to be more dispersed than settlement over any lunar cycle (Table 4, Mann-Whitney  $U$  test comparing angular variances of settlement and settler-production/lunar cycle in 1985–1987,  $P = 0.13$ ). Third, variation (percentage deviation from the mean) in daily settler production during April–July of 1985–1987 was greater than variation in daily spawning out-

TABLE 2. Relations between the dynamics of wind and monthly settlement strength of *T. bifasciatum* over 11 yr (1986–1996) (see also Figs. 6 and 7). The table gives correlations between settlement and onshore wind stress (daily average for month), in raw and de-seasoned time series (see *Methods* for details).

Lag (months)	Entire time series		Wet seasons only		Dry seasons only	
	Raw	De-seasoned	Raw	De-seasoned	Raw	De-seasoned
0	-0.30*	0.07	-0.06	0.08	-0.22	0.08
-1	-0.27*	0.04	0.02	0.10	-0.24	0.01
<i>n</i>	136		77		59	

\*  $P < 0.05$ .

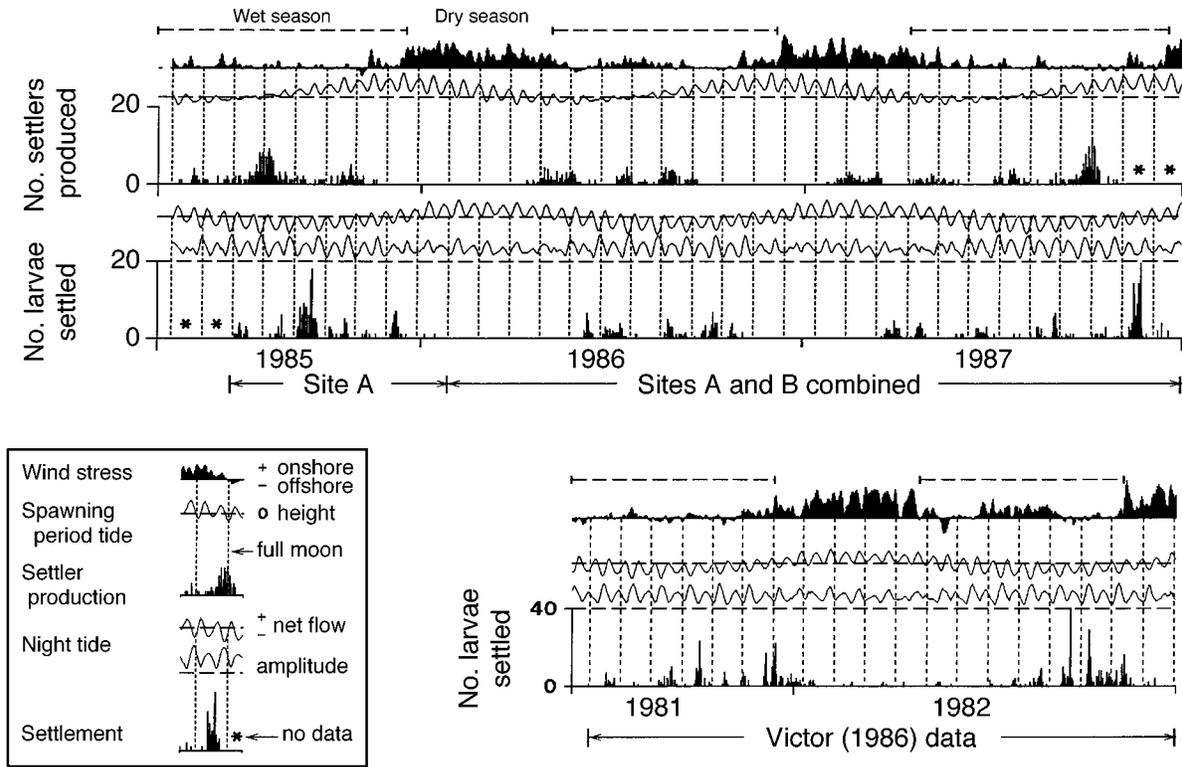


FIG. 8. Time series of daily settlement and settler production by *T. bifasciatum*, and of tidal and wind dynamics during 1981–1982 and 1985–1987 at San Blas. To facilitate their illustration, daily wind stress values were smoothed using a 3-d running mean.

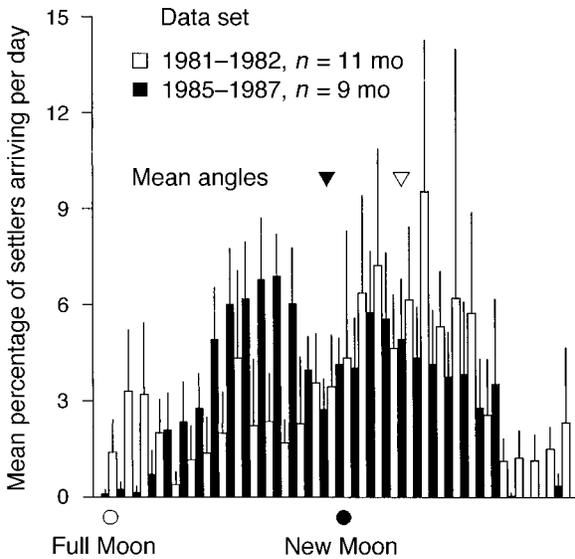


FIG. 9. Mean lunar settlement patterns of *T. bifasciatum* during 1981–1982 and 1985–1987. Mean (+1 SE) levels of settlement per lunar day are derived from months in which at least 30 fish settled ( $n = 9$  and  $11$ , respectively). Triangles indicate the mean angle of each distribution.

put during the same months in 1993 and in 1995 (latter data on activity over 3 mo in 1995 provided by L. Rogers, *personal communication*), but lower than daily variation in settlement that resulted from production during the same time of the year in 1985–1987 (i.e., settlement during May–August): ANOVA,  $F = 37.6$ ,  $P < 0.001$ ; Tukey post hoc comparisons of mean levels of variation in spawning (38%), settler production (115%), and settlement (142%): all combinations differed at  $P < 0.01$ .

