Vol. 267: 267–280, 2004 | MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser | Published February 19

Lunar cyclic population replenishment of a coral reef fish: shifting patterns following oceanic events

Su Sponaugle*, Deanna Pinkard

Marine Biology and Fisheries Division, Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, Florida 33149-1098, USA

ABSTRACT: We examined the relationship between the pelagic environment and the lunar timing of reproduction and recruitment of a coral reef fish by comparing patterns exhibited by fish under normal oceanographic conditions with patterns exhibited by fish that experienced significantly different pelagic conditions (i.e. encounter with meso-scale, low-salinity North Brazil Current [NBC] rings passing by the island of Barbados). We used a 20 mo time series of bluehead wrasse *Thalassoma bifasciatum* recruitment, and compared larval growth and the timing of settlement and (successful) spawning recorded in the otoliths of individual recruits that encountered an NBC ring (RING fish) with those that did not (NO RING fish). Spawning occurred during all times of the lunar cycle, but during NO RING conditions, only those larvae spawned during the first-quarter moon were retained nearshore. Successful NO RING recruits were spawned during the first-quarter moon, grew rapidly as larvae, and settled during the third-quarter moon and neap tides. In contrast, during RING events, larvae spawned during all lunar phases were retained nearshore. Successful RING recruits were spawned over the entire lunar cycle, grew more slowly as larvae, and settled during both quarter moons. Fish settling during the first-quarter moon were of higher condition than third-quarter-moon settlers, which is consistent with the concept of higher predation losses and selective mortality of settlers during less-than-optimum periods. Synchronized settlement patterns can be decoupled from spawning patterns by pelagic processes and flexible larval growth schedules. Variable pelagic conditions may contribute to the maintenance of daily reproduction and flexible growth histories in marine species.

KEY WORDS: Lunar cycle · Reproductive timing · Otolith growth · Pelagic larval duration · Early life-history traits · Settlement cues · *Thalassoma bifasciatum*

INTRODUCTION

Reproduction in benthic marine animals is frequently timed to lunar or tidal amplitude cycles. Lunar or tidal cyclic spawning has been identified for sponges, corals, molluscs, polychaetes, crabs, echinoids and coral reef fishes (e.g. Harrison et al. 1984, Berry 1986, Pearse 1990, Robertson et al. 1990, Lessios 1991, Hayashibara et al. 1993, Fromont & Berquist 1994, Morgan 1995, Domeier & Colin 1997, Reyns & Sponaugle 1999). Even for reef fishes that spawn daily, actual output may vary predictably, so that effective spawning peaks during particular lunar and tidal amplitude phases (Robertson et al. 1999). Where pelagic larval durations are relatively fixed, cyclic spawning patterns should lead to cyclic settlement (Robertson et al. 1988, Meekan et al. 1993), although oceanographic variability and differential larval mortality schedules can insert sufficient noise to obscure the relationship between spawning and settlement (Danilowicz 1997, McIlwain 2002). Further, where larval durations are variable, there can be a decoupling between the timing of spawning and subsequent settlement (Danilowicz & Sale 1999, Robertson et al. 1999). Regardless of the existence of lunar cyclic or uniform spawning patterns, many species exhibit lunar or semi-lunar cyclic patterns of settlement (e.g. for reef fish and crustaceans: Robertson 1992, Thorrold et al.

*Email: ssponaugle@rsmas.miami.edu

1994, Sponaugle & Cowen 1996, Eggleston et al. 1998, Reyns & Sponaugle 1999). Much debate has focused on the underlying reasons for such observed patterns: Are cyclic spawning and settlement patterns a response to adult, larval or juvenile constraints (Robertson et al. 1990)?

Oceanographic conditions or wind stress have been previously implicated in the final transport of late-stage larvae to reefs for settlement (e.g. Thorrold et al. 1994), and recently larvae have been shown to exhibit horizontal swimming capabilities that may enable them to act independently of their surroundings (Leis & McCormick 2002). However, despite the potential and obvious role of currents in transporting larvae, lunar cyclic patterns of settlement often dominate. For example, in Barbados, spatial patterns in larval supply and juvenile abundance were related to spatial patterns in on- and offshore flow along the west coast (Sponaugle & Cowen 1996), but variation in overall current speeds did not account for much variability in temporal patterns of larval supply (Reyns & Sponaugle 1999). Daily and monthly patterns of settlement in Panama over 11 yr were unrelated to wind stress (Robertson et al. 1999). In the Great Barrier Reef, however, a combination of lunar phase and wind explained a greater proportion of variation in recruitment than lunar phase alone (Kingsford & Finn 1997).

Time series measurements of larval supply, when of sufficient duration, often reflect the existence of episodic settlement events, many of which are consistently lunar-cyclic timed yet many orders of magnitude larger than typical monthly pulses (e.g. Sponaugle & Cowen 1996, Reyns & Sponaugle 1999). These episodic events may be due to variation in spawning output, oceanographic conditions that influence the growth, mortality or transport of larvae, or changes in larval behavior that influence onshore transport. The interaction of such conditions with lunar-cyclic replenishment patterns can be difficult to study because long-term data sets and concurrent physical measurements are required.

Recent work has shown that upstream Caribbean islands such as Barbados, West Indies, regularly intercept large (~400 km in diameter; extending vertically to 20 to 30 m) anti-cyclonic rings, shed at the retroflection of the North Equatorial Counter Current and the North Brazil Current (NBC). These rings entrain low-salinity water from the Amazon River (Kelly et al. 2000, Fratantoni & Glickson 2002) and propagate northwestward along the South American coast toward the Lesser Antilles (Richardson et al. 1994, Fratantoni et al. 1995). As these low-salinity rings encounter the Barbados-Tobago ridge, they veer to the north-northwest slightly and often pass directly by or near Barbados (see Cowen et al. 2003). The passage of these water masses frequently impacts the pelagic environment surrounding Barbados (Kelly et al. 2000, Goni & Johns 2001), influencing the transport and growth of fish larvae (Cowen et al. 2003, Sponaugle & Pinkard 2004). Assuming that fish populations of Barbados are largely self-recruited (i.e. geographically isolated island with no upstream source; Cowen et al. 2000), recruits to the reef spend their larval lives in waters surrounding the island and can be influenced by the passage of these oceanographic features. We examined a 20 mo time series of settlement and successful spawning (or 'settler production', sensu Robertson et al. 1999) from Barbados to determine how encounters with such large oceanographic features influence the timing of population replenishment. Fish that encountered an NBC ring during their larval period were compared to those that did not, to identify normal (non-ring) settlement patterns and early life-history traits and determine whether these changed with larval encounter with an NBC ring. Evidence of changes in timing or, alternatively, consistent timing in the face of contrasting pelagic conditions may enable us to better identify constraints operating to generate the observed patterns in population replenishment.

MATERIALS AND METHODS

Study species. The bluehead wrasse *Thalassoma bifasciatum* (Bloch) is a common coral reef fish found throughout the Caribbean. Adults can be observed spawning midday or mid-afternoon every day of the month at most locations. Variation in female size (Petersen et al. 2001), proportion of spawning females (Robertson et al. 1999), amount of sperm released (Shapiro et al. 1994, Petersen et al. 2001), type of spawning event (Marconato et al. 1997), and water velocity (Petersen et al. 2001) can influence fertilization success, potentially resulting in lunar cyclic patterns of effective spawning (Hunt von Herbing & Hunte 1991, Robertson et al. 1999). In Barbados, the percentage of *T. bifasciatum* females spawning reflected a semi-lunar periodicity in egg production, coupled to the new and full moons, although these data were significant only when pooled over 2 lunar phases (Hunt von Herbing & Hunte 1991). After hatching, larvae spend a variable length of time in the plankton prior to settling to the reef, which occurs in pulses associated with particular phases of the lunar and tidal amplitude cycles (Sponaugle & Cowen 1997, Robertson et al. 1999). Larvae undergo metamorphosis while buried in the sand for 3 to 5 d (Victor 1982), after which they emerge onto the reef as fully pigmented recruits.