However, although bouts of settler production and settlement differed in structure and duration, the overall dynamics of settlement did tend to mirror that of settler production (Fig. 8), with a (moderate) cross-correlation between the two time series at  $-43$  d ( $r = 0.52$ ,  $P < 0.01$ ), a lag equivalent to the average PLD.

Settlers produced during different halves of the lunar cycle in 1985–1987 had somewhat different average lunar settlement patterns (Fig. 12, Kuiper two-sample test,  $P < 0.001$ ): most (63%) individuals spawned during the waning moon settled after the new moon, while most (77%) fish spawned during the waxing moon settled before the new moon, and peaks in the settlement distributions of those two classes of settlers were 6 d apart.

*Settler production and environmental dynamics.*— There were significant but weak negative correlations

TABLE 3. Relations between the dynamics of settlement of *Thalassoma bifasciatum* and concurrent onshore wind stress and nocturnal tides, all year round (All), during the wet season (Wet), and during the high-settlement months (HM) (see *Methods* for details).

Activity level	Type of correlation	Cross correlations of settlement vs.:								
		Wind			Nocturnal tides					
		All	Wet	HM	No. hrs flooding <sup>†</sup>			Amplitude		
				All	Wet	HM	All	Wet	HM	
Daily (log[(settlers/d) + 1])										
1985–1987	Raw	-0.20**	-0.04	-0.01	-0.18**	-0.04	-0.01	0.03	0.01	0.01
	Diff.	0.01	0.01	0.07	0.02	0.04	0.01	0.01	0.01	0.03
1981–1982	Raw	-0.12*	0.02	0.15	-0.06	0.03	0.13	-0.02	-0.01	-0.07
	Diff.	0.04	-0.01	0.09	-0.05	0.01	-0.06	-0.04	-0.01	-0.05
Lunar-quarterly (log[(settlers/quarter) + 1])										
1985–1987	Raw	-0.37**	-0.03	-0.01	-0.35**	-0.13	-0.04	0.08	0.06	0.07
	Diff.	-0.02	0.06	-0.01	-0.15	-0.21	-0.14	0.15	0.15	0.20
1981–1982	Raw	-0.26	-0.05	0.17	-0.11	-0.05	0.19	0.03	0.05	0.01
	Diff.	-0.02	-0.06	0.11	0.06	-0.07	0.02	0.02	0.11	0.06

Notes: For type of correlation, “Raw” refers to correlations between raw series; “Diff.” refers to correlations between series after differencing to remove autocorrelations. For daily activity levels 1985–1987, number of months for All = 30, Wet = 21, and HM = 15. For the period 1981–1982, number of months for All = 20, Wet = 13, and HM = 10.

\*  $P < 0.05$ ; \*\*  $P < 0.01$ . Significance levels were adjusted for multiple comparisons using the Bonferroni technique.

<sup>†</sup> Correlations of settlement vs. net-flow follow essentially the same pattern as those between settlement and hours of flood tide/night.

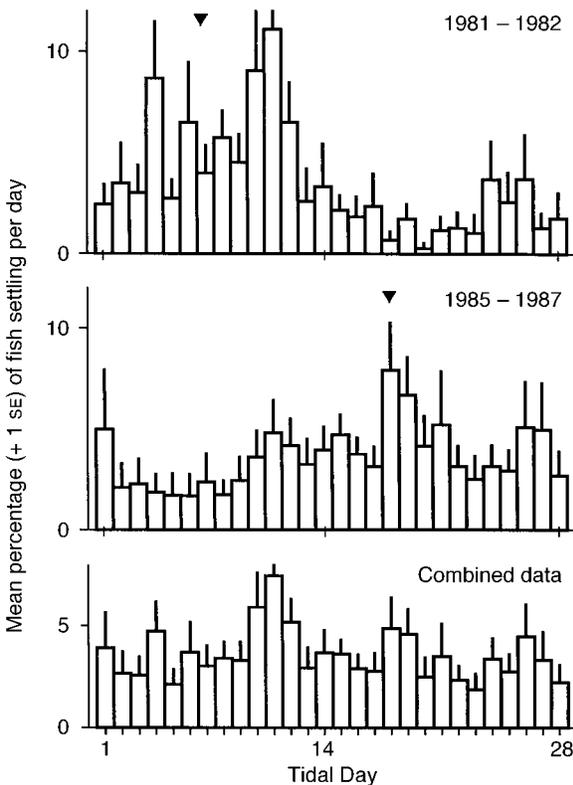


FIG. 10. Mean normalized tidal-amplitude cycles of settlement by *T. bifasciatum* during 1981–1982 ( $n = 11$  cycles), 1985–1987 ( $n = 15$  cycles), and both periods combined. Day 1 is the day with the largest nocturnal tidal amplitude in the cycle. Triangles indicate the mean angle of each distribution in which activity was significantly concentrated in one part of the tidal-amplitude cycle.

between both daily and quarterly levels of settler production and concurrent onshore wind stress throughout the year and during the wet season, but not during the high-production months (Fig. 8, Table 5). There also were significant, but weak, negative correlations between daily settler production and onshore wind stress on the preceding day, in high-activity months as well as wet seasons and year round. Those relationships persisted after the time series were differenced to remove autocorrelations, including seasonal effects (Table 5). There were no indications of a nonlinear relationship between settler production and concurrent onshore wind stress during the wet seasons (Fig. 11B, Kolmogorov-Smirnov two sample tests comparing the daily and lunar-quarterly frequency distributions [latter not shown],  $P \gg 0.05$  in both cases). Thus there were weak inverse links between onshore-wind and settler-production dynamics at both the seasonal and subseasonal levels.

There were weak negative correlations between settler production and afternoon (spawning period) tide height year round (i.e., an inverse seasonal relationship), but not during either the wet season, when spawning-period tides were at near their seasonal minimum (see Figs. 5 and 8), or during the high-production months (Table 5).