Field sampling. To examine the effect of NBC rings on the timing of settler production (i.e. spawning that successfully resulted in settlers), growth of larvae, and timing of settlement, juvenile *Thalassoma bifasciatum* were censused and collected biweekly at 3 sites along the west coast of Barbados for 20 mo (April 1996 to November 1997; see Sponaugle & Pinkard 2004 for census sites, techniques and collection methods). To reconstruct a settlement record, the otoliths of collected individuals were analyzed to measure age and the timing of events during the larval and juvenile periods. Otolith increments in *T. bifasciatum* are deposited daily (Victor 1982) and record life-history events such as settlement and metamorphosis (Victor 1983, Searcy & Sponaugle 2001). Fish length and otolith length are strongly correlated, and otolith increment widths provide a relative measure of growth (Searcy & Sponaugle 2001).

To identify the age structure of new recruits, up to 15 individuals were selected randomly from each biweekly collection for otolith analysis. In total, 274 fish were selected for otolith analysis. Techniques are described in detail in Sponaugle & Pinkard (2004), but briefly, the sagittal pair of otoliths was dissected out and placed on a microscope slide in a drop of medium viscosity immersion oil. After clearing, the sagittae were read at 400× oil-immersion magnification through a Leica DMLB microscope, equipped with a polarized filter between the light source and the first stage. The image was transferred to a computer through a Dage MTI video camera and frame grabber, and sharpened and analyzed with Image Pro Plus 4.5 image analysis software. All otoliths were read by one person (S.S.), and each reading entailed the identification of all otolith increments as larval, metamorphic or juvenile, and the enumeration of those increments along the longest radius from the otolith core to edge. The characteristic metamorphic band enables the identification of timing of settlement (inner edge) and emergence (outer edge) and separates larval from juvenile increments. From these data, we obtained measures of juvenile age (post-emergence age), timing of settlement, pelagic larval duration (PLD), timing of successful spawning (i.e. successful production of recruits), and otolith growth rates (increment widths) for the larval and juvenile periods. For the estimate of larval duration and successful spawning, 2 d were added to the total number of larval increments to account for the incubation period (Victor 1982, Sponaugle & Cowen 1997, Robertson et al. 1999).

Data analysis. Census-derived density estimates and otolith-derived age structure data were combined to create a scaled settlement record for the entire 20 mo period (March 1996 to October 1997). Each biweekly collection of juveniles was assumed to have the same age-structure as the proportion of fish randomly selected from that collection for otolith aging. We further assumed that the biweekly collections would not interject cyclic behavior in the back-calculated settlement patterns. We used similar techniques to reconstruct a scaled record of successful spawning. To identify cyclic behavior over time, the scaled and raw otolith data were normalized by log-transformation prior to computing each autocorrelation function (ACF; Jassby & Powell 1990). Where lunar (~30 d) or semi-lunar (~15 d) cycling was evident, the untransformed data were collapsed into a single lunar month. Fish that settled or had been spawned on each day were assigned a lunar day (lunar day 1 = new moon). The collapsed dataset was analyzed using Rayleigh circular statistics (Batschelet 1981). Where the Rayleigh test indicated that distributions were non-uniform over the lunar month, the mean day(s) about which the data were distributed was calculated. The scaled and raw otolith data were similarly distributed over the lunar cycle (see 'Results'), so the raw data were used in all further analyses. Although the tidal amplitude cycle may play an important role in the supply of late-stage larvae to Barbados (e.g. Reyns & Sponaugle 1999), the lunar and tidal amplitude cycles are very closely related around Barbados, so for simplicity, all analyses were made using the lunar cycle.

The presence of NBC rings in the vicinity of Barbados was determined from hydrographic records from a conductivity-temperature (CT) sensor moored in 290 m-depth water, 2 km off the west coast of the island (Kelly et al. 2000). A ring was considered to be present on days when salinities at 10 to 13 m depth were less than 34.5 (Cowen et al. 2003). The low-salinity Amazon River water entrained in NBC rings is less dense, thus surface salinities are the most consistent and apparent signature of the presence of a ring.

Otolith aging enabled calculation of the actual dates when larvae were in the water column, thus, whether they encountered a ring while there. The term 'encounter' is used to indicate temporal concurrence of larvae and an NBC ring in the waters surrounding Barbados. Although we did not track larvae in the water column, *Thalassoma bifasciatum* larvae were collected from within NBC ring waters during cruises within this time period (Cowen et al. 2003). Based on these observations, the local (island) source of larvae, and the enormous diameter and vertical extent of NBC rings, the assumption of larval 'encounter' with NBC ring water is most parsimonious.

To account for possible delays in the response of otolith accretion to environmental events (e.g. McCormick & Molony 1992), we selected a window of a week to test for the influence of ring encounter.

This period was a trade-off between allowing maximum otolith responses and maintaining adequate sample sizes. Based on their age and timing of collection, aged fish were divided into those that encountered an NBC ring for at least 7 d (RING fish) during the first 40 d of their larval period and those that did not encounter an NBC ring at any time during their larval period (NO RING fish). The overall mean PLD of fish collected in Barbados was 49.4 d (±10.3). Therefore, 40 d was chosen as the cutoff, so that fish with relatively short PLDs could be included in the analyses. Fish that encountered a ring for less than 7 d (n = 49; 17.9%) were eliminated from further RING/NO RING analysis. The eliminated fish were from various collection dates and did not exhibit any unique lunar cyclic patterns that would alter the overall patterns.

The timing of settlement and (successful) spawning over a lunar month was compared for RING and NO RING fish by first calculating the autocorrelation function and then using Rayleigh circular statistics as before. Because there were distinct lunar patterns in the timing of settlement and successful spawning (see 'Results'), aged fish were grouped by the lunar phase in which they were spawned. Each lunar phase encompassed the day of each quarter phase ± 3 d: new moon = Days 27 to 4; first quarter = Days 5 to 11; full moon = Days 12 to 18; third quarter = Days 19 to 26. Mean larval otolith growth trajectories (mean otolith increment widths) were calculated for each group and compared for RING and NO RING fish using repeated measures MANOVA techniques (SYSTAT Version 8.0: Wilkinson 1992, Chambers & Miller 1995).

Previous work with *Thalassoma bifasciatum* revealed an inverse relationship between otolith growth rate and pelagic larval duration (Searcy & Sponaugle 2000). To examine whether PLD differed in the presence of NBC rings, nonparametric ANOVA tech-

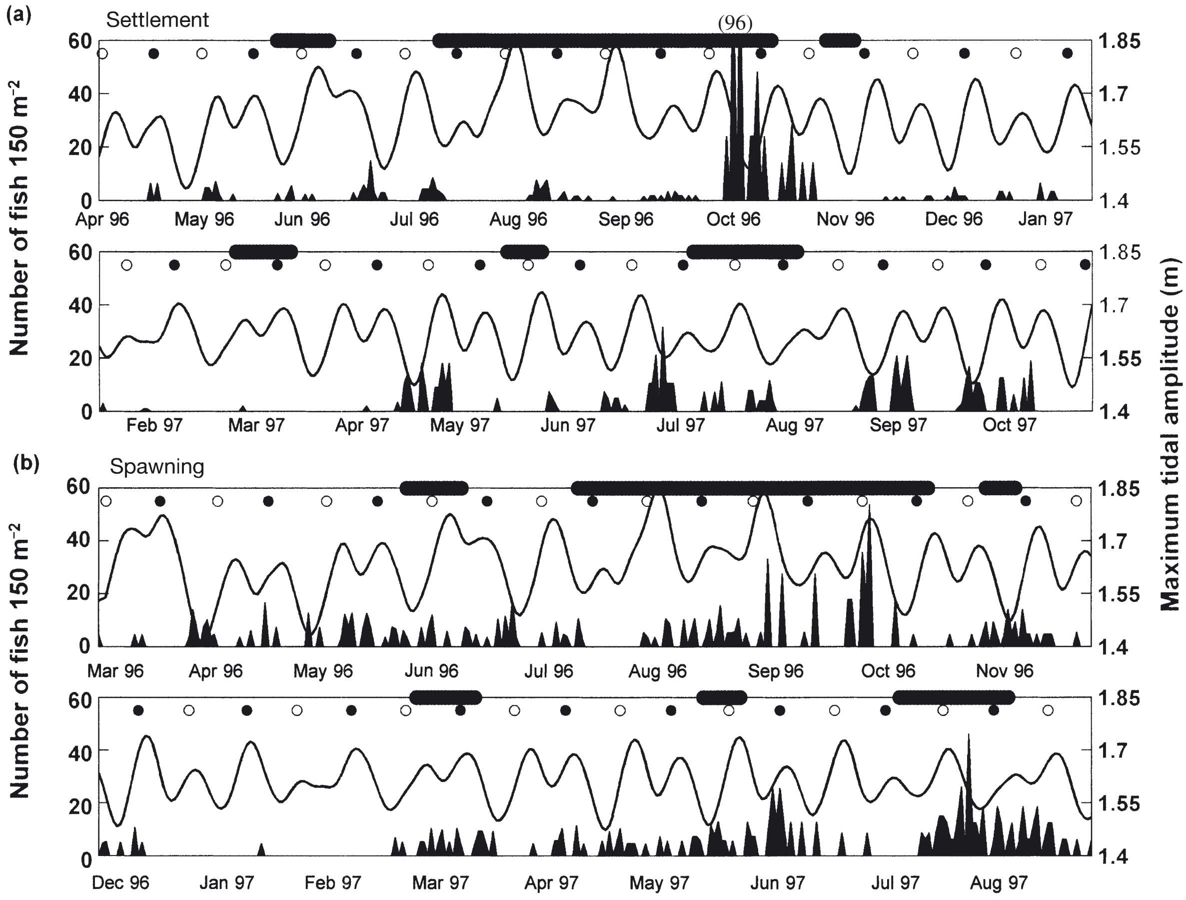

Fig. 1. *Thalassoma bifasciatum*. Raw records of (a) settlement and (b) successful spawning at Barbados over a 20 mo time period. Timing of settlement and spawning was back-calculated from otoliths of collected new recruits; magnitude of events was obtained from biweekly census data. The magnitude of the large settlement pulse in October extends beyond the plot and is indicated by the number in parentheses. Heavy black bars refer to the nearshore presence of North Brazil Current (NBC) rings (salinity ≤ 34.5). ● = new moon; ○ = full moon. Maximum amplitude tides are plotted as a continuous line

niques (Kruskal-Wallis [KW] test) were used on ranked data to compare the PLDs of RING and NO RING fish that were spawned on particular lunar phases. Original values were ranked due to low sample sizes. Where ANOVA results were significant, post-hoc Tukey tests were used to identify pair-wise differences. Post-emergence growth was similarly compared among fish spawned on a particular lunar phase that did or did not encounter an NBC ring during their larval period. Juvenile otolith growth during the first 3 d following emergence was compared among groups using the same nonparametric ANOVA techniques.

Finally, the relative condition of RING and NO RING settlers, as measured by mean PLD and metamorphic band width, at each of the quarter moons was compared by using nonparametric ANOVA techniques. Metamorphic band width is correlated with fast growth and short PLDs, and likely reflects relative condition at settlement (Searcy & Sponaugle 2001). Metamorphosis is an energetically costly, non-feeding period during which somatic growth is negligible and relative otolith accretion is likely a continuation of larval otolith accretion at the time of settlement. Higher-condition larvae may be more likely to survive this period (Searcy & Sponaugle 2001).

RESULTS

The raw record of *Thalassoma bifasciatum* settling to Barbados over 20 mo was simultaneously cyclic and episodic. Settlement was semi-lunar with peaks at the quarter moons and minimum amplitude tides (Figs. 1a & 2a, Table 1). Some peaks were of much larger magnitude than others, but the overall timing of the peaks was semi-lunar. The pattern exhibited by fish scaled according to the census data (i.e. reflecting observed densities) was similar to that exhibited by the aged fish alone (Fig. 2a). Likewise, back-calculated spawning patterns were similar for all (scaled) fish and those that were aged: raw spawning patterns were acyclic, in that spawning was evenly distributed over the lunar cycle (Figs. 1b & 2b, Table 1). Based on the similarity between aged fish and fish scaled according to census densities, all remaining analyses were conducted using only aged fish.

When fish were divided into those that encountered an NBC ring during their larval period (RING fish) versus those that did not (NO RING fish), patterns of settlement and spawning differed: NO RING fish exhibited a weak semi-lunar settlement pattern with a non-significant peak near the first-quarter moon and a significant peak at the third-quarter moon, whereas

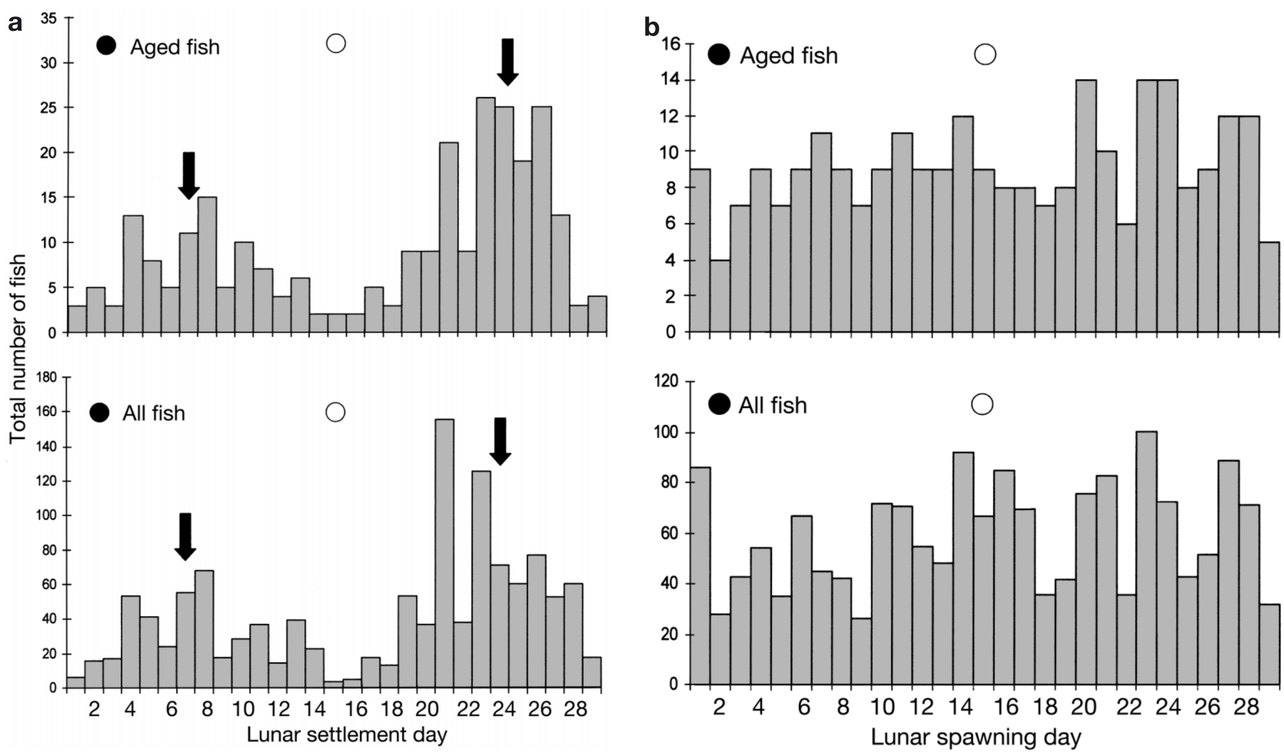

Fig. 2. *Thalassoma bifasciatum.* Distribution of (a) settlement and (b) spawning over the lunar cycle for all fish (i.e. aged fish from biweekly collections multiplied by biweekly census densities), and aged fish alone. ● = new moon; ○ = full moon. Arrows indicate mean days about which settlement was distributed

RING fish exhibited significant semi-lunar peaks of settlement associated with the quarter moons (Fig. 3, Table 1). Spawning also differed significantly between the 2 groups of fish: NO RING fish were spawned successfully, mainly on the first-quarter moon, whereas RING fish were spawned evenly over the lunar cycle (Fig. 4, Table 1).