To accommodate the possibility that sagittal increment counts provide better estimates of the PLD than lapillae, we repeated all the cross-correlation analyses for settler production vs. winds and tides using a “sagittal-PLD” (lapillal PLD + 5 d). Although, for brevity, the results are not presented here, those analyses produced the same pattern of results as the analyses described above that used lapillal PLDs.

A) Settlement vs. wind

B) Settler production vs. wind

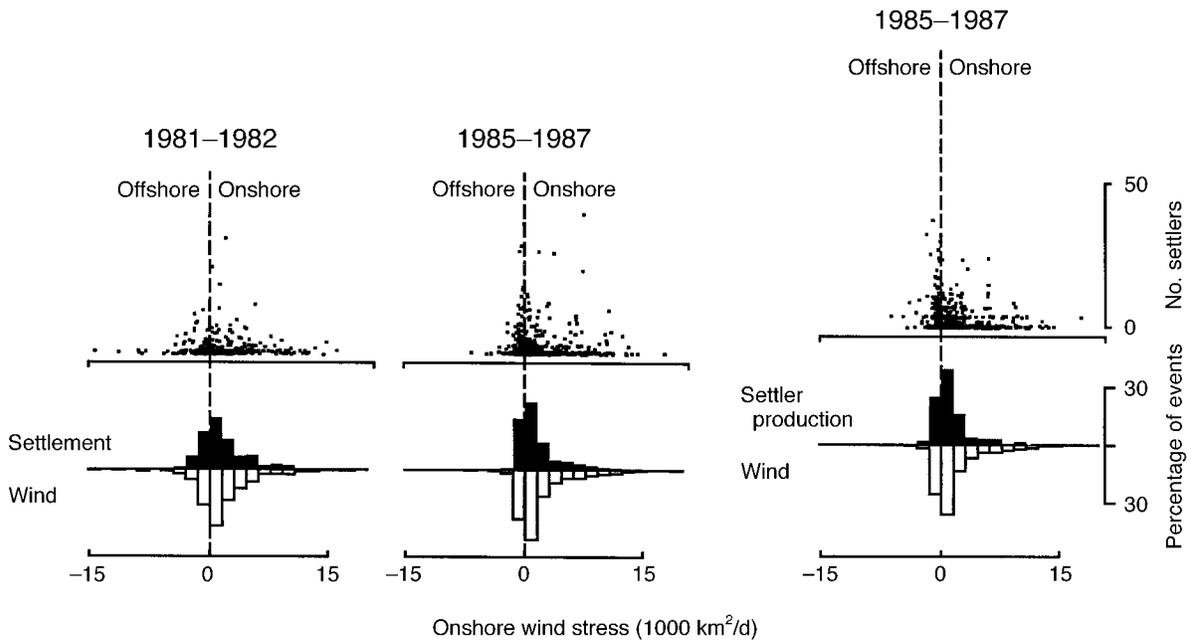


FIG. 11. Relationships between onshore wind stress and (A) daily settlement and (B) settler-production activity by *T. bifasciatum* during the wet seasons of 1981–1982 (settlement only) and 1985–1987 (settlement and settler production). Scatterplots show the size of each settlement event vs. the level of concurrent onshore wind stress. Histograms show the frequency distributions of settlement (or settler production) events and wind-stress events, i.e., the proportion of events that occurred on days with different levels of wind stress, and the proportion of all days with different levels of wind stress, respectively.

*Patterns of variation in pelagic larval durations*

The 776 fish whose otoliths we analyzed had PLDs ranging from 29 to 67 d, with a median of 44 d. The frequency distribution of PLDs was skewed towards long durations, although most fish had PLDs within 10% of the median (Fig. 13). PLDs varied in a consistent manner among fish spawned at different stages of the lunar cycle: the production of fish with short, average, and long PLDs peaked during different lunar phases (see mean angles in Fig. 14), several days before the new moon for those with short PLDs (Rayleigh  $Z = 36.4$ ,  $P < 0.001$ ), several days after the full moon for those with average PLDs (Rayleigh  $Z = 61.1$ ,  $P <$

0.001), and several days after the new moon for those with long PLDs (Rayleigh  $Z = 203.6$ ,  $P < 0.001$ ). In addition, variation in the PLD was highest among fish spawned just before the new moon (Rayleigh test of circular distribution of daily CVs (coefficient of variation) of PLDs:  $Z = 11.8$ ,  $P < 0.001$ , mean angle = 2 d before the new moon).

Overall, settlement by fish with short, average, and long PLDs was equally concentrated around the new moon: the mean angle of the average normalized distribution of settlement over the lunar cycle by individuals of each of those three age classes was within 1 d of the new moon, and there were no significant dif-

TABLE 4. Levels of dispersion (angular variance; see Batschelet 1981) of spawning, settlement, and settler production over the lunar cycle.

Activity	Period	Angular variance		
		Median	Range	<i>n</i>
Spawning (1993)				
Percentage of females spawning per day		1.87	1.62–1.89	3
Mean output per female per day		1.89	1.45–1.90	3
Settlement				
No. fish settling per day	1985–1987	0.76	0.22–1.56	15
	1981–1982	0.66	0.33–1.40	10
Settler production				
No. fish produced per day	1985–1987	1.07	0.32–1.78	15