Dividing the fish into groups based on when they were spawned demonstrates that the shift in overall settlement patterns between NO RING and RING fish was a result of a shift by full- and third-quarter-moon spawned fish from weak lunar (unimodal) or acyclic settlement patterns (during NO RING periods), to semi-lunar (bimodal) settlement during the quarter moons under RING conditions (Fig. 5). Fish spawned during the new and first-quarter moons exhibited a strong lunar (unimodal) and weak semi-lunar settlement pat-

Table 1. *Thalassoma bifasciatum.* Autocorrelations for density-normalized settlement and successful spawning data (log[number fish d^{-1}] + 1). All fish = daily time series of scaled abundance data; aged = all aged fish. NO RING fish did not encounter a North Brazil Current ring for at least 7 d during the first 40 d of larval life; RING fish did. NS indicates a time series with autocorrelation values resulting in $p > 0.05$, and * indicates a time series that results in $p < 0.05$. NA: not applicable. Time series with significant cycling includes the approximate periodicity (i.e. day) of cycling in parentheses. Approximate periodicities are also included in cases where cycling is apparent, although NS. Rayleigh test statistics are reported (2 for each test where cycling was semi-lunar) for time-series data that cycled significantly (or were NS). Z = Rayleigh test statistic. Mean day(s) = mean day about which the data were distributed

		Maximum autocorrelation test results	Rayleigh test results: n	Rayleigh test results: Z	Rayleigh test results: Mean day(s)
Settlement	All fish	NS (17 d)	448, 786	33.3*, 99.0*	7, 24
	Aged fish	*(17d)	99, 143	8.3*, 32.1*	7, 24
	NO RING fish	*(15 d)	14, 48	0.9 (NS), 3.4*	NA, 24
	RING fish	*(17 d)	68, 94	7.6*, 22.8*	6, 25
Spawning	All fish	NS			
	Aged fish	NS			
	NO RING fish	*(15 d)	40, 22	4.3*, 0.5 (NS)	8, NA
	RING fish	NS			

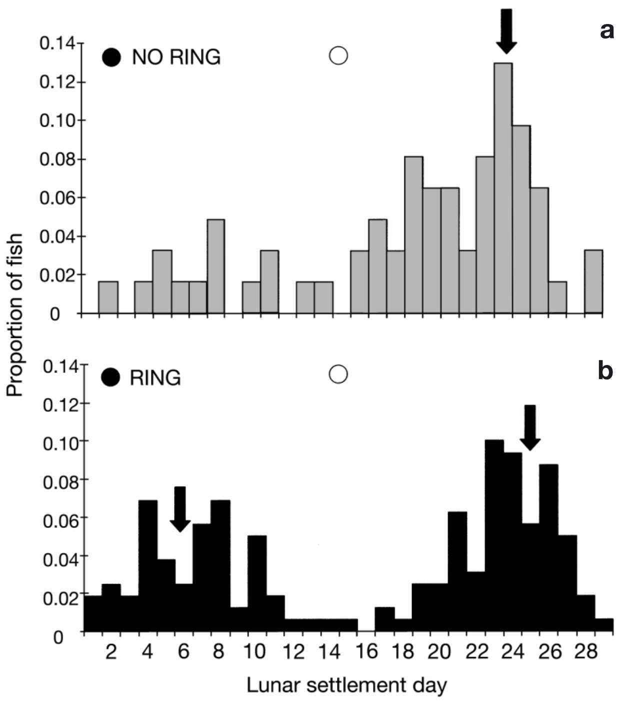

Fig. 3. *Thalassoma bifasciatum.* Distribution of settlement over the lunar cycle for (a) NO RING fish (gray bars) that did not encounter a North Brazil Current (NBC) ring for at least 7 d during their larval period, and (b) RING fish (black bars) that encountered an NBC ring for at least 7 d during their larval period. ● = new moon; ○ = full moon. Arrows indicate mean days about which settlement was distributed

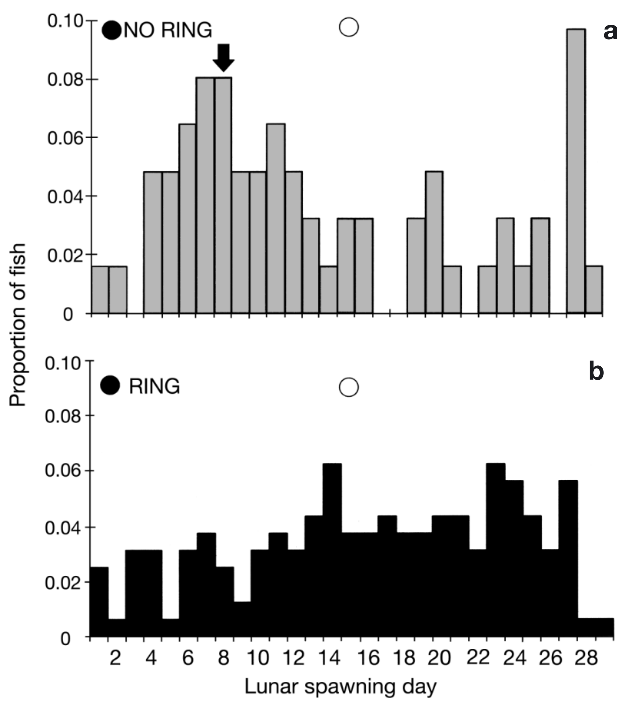

Fig. 4. *Thalassoma bifasciatum.* Distribution of successful spawning over the lunar cycle for (a) NO RING fish (gray bars) that did not encounter a North Brazil Current (NBC) ring for at least 7 d during their larval period, and (b) RING fish (black bars) that encountered an NBC ring for at least 7 d during their larval period. ● = new moon; ○ = full moon. Arrow indicates mean day about which spawning was distributed

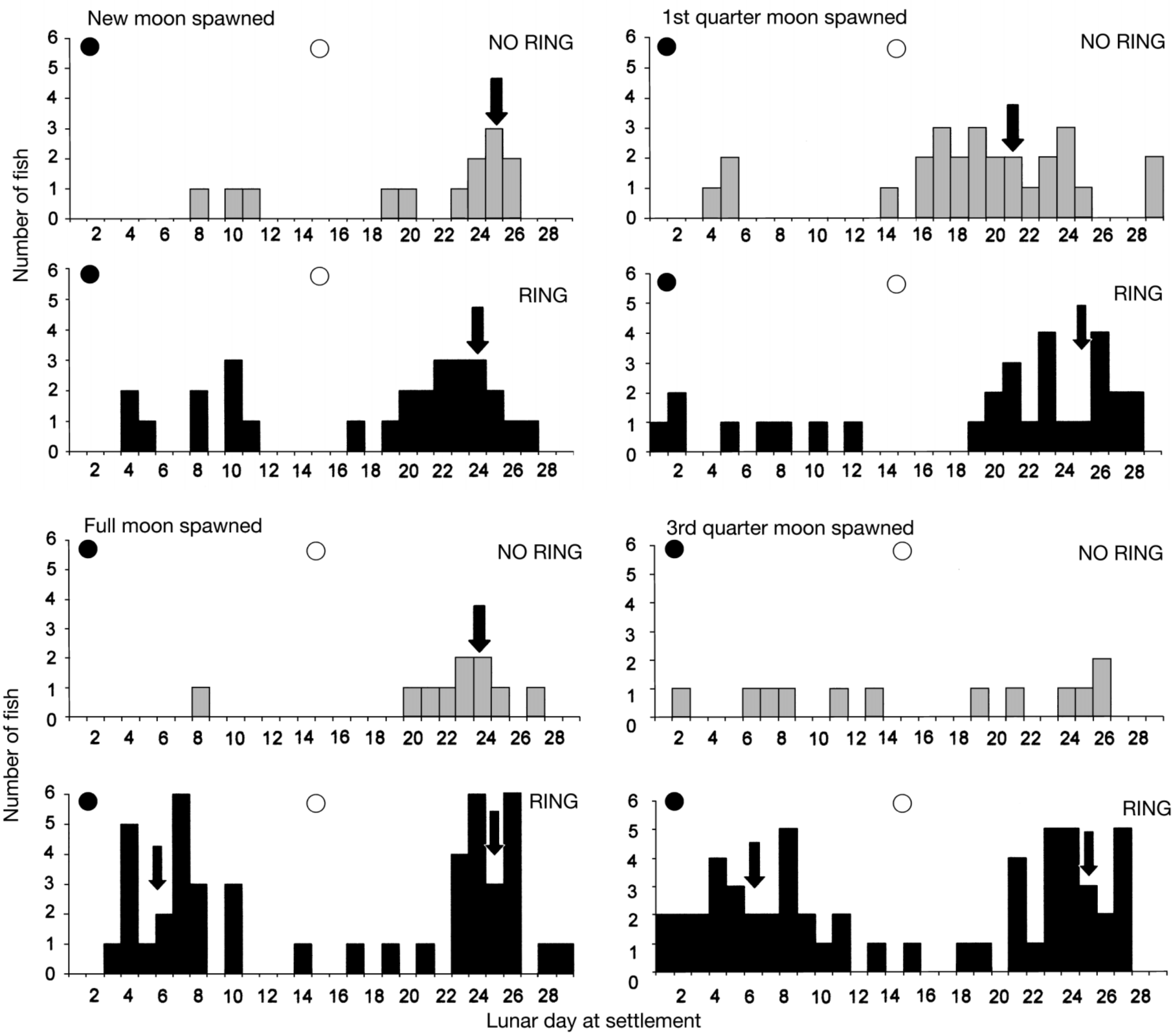

Fig. 5. *Thalassoma bifasciatum.* Distribution of settlement over the lunar cycle for groups of fish spawned during different lunar phases (● = new moon, ○ = full moon). NO RING fish (gray bars) did not encounter a North Brazil Current (NBC) ring for at least 7 d during their larval period, and RING fish (black bars) did. Arrow indicates mean day about which spawning was distributed

tern, whether or not they encountered an NBC ring. It should be noted, however, that sample sizes were particularly low for full- and third-quarter-moon spawned fish spawned during NO RING periods, and therefore strong patterns may not have been evident.

The larval otolith-growth trajectories of NO RING fish differed according to when fish were spawned. There was high variation in the otolith growth trajectories among spawning lunar phases: fish spawned on the first-quarter moon and full moon tended to have higher larval growth rates than did fish spawned on the new and third-quarter moons (Fig. 6). Low sample sizes precluded MANOVA comparisons for NO RING fish, but the trajectories of RING fish could be statistically compared. RING fish spawned on different lunar phases exhibited similar larval otolith growth trajectories (Fig. 6; MANOVA: $p = 0.14$ to 0.99). Comparison of RING and NO RING trajectories for fish spawned on each lunar phase demonstrated that growth trajectories did not differ between NO RING and RING fish that were spawned during the new and third-quarter moons (Fig. 7, Table 2). For fish spawned during the first-quarter and full moons, otolith growth trajectories of NO RING fish were consistently higher than RING fish throughout the larval period (Fig. 7). The trajectories were significantly higher for full-moon spawned fish and marginally non-significant for fish spawned on the first-quarter moon (Table 2).

As a result of generally higher larval growth rates, the PLDs of all NO RING fish generally were shorter

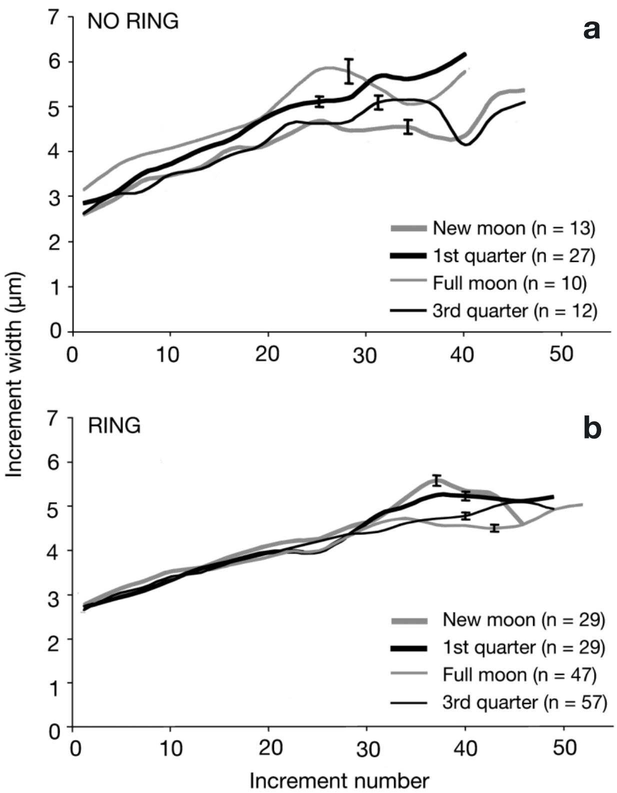

Fig. 6. *Thalassoma bifasciatum.* Larval otolith growth trajectories for (a) NO RING fish that did not encounter a North Brazil Current (NBC) ring; and (b) RING fish that did encounter an NBC ring during their larval period. Fish were separated by the lunar phase in which they had been spawned. Representative sample standard error bars are included for one increment on each line

than RING fish (Figs. 8 & 9). Division of the fish by the lunar phase in which they were spawned demonstrated that there was a significant influence of lunar phase and ring presence, as well as a significant interaction (KW test: RING: $p < 0.001$, df = 1; Lunar phase: $p = 0.047$, df = 3; RING × Lunar phase: $p = 0.013$, df = 3). NO RING fish spawned on the first-quarter and full moons had significantly shorter mean PLDs than did NO RING fish spawned on the third-quarter and new moons (Fig. 9). Fish spawned during the first-quarter and full moons had significantly higher mean PLDs in the presence of rings than not, but the mean PLD of those spawned during the new and third-quarter moons did not differ significantly in the presence of rings (Fig. 9). The mean PLD of RING fish spawned during the full moon was significantly higher than RING fish spawned during the first-quarter or new moon.

To examine whether condition differed among fish settling during different lunar phases, the PLD and metamorphic band width of RING fish settling during each quarter moon were compared to each other. While the overall mean PLD of fish settling during the quarter moons was longer during RING events relative to NO RING fish (KW test: RING: $p = 0.001$, df = 1), there was no significant difference in PLD among RING fish settling during the quarter moons (KW test: Lunar phase: $p = 0.226$, df = 1; RING × Lunar phase: $p = 0.272$, df = 1). However, mean metamorphic bandwidth was consistently higher for fish settling during the first-quarter moon (KW test: RING: $p = 0.014$, df = 1; Lunar phase: $p = 0.044$, df = 1; RING × Lunar phase: $p = 0.433$, df = 1; Fig. 10).

As a means of determining whether differences in larval life-history traits as a function of ring encounter or lunar phase were expressed in juvenile life, post-settlement otolith growth trajectories were examined. Unlike larval growth, mean juvenile otolith growth during Days 1 to 3 post-emergence was unrelated to spawning phase and encounter with rings (KW test: RING, Lunar phase, RING × Lunar phase: $p > 0.05$).

DISCUSSION

Benthic marine organisms frequently exhibit synchronized spawning and settlement patterns, the ultimate causes of which have been widely discussed, yet remain largely unresolved (Robertson et al. 1990, Morgan 1995, Sancho et al. 2000). This study was undertaken to identify cycles of settlement and successful spawning for a common coral reef fish and to determine whether encounters with episodic meso-scale oceanographic features would disrupt these patterns. Examination of changes in rhythmic behavior has the potential to shed light on both proximate and perhaps ultimate causes of reproductive synchrony.

Examination of the spawning dates of successful recruits, *in situ* observations, and previous reports demonstrate that *Thalassoma bifasciatum* spawns daily at Barbados. Regardless of whether or not actual spawning output is continuous or peaks over the lunar month (e.g. Hunt von Herbing & Hunte 1991, Robertson et al. 1999), recruits that settled to Barbados over a 20 mo time period were spawned during all periods of the lunar cycle. Fish that were spawned evenly over the lunar cycle settled with semi-lunar periodicity during the quarter moons and minimum amplitude tides. Thus, synchrony at settlement was decoupled from spawning patterns. The particularly unique aspect of the present study, however, is the finding that these patterns differed when fish were separated according to whether or not they encountered large oceanographic features during their larval period.