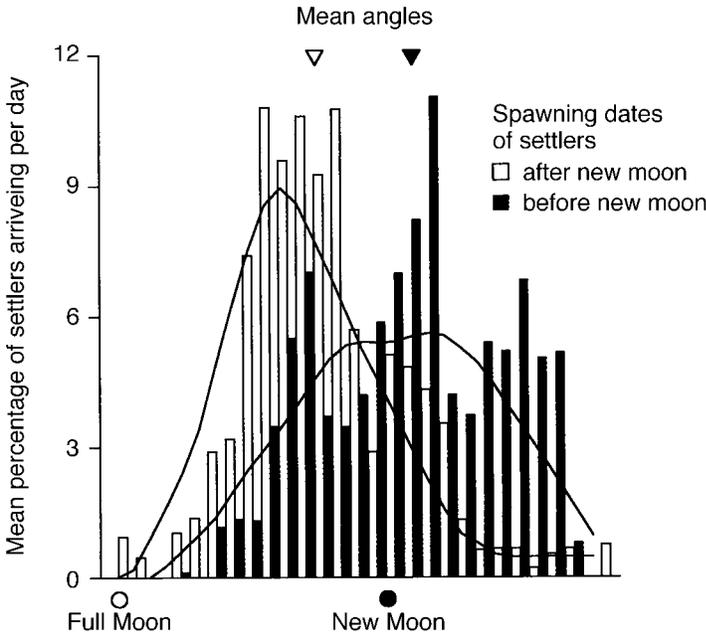


FIG. 12. Mean lunar settlement patterns of *T. bifasciatum* spawned in two halves of the lunar cycle in 1985–1987: from the new moon to the full moon – 1 d, and from the full moon to the new moon – 1 d. Lowess smoothing lines indicate the underlying unimodal patterns. Triangles indicate the mean angle of each distribution.

ferences between those three distributions (two-sample Kuiper tests, all  $P > 0.05$ ).

DISCUSSION

*Seasonality of reproduction*

Settlement of *T. bifasciatum* in San Blas is distinctly seasonal, with a predictable minimum during the dry season and a maximum in mid- to late wet season. Hunt von Herbing and Hunte (1991) concluded that a similar seasonal pattern of settlement by *T. bifasciatum* at Barbados (see also Tupper and Hunte 1994) was simply a reflection of the seasonality of spawning. Seasonal variation in spawning may also contribute to settlement seasonality at San Blas. Although our data indicate only weak negative effects of onshore winds on the short-term dynamics of spawning and settler production, larger and more persistent effects may occur in the dry

season when those winds are strong and persistent, and produce rough turbid conditions on inshore reefs. In other species of reef fishes in our study area, populations that live on reefs exposed to effects of the trade-winds have markedly reduced dry-season spawning relative to populations living in habitats sheltered from those effects (Robertson 1990, Clifton 1995).

Seasonal variation in wind potentially could also affect settlement seasonality of *T. bifasciatum* through adverse effects of wind-driven turbulence on fertilization success (Petersen et al. 1992) that would limit larval production during the dry season. Winds may also affect survival of fish larvae through its indirect effects on their feeding (cf. Peterman and Bradford 1987, MacKenzie and Leggett 1991). During the dry season a gradient develops in the distribution of fish eggs and larvae across the continental shelf around our

TABLE 5. Relations between the dynamics of settler production of *Thalassoma bifasciatum* in 1985–1987 and concurrent onshore wind stress and spawning-period tides, all year round (All), during the wet seasons (Wet), and during the high-production months (HM). Spawning period tide = height at ~mid-spawning period (1300 h). See *Methods* for details.

Activity level	Cross correlations of settler production vs.:						
	All	Wind			Spawning period tide		
		Wet	HM	All	Wet	HM	
Daily (log[(fish/d) + 1])							
Raw: lag = 0	-0.23**	-0.13**	-0.11	-0.14**	-0.09	0.10	
lag = -1	-0.25**	-0.17**	-0.15*				
Diff: lag = 0	0.02	0.03	0.04	0.01	0.01	0.01	
lag = -1	-0.10*	-0.13*	-0.16*				
Lunar-quarterly (log[(fish/quarter) + 1])							
Raw: lag = 0	-0.39**	-0.27*	-0.12	-0.29**	-0.20	0.16	
Diff: lag = 0	-0.12	-0.26*	-0.23	-0.08	-0.20	-0.11	

Note: Number of months for All = 30, wet = 21, and HM = 15.

\*  $P < 0.05$ ; \*\*  $P < 0.01$ . Significance levels were adjusted for multiple comparisons using the Bonferroni technique.

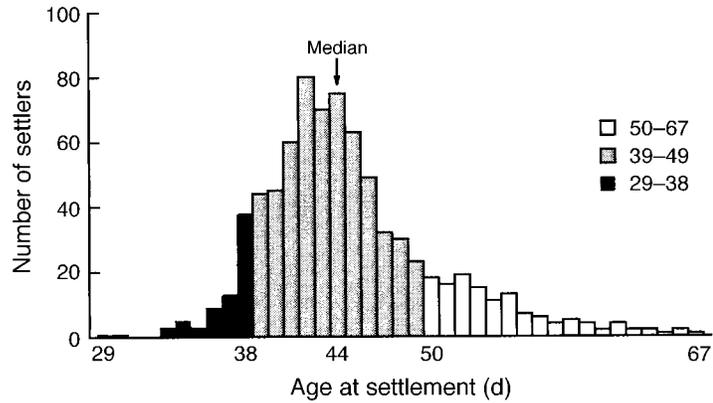


FIG. 13. Frequency distribution of pelagic larval durations of *Thalassoma bifasciatum* that settled in San Blas in 1985-1987;  $n = 776$ .

study area, with egg and larval densities increasing inshore along the continental shoreline to the south of San Blas Point. That gradient is not evident during the wet season (L. D’Croz and D. R. Robertson, unpublished data). Wind-driven transport of eggs and larvae to high-turbidity, high-energy, inshore habitats may reduce their survivorship, contributing to low settlement by *T. bifasciatum* during the dry season.

Other seasonally variable factors that affect growth, mortality, and movements of larvae at various stages of their development likely also contribute to seasonality of settlement of *T. bifasciatum* at San Blas. Those variables include sea temperature, which roughly parallels settlement seasonality. Rainfall seasonality, which also parallels settlement seasonality of *T. bifasciatum*, might be expected to produce seasonal fluctuations in terrestrial nutrient input, and hence availability of food for fish larvae. However, there is no

evidence of any seasonal fluctuation in plankton abundance (D’Croz and Robertson 1997) that is either parallel to, or the inverse of, the seasonal pattern of settlement by *T. bifasciatum*. Thus, while effects of other variables cannot be discounted, at present the only evidence of environmental forcing of reproductive seasonality is that strong onshore winds during the dry season probably depress spawning capacity, possibly reduce fertilization success, and likely reduce survivorship of eggs and larvae by moving them into shoreline habitats.