The nearshore passage of NBC rings in the vicinity of Barbados can lead to several transport-related results depending on the ring structure, angle of impingement

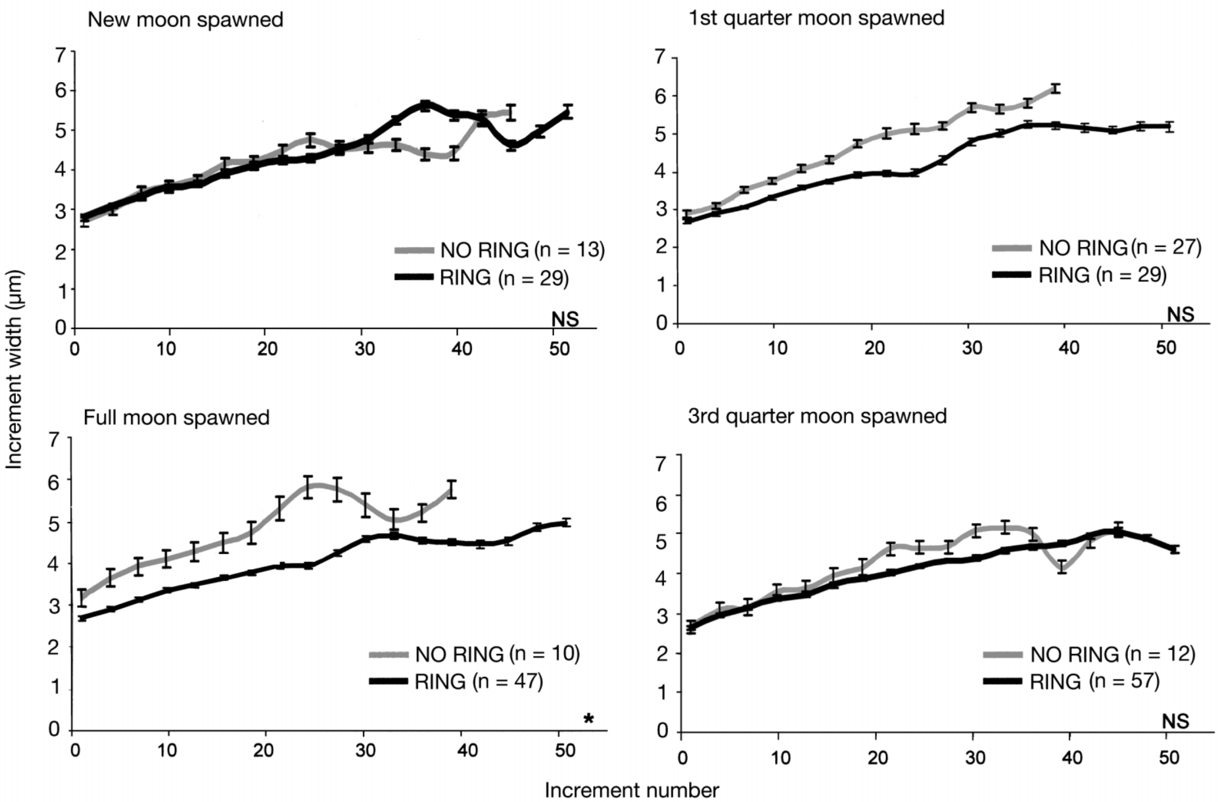

Fig. 7. *Thalassoma bifasciatum.* Larval otolith growth trajectories (mean ± SE) for NO RING fish that did not encounter a North Brazil Current (NBC) ring and RING fish that did encounter an NBC ring during their larval period. Fish were separated by the lunar phase in which they had been spawned

and vertical distribution of larvae (Cowen et al. 2003). Island larvae can either be advected (flushed) out to sea and lost to the island system, or retained nearshore for longer time periods. Because our study is based entirely on successful recruits, larvae lost to sea were not included in the analysis. Therefore, fish that encounter an NBC ring and survive to settle are most likely those that experienced enhanced nearshore retention.

Despite daily spawning by *Thalassoma bifasciatum*, under normal (non-ring) conditions, successful recruits (survivors) were those that were spawned mostly during the first-quarter moon and neap tides. Larvae spawned during this time had faster growth rates and shorter PLDs, and therefore likely experienced higher survivorship. Preferential survival of offspring spawned during neap tides is consistent with a hypothesis that offshore transport would be

Table 2. *Thalassoma bifasciatum.* Summary of repeated measures MANOVA results for growth of recruits to Barbados by the lunar phase they were spawned. NO RING fish did not encounter a North Brazil Current ring for at least 7 d during the first 40 d of larval life; RING fish did. df_h = hypothesis degrees of freedom. df_e = error degrees of freedom. Wilk's λ = multivariate test statistic. *$p < 0.05$; NS = non significant; NA = not applicable. Trend refers to the results of a Tukey's post-hoc analysis with significance at $p < 0.05$

	New moon NO RING vs RING	1st quarter NO RING vs RING	Full moon NO RING vs RING	3rd quarter NO RING vs RING
n	42	56	57	69
df_h	30	30	30	30
df_e	11	27	26	38
Wilk's λ	0.232	0.332	0.241	0.598
F	1.213	1.813	2.727	0.852
P	0.383 (NS)	0.061 (NS)	0.006*	0.671 (NS)
Trend	NA	NA	NO RING > RING	NA

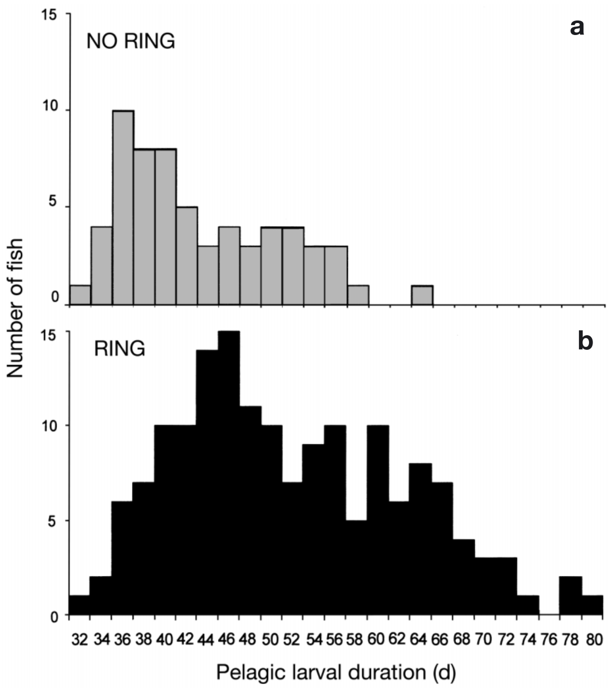

Fig. 8. *Thalassoma bifasciatum.* Pelagic larval durations of recruits to Barbados over a 20 mo time period for (a) NO RING fish (gray bars) that did not encounter a North Brazil Current (NBC) ring; and (b) RING fish (black bars) that did encounter a NBC ring during their larval period

reduced during minimum amplitude tides. Because there is no corresponding spawning peak during the neap tides associated with the third-quarter moon, there is at least another cyclical process contributing to this pattern of egg and larval transport. The timing of neap tides with semidiurnal flood/ebb, for example, can result in an inequity in the transport-related advantages of offspring spawned during a particular time of day for each quarter moon. However, the specific timing of the critical window(s) in the early life of eggs and larvae, early swimming capabilities of larvae, and their susceptibility to starvation and predation are unknown at this time; therefore, it is presently impossible to know which factors may be more or less important. Regardless of these additional factors, spawning during minimum-amplitude tides associated with the first-quarter moon should reduce offshore dispersal and enhance nearshore retention of offspring.