*Short-term dynamics of spawning*

Our 3 mo daily sampling during 1993 revealed a pattern of continuous but weakly semilunar spawning, overlaid by erratic shorter term fluctuations in output. L. Rogers (personal communication) measured spawning activity by *T. bifasciatum* in our study area over a

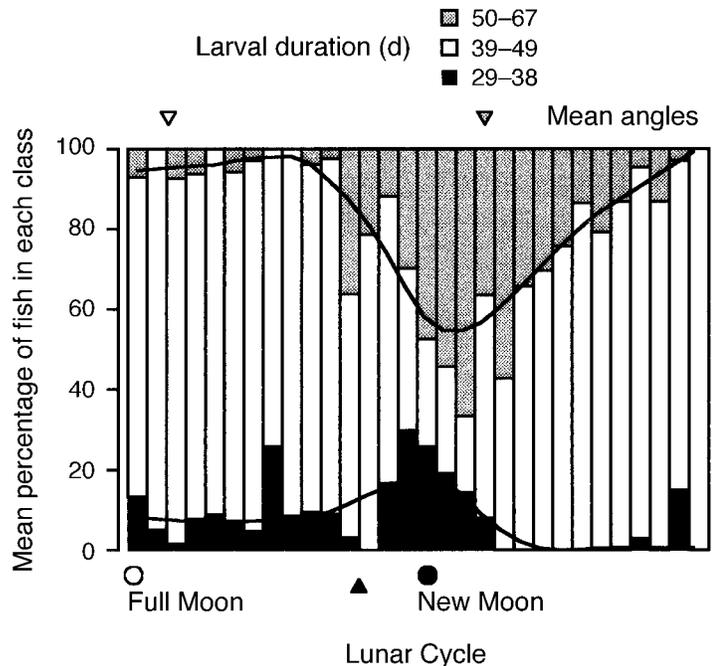


FIG. 14. Mean proportional abundances of fish with short (29-38 d), average (39-49 d), and long (50-67 d) pelagic larval durations among fish produced on each day of the lunar cycle ( $n = 11$  lunar cycles during which at least 30 fish settled in 1985-1987). Lowess smoothing lines indicate the underlying circular distributions for short and long PLD classes. Triangles indicate the mean angle of the unimodal distribution of each age class.

92-d period in April–July, 1995, by bidaily (every second day) sampling of different reefs among a cluster of six patch reefs. Spawning occurred continuously throughout that period: an average of 87% of females spawned per day (SE 2.5%, range 20.5–100%) and average daily per capita egg production was equal to 32.1% of the potential maximum (SE 2.2%, range 6–62%). Levels of daily variation in output during his and our sampling periods were very similar (Levene's test,  $P = 0.665$ ). The similarity of our and Rogers' observations, as well as R. R. Warner's (*personal communication*) more fragmented observations during several wet seasons in the 1980s, indicates that continuous egg production is typical in our study area, at least during early to mid-wet season.

At both San Blas (present results) and Barbados (Hunt von Herbing and Hunte 1991) spawning of *T. bifasciatum* is linked in the same way to both the tidal regime and the lunar cycle; activity peaks around the new and full moons, when spawning-period tidal heights are largest. Because those spawning peaks coincide with both extremes of lunar conditions, activity most likely is tracking the tidal regime. The tidal regime on the Caribbean coast of Panama is more strongly influenced by the lunar declinational cycle (period = 27.3 d) than the synodic lunar cycle (period = 29.5 d) (see Barnwell 1976). As a result the tidal cycle at San Blas is, on average, ~2 d shorter than the "lunar" cycle (NOAA 1981–1993), and the timing of "large early afternoon tides" relative to the new and full moons will vary through time (cf. Barnwell 1976). Consequently, if spawning by *T. bifasciatum* at San Blas is tracking spawning-period tidal heights, then the long-term average "lunar" pattern of activity may simply be acyclic (see also *Discussion: Short-term dynamics of settlement; lunar and tidal patterns*). Our data set on spawning is too small to assess that possibility, and for the remainder of this discussion we will assume that spawning is weakly semilunar. However, that issue could be resolved by determining what the pattern of spawning is during several months when the phase relationship between the lunar and tidal cycles is distinctly different to what it was in April–June 1993.

Biweekly (once every two weeks) peaks of spawning output could represent an adaptive response to effects of the tidal regime on the flushing of eggs away from the near-reef environment (cf. Johannes 1978, Robertson 1983). While the lack of a correlation between settler-production dynamics and concurrent tidal conditions could indicate that tides actually have no effect on egg survivorship, such effects may exist but be masked by effects of varying mortality later in the larval life. Alternatively that tide-related spawning pattern may represent an adaptation to tidal effects that prevail over much of the Caribbean-wide range of *T. bifasciatum*, but, due to the weakness of the tidal regime, are of little or no biological significance at San Blas.

The medium-term (~2 wk) fluctuations in spawning

at San Blas during 1993 were overlaid by day to day fluctuations in output that were weakly correlated with short-term fluctuations in light, wave action, and wind conditions on preceding days. Such lagged responses indicate that those factors have a delayed effect on females' egg-production machinery. Increased wave action, currents, and turbidity due to increased winds may reduce egg production by reducing feeding efficiency and increasing metabolic costs of general maintenance. Light, on the other hand, may positively affect feeding efficiency.