Retention of eggs and larvae close to shore where nutrients are higher (Hernandez-Leon 1988, Rissik et al. 1997) enhances larval growth (Searcy & Sponaugle 2000; evident in the higher larval otolith growth of fish spawned during the first-quarter moon, and the first few full moon days immediately following this). Faster growth leads to faster attainment of minimum settlement condition (Searcy & Sponaugle 2000), thus the PLDs of these fish also were shorter. Reduced offshore transport, enhanced growth, and shorter PLDs should combine to increase the survivorship of larvae spawned under normal conditions during the first-quarter moon.

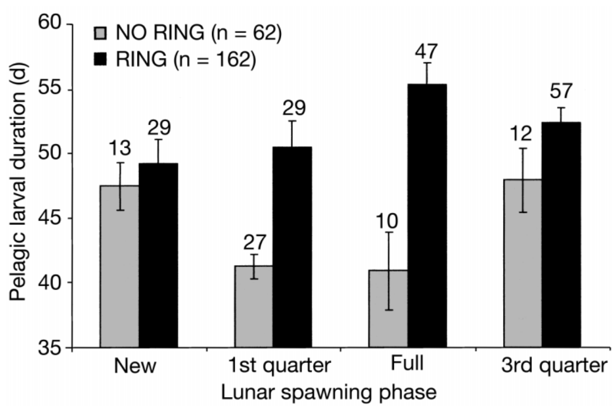

Fig. 9. *Thalassoma bifasciatum.* Mean (±1 SE) pelagic larval duration for fish spawned during each of the 4 lunar phases. NO RING fish did not encounter a North Brazil Current (NBC) ring during their larval period, and RING fish did. Sample sizes are indicated by a number at the top of each bar

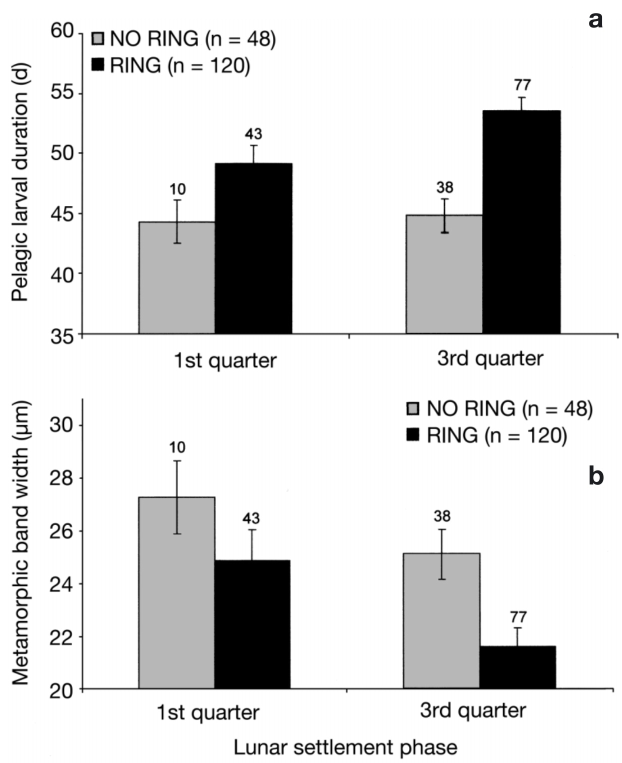

Fig. 10. *Thalassoma bifasciatum.* Mean (±1 SE) (a) pelagic larval duration and (b) metamorphic band width (proxy for condition) of fish settling during the quarter moons. NO RING fish did not encounter a North Brazil Current (NBC) ring during their larval period and RING fish did. Sample sizes are indicated by a number at the top of each bar

The spawning periodicity exhibited by NO RING fish disappeared entirely when fish encountered an NBC ring during their larval period. During RING conditions, successful settlers were spawned over all periods of the lunar cycle. Larvae spawned during all lunar phases were retained equally when NBC rings were present. The nearshore presence of these large ring features not only changed transport-related processes, but also significantly changed the signature of the water mass. Water salinities were reduced during ring events and there was likely a concomitant shift in prey that resulted in significantly reduced growth for larvae (Cowen et al. 2003, Sponaugle & Pinkard 2004). Thus, although all larvae were retained nearshore (i.e. generally a high-growth environment) during these events, overall larval growth rates were significantly reduced rather than enhanced (Sponaugle & Pinkard 2004). This was most noticeable for fish that were spawned during the first quarter and full moons. Otolith growth trajectories for fish spawned during the new and third quarter moons did not differ significantly between fish that did or did not encounter an NBC ring. Assuming these fish were normally transported farther offshore into waters with fewer prey, offshore growth rates were not significantly higher than growth during ring events. Likewise, mean PLDs were more similar among lunar spawning phases for RING fish (only the PLD of full-moon spawned fish was significantly longer than first-quarter and new-moon spawned fish). Thus, significant differences in larval growth and PLD that normally exist among fish spawned during different lunar phases were tempered when fish encountered an NBC ring.

Settlement of *Thalassoma bifasciatum* during NO RING conditions was weakly semi-lunar but peaked significantly only on the third-quarter moon, whereas during RING events, settlement was clearly semi-lunar with significant peaks at both quarter moons. Peak settlement during the third-quarter moon did not change for RING versus NO RING fish, but fish that encountered a ring also settled frequently during the first-quarter moon, resulting in the shift from weakly semi-lunar (almost lunar) to semi-lunar cyclic settlement with ring encounter.

Successful recruitment of RING fish during both quarter moons demonstrates that settlement and survival of *Thalassoma bifasciatum* is possible during both of these lunar phases. The semi-lunar nature of the patterns during RING conditions suggests that tides play a significant role in the settlement of this species, independent of spawning. Since RING fish were generally of lower condition than NO RING fish, it is conceivable that the longer a larva spends in the plankton, the trade-off between remaining in the plankton and settling changes, resulting in the larva becoming less selective with regard to the timing of settlement. However, in contrast to this idea, and regardless of larval encounter with rings, first-quarter-moon settlers were always of higher condition than third-quarter-moon settlers.

Results of this study are consistent with the concept of larvae reaching a minimum condition to settle (Searcy & Sponaugle 2000) and then settling on the nearest quarter moon. The lack of first-quarter-moon settlers during NO RING conditions is likely the result of larvae from other spawning phases being relatively unavailable. Only larvae spawned during the first-quarter moon survived to recruit, and based on their rapid growth, their settlement was correspondingly coupled to the third-quarter moon. Therefore, depending on pelagic conditions (presence or absence of a NBC ring), the degree of spawning-settlement coupling may vary. Pelagic conditions affect the transport, growth and survivorship of larvae, each of which can decouple the relationship between spawning and settlement (Danilowicz 1997).

It is also possible that transport conditions during the quarter moons/neap tides change with the presence of NBC rings such that settlement is more likely during the first-quarter moon than it is during NO RING conditions. Ring events have been known to generate internal tides due to stratification, resulting from the presence of low-salinity water (Krauss 1999), and internal tides and tidal bores generally occur more frequently during quarter moons (Pineda 1995). However, during the first 7 mo of this study period, brachyuran post-larvae (megalopae) exhibited semi-lunar settlement pulses regardless of the presence of NBC rings (Reyns & Sponaugle 1999). So, while we cannot eliminate the possibility of such a change in transport mechanisms, the data are more consistent with there simply being a lack of NO RING larvae available for settlement during the first-quarter moon.

Settlement during the third-quarter moon was a consistent observation throughout this study regardless of larval encounter with NBC rings. Synchronization of settlement with the third-quarter moon is a widespread phenomenon among fishes and crustaceans at Barbados. Nightly time-series collections from light traps at Barbados demonstrated that many fish species settle during the third-quarter moon and neap tides (Sponaugle & Cowen 1996). Similarly, settlement of brachyuran crabs to Barbados was frequently semi-lunar, peaking on the quarter moons and neap tides, but often with a dominant pulse on the third-quarter moon (Reyns & Sponaugle 1999). Minimum amplitude tides may be easier to swim against and nights become progressively darker between the third-quarter and new moon, potentially reducing losses to predation (Sponaugle & Cowen 1997). The converse occurs during the first-quarter moon: brighter nights during the first-quarter moon should reduce settler survival. Yet fish that encountered a NBC ring frequently settled during the first-quarter moon. The fact that first-quarter-moon settlers were consistently of higher condition may reflect higher predation and greater selective mortality, such that only the highest-condition fish survive. Alternatively, settlement during the first-quarter moon may be relatively more common during ring events because the water is less transparent during these times (Cowen et al. 2003), potentially reducing moonlight to a level similar to that seen during third-quarter moon periods.