The availability of plankton, the primary food of *T. bifasciatum* (Randall 1967; D. R. Robertson and S. Swearer, *personal observations*), typically is highly variable on small spatial and temporal scales (e.g., Youngbluth 1979, Hamner et al. 1988). Schultz and Warner (1991) proposed that the considerable variation in egg production that they found among populations of *T. bifasciatum* on different reefs on San Blas Point was driven by spatial variation in the plankton supply. L. Rogers (*personal communication*) found that, in the field, females of *T. bifasciatum* rapidly (within ~2 d) increase their clutch sizes in response to supplemental feeding. Occasional substantial differences that he (L. Rogers, *personal communication*) found in egg production levels among adjacent reefs on the same day in 1995 are consistent with such short-term responses by females of *T. bifasciatum* to small-scale spatio-temporal variation in the food supply. Other planktivorous reef fishes show considerable short-term variability in spawning that may be related to short-term variation in plankton supplies (Robertson et al. 1990, Tyler and Stanton 1995). Thus both continuous spawning by *T. bifasciatum* at average levels well below the potential maximum and fluctuations in output on a variety of time scales may reflect fluctuations in a limited food supply, in combination with continuous allocation of resources to growth as well as reproduction (Schultz and Warner 1991).

The correlations we observed between spawning output and wind, light, and swell were all quite weak. Each of those factors probably has little explanatory power because spawning capacity is affected in different ways by the simultaneous action of a variety of factors that act on different time scales.

#### *Short-term dynamics of settlement*

*Lunar and tidal patterns.*—Geographic variation within the Caribbean in both the structure of the tidal regime and its relationship to the lunar cycle presents opportunities to distinguish between effects of those factors on settlement dynamics both within and among locations. Sponaugle and Cowen (1997) compared the settlement dynamics of *T. bifasciatum* at San Blas and Barbados from that perspective, because those two sites differ in the structure of their tidal regimes (at Barbados the tidal range is twice as large and the semidiurnal tidal signal is stronger) and in the closeness of the

linkage between the tidal and “lunar” cycles (both cycles have a  $\sim 29.5$ -d period at Barbados, while the tidal cycle is  $\sim 2$  d shorter than the lunar cycle at San Blas; Sponaugle and Cowen 1997 and see *Discussion: Short-term dynamics of spawning*). They analyzed Victor’s (1986a) data on settlement by *T. bifasciatum* at San Blas in 1981–1982 and found a marginally stronger relationship with the tidal-amplitude cycle than the lunar cycle. They also found that settlement was linked to the tidal/lunar cycle at Barbados. Substantial differences in the timing of settlement relative to both the tidal and lunar cycles at those sites led them to propose that settlement dynamics at both sites are related primarily to tidal conditions rather than lunar factors, with a stronger tidal link at Barbados.

Two large data sets (1.7 yr and 2.5 yr, spread over a 7-yr period) on settlement by *T. bifasciatum* at San Blas both demonstrated similar broad peaks of activity around the new moon, although with several days difference in the timing of those peaks in each period. Our time series analyses showed no evidence of any consistent relationship between settlement and the tidal regime during the wet seasons and high-settlement months of 1981–1982 and 1985–1987. Sponaugle and Cowen (1997) tested the structure of generalized tidal-amplitude cycles of settlement at San Blas and Barbados that they derived by pooling data from different months. To assess the consistency in any such relationship at San Blas we tested the structure of average normalized tidal-amplitude cycles of settlement. Our analyses showed that, while settlement did peak during one part of the tidal-amplitude cycle during both 1981–1982 and 1985–1987, those two peaks were 11 d out of phase. The average cycle for both periods combined showed no evidence of any peak. The difference in the tidal-cycle timing of peak activity during those two periods probably is due simply to interannual variation in the timing of large-amplitude tides relative to the lunar cycle: the median date of day 1 of the tidal-amplitude cycle was 5.5 d before the new moon (range, 1 d after to 9 d before) during high-settlement months in 1981–1982, vs. 15 d before the new moon (range, 6–21 d before) in 1985–1987 (NOAA, 1981–1987). The fact that there were much larger differences in the tidal patterning of settlement than in the lunar patterning of settlement during those two periods leads us to conclude that the dynamics of settlement of *T. bifasciatum* at San Blas are functionally related to the lunar cycle, but not to the tidal regime.

Although the tidal range is small at San Blas, the seasonal peak of settlement by *T. bifasciatum* occurs when nocturnal off-reef tidal flows are at their seasonal maximum, i.e., when tidal flows seem most likely to hinder the nocturnal movements of settlers to reefs. The combination of this seasonal relationship between settlement and the tidal regime, and the lack of any consistent relationship between the sub-seasonal dynamics of settlement and tides indicates that either tidal

currents at Panama are too weak to affect transport-mediated settlement activity by *T. bifasciatum*, or that settlement is not primarily dependent on transport mechanisms.

A lunar pattern of settlement by *T. bifasciatum* very similar to that observed at San Blas also appears to occur at St. Croix (see Caselle and Warner 1996, and Masterson et al. 1997). As the tidal range at St. Croix is even smaller than that at San Blas (NOAA 1981–1993); the similarity in the lunar patterning of settlement at those sites suggests that the influence of lunar factors on settlement periodicity predominates when tidal fluxes are weak. Two studies that used different methods reached different conclusions about the lunar periodicity of settlement by *T. bifasciatum* at Barbados: Hunt von Herbing and Hunte (1991) used otolith back calculation to estimate the settlement dates of individuals sampled at monthly intervals over one year. They found no lunar periodicity (when they pooled data from all months), but pointed out that density-dependent post-settlement mortality may have confounded their attempt to reconstruct the lunar settlement pattern. They did not examine possible links between settlement and the tidal regime. Sponaugle and Cowen (1997) estimated the daily dynamics of settlement of *T. bifasciatum* at Barbados indirectly, using a length/post-settlement-age relationship (derived from a subsample of fish) to back calculate the settlement dates of all new recruits obtained in biweekly collections. They concluded, after testing the structure of a single cycle of activity (derived by pooling data from six cycles) that its settlement was lunar/tidal cyclic and peaked  $\sim 8$  d before the new moon, i.e.,  $\sim 10$  d out of phase with the lunar pattern of settlement at Panama (and St. Croix). They then proposed that settlement of *T. bifasciatum* is functionally related to tidal conditions rather than lunar factors at Barbados: large tidal fluxes can limit the ability of larvae to swim to settlement habitats, and activity peaks during neap tides when such fluxes are weakest.

Two large time series of settlement from San Blas showed that, at a single site, there can be both pronounced interannual variation in the relationship between settlement and the tidal regime, and considerable inter-mensural variation in the relationship between settlement and the lunar cycle. The existence of such within-site variability indicates that multiyear data sets that span a range of seasonal conditions, and that rely on direct methods to estimate daily settlement dynamics, will be needed from other sites before firm conclusions can be reached about geographic variation in the relative influence of tidal and lunar factors on the settlement dynamics of *T. bifasciatum* or other species. Large time series will be particularly important for sites, such as Barbados, where the tidal regime might be expected to have relatively strong effects on settlement dynamics, and where differences in methodology

make it difficult to satisfactorily account for the results of different studies at the same and different locations.

*Settlement vs. wind dynamics.*—Fluctuations in prevailing winds might well be expected to influence settlement dynamics of *T. bifasciatum* at San Blas if those are affected either by the prevailing, long-shore large-scale current (cf. Roberts 1997) or more localized wind-generated surface flows. However, although wind and settlement have inverse seasonalities, we found no indications of any consistent, and hence functional, relationship between the subseasonal dynamics of settlement and wind on either the daily, lunar-quarterly, semi-lunar, or monthly time scales.

Victor (1984) proposed that transport of large patches of competent larvae from offshore habitats to inshore reefs in San Blas was responsible for the strong concordance of daily settlement dynamics of *T. bifasciatum* that he found over an area much larger than our study area. However, such concordance could arise independently of such a transport mechanism: relatively stationary patches of larvae could develop on the narrow continental shelf throughout San Blas. Transport-independent settlement behavior by larvae in those patches could be triggered by some environmental factor or cue(s), resulting in concurrent settlement on spatial scales that reflect the sizes of larval patches. The lack of any clear involvement of wind (or tides) in the short-term settlement dynamics of *T. bifasciatum* at San Blas indicates that either (1) currents that usually deliver settlers effectively operate independently of short-term fluctuations in wind (and tides) or (2) mechanisms other than transport of settlers to settlement habitat are primarily responsible for settlement dynamics.

Shenker et al. (1993) and Thorrold et al. (1993) found correlations between fluctuations in wind stress and the dynamics of supply of “larval” reef fishes in the Bahamas, as did Milicich (1994) for settlement-stage larvae, and Kingsford and Finn (1997) for “pre-settlement” fishes on the Great Barrier Reef. Sponaugle and Cowen (1996) found some evidence that wind-driven changes in major long-shore currents occasionally affect the dynamics of recruitment of two reef fishes at Barbados. Those studies either were performed at locations at which prevailing large-scale nearshore currents flow more or less parallel to prevailing winds (Shenker et al. 1993, Thorrold et al. 1993, Milicich 1994, Kingsford and Finn 1997, Sponaugle and Cowen 1997), and/or found effects in habitats in which currents are likely to be strongly affected by wind (a small channel [Shenker et al. 1993, Thorrold et al. 1993] or a lagoon on the windward side of a reef [Kingsford and Finn 1997]) or variation in wind direction (the lee side of a high island, Milicich 1994 and see also Hawkins and Hartnoll 1982). In some cases they also used sampling methods likely to be susceptible to wind effects (anchored, surface-fishing nets: Shenker et al. 1993, Thorrold et al. 1993). Most of those studies also were performed at small, isolated islands or reefs

(Cowen and Castro 1994, Milicich 1994, Caselle and Warner 1996, Kingsford and Finn 1997, Sponaugle and Cowen 1997). Other studies have shown that the relationship between local geography and the directions of prevailing winds and nearshore currents determines how winds affect settlement dynamics of shore organisms (Roughgarden et al. 1988, Farrell et al. 1991). The wind regime may have no consistent effect on settlement dynamics of *T. bifasciatum* at San Blas Point due to the nature of that relationship at that site. At our study site prevailing winds blow at  $\sim 135^\circ$  to the prevailing current, which runs along a continental shore. Due to porosity of the Point's reef system and major water flows along most of the periphery of that system, oceanic water enters that system from most directions. The reef system of the Point is in a lee only from the west winds, which are a minor component of the wind regime (Fig. 1). Hence little of that reef system is strongly shadowed from effects of either the prevailing wind or major currents, and the prevailing wind may have quite different effects on surface currents and the transport of larvae to and within the reef complex at San Blas Point than it does at the sites referred to above. Further, both waters to seaward of San Blas Point, and a large ( $\sim 100$  km<sup>2</sup>), deep (to 50 m) bay to the south of that point (Fig. 1) could provide habitat for reef fish larvae, and act as sources of settlers. If settlers move to reefs on the Point from any direction, then currents, with or without wind influences, might simply influence the direction of delivery rather than its occurrence.

Although nearshore current regimes at islands and continental shelves share some important structural features (Cowen and Castro 1994), the results of our study indicate that attention needs to be paid to situations on continental shores, and to sites with varying prevailing-wind/prevailing-current relationships, before an understanding of the general importance of wind effects on the settlement dynamics of Caribbean reef fishes is possible.

#### *Short-term dynamics of settler production*

*Relationship to winds and tides.*—While the prevailing wind has weak short-term effects on spawning during the wet season, and may have stronger adverse seasonal effects on spawning, our data indicate that that wind has, at most, very weak effects on the dynamics of settler production during the wet season, i.e., the settler production that leads to most of the year's settlement. Thus any influence of winds (and tides) on either short-term spawning output or the survival of eggs and hatchling larvae during the wet season evidently is largely overwhelmed by events occurring later in the larval life that determine the temporal pattern of variation in the survival to settlement of daily and monthly cohorts of larvae produced over the course of the year.

*Relationships to spawning and settlement.*—There are distinct differences in the short-term dynamics of

spawning, settler production, and settlement. Spawning is much more continuous than settler production, which in turn is more continuous than settlement. Those differences between spawning and settler-production dynamics indicate that larvae produced at different phases of the same and different lunar cycles over the course of a single wet season experience widely varying levels of survivorship to settlement. The dynamics of settlement and settler production are more closely linked than those of spawning and settler production, due to most larvae having near-average PLDs. However, settlement is not only much less continuous than settler production, but is, overall, lunar cyclic rather than (very weakly) semilunar cyclic (or acyclic?) like settler production. Those differences, when combined with the fact that larvae with both short and long PLDs settle as close to the new moon as do larvae with average PLDs, indicate that larval avoidance of settlement around the full moon by advancement or delay of settlement makes a substantial contribution to settlement dynamics and the linkage of a lunar pattern of settlement to a weakly semilunar pattern of spawning and settler production.

#### *Advantages vs. costs of delaying metamorphosis*

The ability to extend the larval life and delay metamorphosis has been viewed as an adaptation to larval development in habitats that are distant from settlement habitats (Jackson and Strathmann 1981, Victor 1984, Cowen 1991), and/or the control of settlement by infrequent, short-duration transport mechanisms (Cowen 1991, Jenkins and May 1994). An alternative hypothesis (Sponaugle and Cowen 1996) is that the ability to delay metamorphosis enables a larva to choose when it settles, by waiting to do so during a particular lunar phase. While those authors' data on the pattern of variation in the PLD of a Caribbean goby is consistent with that idea, they lacked observational data on that species' lunar spawning pattern, on patterns of variation in the PLD of fish spawned during different lunar phases, and on the lunar patterns of settlement of larvae with different PLDs. Our study extends on theirs in several ways and offers support for that hypothesis as applied to *T. bifasciatum*, by showing that systematic variation in the PLD among larvae spawned at different lunar phases makes a major contribution to the linkage of a weakly semilunar spawning pattern to a broadly lunar settlement pattern.

Mortality of pelagic larvae is high and the longer a competent larva spends in the plankton waiting to settle, the lower must be its chance of doing so. Thus it is reasonable to expect that fish with extended PLDs would have substantially lower average settlement success, relative to fish with near-average PLDs, and that spawning that consistently produces larvae that must extend their PLDs in order to settle around the new moon will produce a substantially lower average return for effort. Is that the case with *T. bifasciatum*?

The similarity between the average lunar cycles of spawning and settler production indicates that fish that tend to have long PLDs (i.e., those spawned around the new moon) experience at most a small reduction in average settlement success relative to larvae that have near-average PLDs (whose production is concentrated around the full moon). Settler production varies considerably in different months over the course of any year, and, in different months, eggs that are spawned during one lunar phase experience very different levels of settlement success relative to eggs spawned during another lunar phase. Thus, although fish spawned around the new moon have low settlement success (relative to other members of their monthly cohort) in some months, they have higher relative settlement success in others. High relative settlement success by fish with long PLDs evidently occurs in a sufficient number of months that their average relative level of success is similar to that of fish with near-mean PLDs. Thus, although there will be differences in the return for effort from spawning during different phases of any particular lunar cycle, on average, the relative return for effort is about the same for spawning during each lunar phase.

#### *Conclusions*

Transport of settlers to settlement habitat is of primary importance to the settlement dynamics of a range of marine organisms in a variety of situations. Winds and tides have major effects on such transport at some locations, and most recent studies have found them to have (usually relatively weak) effects on the settlement dynamics of tropical reef fishes. However, winds and tides apparently have no effect on the short-term dynamics of settlement of our study species during the 8-mo wet season, when most of its settlement occurs. Either transport of settlers of that species is not primarily dependent on winds and tides, or settlement dynamics are not primarily dependent on transport mechanisms. On the other hand, strong, consistent prevailing winds may have major effects on settlement seasonality of various reef fishes in San Blas by depressing spawning and reducing survivorship of eggs and larvae during the ~4-mo dry season.

Nearshore current regimes on continental shelves may be structurally similar to those at isolated islands that have self-recruiting reef fish populations, and small reefs within large reef complexes on such shelves may have self-recruiting reef fish populations (Jones and Milicich 1996). Analysis of prevailing nearshore currents indicates that, on the coast in the San Blas area, larvae of *T. bifasciatum* and other reef fishes likely settle in the general vicinity of where they are spawned (Roberts 1997). Hence it is reasonable to expect that the dynamics of spawning, larval survivorship, and settlement of reef fishes at sites such as San Blas will be strongly influenced by the local peculiarities of the coastal environment. Differences between our results and those of studies at other sites may be due to geo-

graphic variation in tidal regimes and the relationship between prevailing winds, nearshore currents, and local geography.

Our conclusions for *T. bifasciatum* at San Blas are based on two multiyear data sets that spanned the full range of seasonal conditions under which reproduction occurs. Similar-sized data sets may generally be required to assess the consistency of relationships between settlement and environmental dynamics in tropical species that have broad reproductive seasonalities, to accommodate not only the considerable variation that occurs in the temporal patterning of settlement and environmental change across time scales ranging from days to years, but also complex patterns of geographic variation in environmental regimes.

The ability of competent larvae of marine organisms to delay settlement has been considered primarily in relation to the degree of spatial separation of larval and adult habitats. However, in many reef fishes, and particularly those whose larvae develop near where they were spawned and will settle, such an ability may be related primarily to the exercise of choice in the timing of settlement and the linkage of short-term spawning and settlement dynamics. Monthly variation in settlement success of larvae spawned during different lunar phases may be sufficiently great that, averaged over the long term, larvae that are obliged to delay settlement achieve close to the same relative level of settlement success as normal-duration larvae. Thus spawning that consistently produces larvae that are likely to delay metamorphosis may offer a return for effort very close to that from spawning that produces normal-duration larvae.

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