The degree to which RING versus NO RING conditions represent 'normal' is debatable. In fact, during this study more fish were influenced by an NBC ring for at least 7 d than were not (all fish: n = 872 RING vs 198 NO RING; aged fish: n = 162 RING vs 62 NO RING). We cannot determine whether fish are more or less likely to recruit successfully with the encounter of an NBC ring because there can be conflicting effects. For example, contact with an NBC ring inevitably reduces the growth of larvae, but simultaneously may enhance retention and reduce loss to offshore environments (Cowen et al. 2003). Conversely, encounter with some NBC rings can sharply reduce nearshore larval retention (Cowen et al. 2003), but this study did not track those lost fish. Fish used in this analysis clearly were able to recruit regardless of their encounter with normal or NBC ring conditions. Such variation in pelagic conditions and resulting selective mortality, or lack thereof, of fish spawned during particular lunar phases may contribute to the persistence of daily spawning. If fish spawned during the first-quarter moon are consistently the only ones to survive under normal conditions, over long time periods fish in such a self-recruiting population should minimize losses and spawn exclusively during the most favorable time. However, variable pelagic conditions would tend to operate against this adaptation, as successful recruits over the 20 mo time period exhibited a broad set of early life-history traits.

Do any of these observations shed light on ultimate causes of synchronized reproduction? Lunar synchrony of adult spawning is likely unimportant for optimizing larval survival: under NO RING conditions there was preferential survival of offspring depending on when they were spawned, but adults either exhibited no lunar patterns of spawning or at least not peaks on the quarter moons (Hunt von Herbing & Hunte 1991). Further, the selective advantage of spawning time changed with pelagic conditions. Spawning does not appear to be timed to promote dispersal or distant transport off-reef, since the survivors during NO RING conditions were larvae spawned during minimum amplitude tides. These larvae had the fastest growth and shortest PLD, thus likely the highest survival rates. Aggregation of spawners on downstream locations and spawning on outgoing tides may remove young from the immediate vicinity of the reef as well as enhance fertilization success (Warner 1988, Hensley et al. 1994); however, spawning during neap tides would tend to retain larvae closer to the natal population than spawning during spring tides. There is generally high diversity and plasticity in the timing of spawning by reef fishes (e.g. Colin & Bell 1991, Sancho et al. 2000). Understanding more about the scales of dispersal, as well as the critical periods during larval life, would shed light on the underlying use of cues, and at what points the combination of environmental cues and processes play an important role in larval survivorship.

Flexibility or plasticity in the length of larval life may enable larvae to more closely time settlement to optimum periods (Sponaugle & Cowen 1994, Robertson et al. 1999); however, long PLDs also often reflect low condition in *Thalassoma bifasciatum*. Once a minimum settlement condition is attained and the appropriate settlement habitat is near, is there anything to be gained by remaining in the plankton where mortality rates are high? There is probably a trade-off between remaining in the plankton until an optimal settlement time and settling as soon as possible at a suboptimal time. During suboptimal settlement periods, stronger selective pressures may result in higher mortality and stronger selection for high-condition settlers (see Sogard 1997 for review of size-selective mortality). First-quarter moon settlers were consistently of higher condition than third-quarter moon settlers, suggesting that only relatively high-condition larvae may be able to settle and survive during less optimum conditions. Low condition larvae may delay settlement until an optimal settlement time, or settle immediately and experience lower survival during suboptimal periods. Either process results in the observation of heightened settlement synchrony of low condition fish with more optimal times. Comparable data on the relative condition of late-stage larvae settling during those periods is needed to determine whether this occurs by behavioral choice or preferential survival of settlers.

Following settlement, many of the differences in larval growth related to ring encounter and spawning lunar phase did not persist in the juvenile phase. There were no significant differences in juvenile growth during the first 3 d on the reef among fish that were spawned during different lunar phases. This is consistent with results found for all fish combined, and likely reflects differences in the constraints of a benthic existence (Sponaugle & Pinkard 2004). The opposing constraints experienced by larvae and juveniles likely further contribute to the persistence of daily spawning and flexible growth schedules exhibited by *Thalassoma bifasciatum*.

In summary, observed synchrony in temporal patterns of successful spawning and settlement in a coral reef fish varies depending on the oceanographic conditions encountered by larvae. Larval encounter with meso-scale low salinity ocean-current rings influences larval transport and growth, and leads to a shift in the synchrony of population replenishment. Such variability in pelagic conditions may contribute to the flexibility in reproduction and larval growth. Overall, the multitude of processes occurring during the early life of reef fishes can substantially obscure the linkages between events occurring during larval life and successful recruitment.

Acknowledgements. This manuscript benefited from the comments of R. Cowen, C. Paris, K. Grorud-Colvert, M. Sullivan, M. Kiflawi and 4 anonymous reviewers. S. Dorsey, N. Reyns, S. Searcy, C. Masterson, and M. Frey collected the samples. C. Paris assisted with the interpretation of the physical data and J. Fortuna designed the image processing macros and database. The fieldwork for this project was supported by National Science Foundation Grant No. OCE-9521104 to R. Cowen, K. Lwisa and E. Schultz. Data analysis was supported by NSF Grant No. OCE-9986359 to S.S.

LITERATURE CITED

Batschelet E (1981) Circular statistics in biology. Academic Press, New York

Berry AJ (1986) Semi-lunar and lunar spawning periodicity in some tropical littorinid gastropods. J Mollusc Stud 52: 144–149

Chambers RC, Miller TJ (1995) Evaluating fish growth by means of otolith increment analysis: special properties of individual-level longitudinal data. In: Secor DH, Dean JM, Campana SE (eds) Recent developments in fish otolith research. University of South Carolina Press, Columbia, p 155–175

Colin PL, Bell LJ (1991) Aspects of spawning of labrid and scarid fishes (Pisces: Labroidei) at Enewetak Atoll, Marshall Islands with notes on other families. Environ Biol Fish 31:229–260

Cowen RK, Lwiza KMM, Sponaugle S, Paris CB, Olson D (2000) Connectivity of marine populations: Open or closed? Science 287:857–859

Cowen RK, Sponaugle S, Paris CB, Fortuna JL, Lwiza KMM, Dorsey S (2003) Impact of North Brazil Current rings on local circulation and coral reef fish recruitment to Barbados, West Indies. In: Goni GJ, Rizzoli PM (eds) Interhemispheric water exchange in the Atlantic Ocean. Elsevier, Amsterdam, p 443–462

Danilowicz BS (1997) A potential mechanism for episodic recruitment of a coral reef fish. Ecology 78:1415–1423

Danilowicz BS, Sale PF (1999) Modelling settlement in open populations of reef fishes. Ecol Model 121:261–276

Domeier ML, Colin PL (1997) Tropical reef fish spawning aggregations: defined and reviewed. Bull Mar Sci 60: 698–726

Eggleston DB, Lipcius RN, Marshall LS, Ratchford SG (1998) Spatiotemporal variation in postlarval recruitment of the Caribbean spiny lobster in the central Bahamas: lunar and seasonal periodicity, spatial coherence, and wind forcing. Mar Ecol Prog Ser 174:33–49

Fratantoni DM, Glickson DA (2002) North Brazil Current ring generation and evolution observed with SeaWiFS. J Phys Oceanogr 32-3:1058–1074

Fratantoni DM, Johns WE, Townsend TL (1995) Rings of the North Brazil Current: their structure and behaviour inferred from observations and a numerical simulation. J Geophys Res 100:10 633–10 654

Fromont J, Bergquist PR (1994) Reproductive biology of three sponge species of the genus *Xestospongia* (Porifera, Demospongiae, Petrosida) from the Great Barrier Reef. Coral Reefs 13:119–126

Goni G, Johns WE (2001) A census of North Brazil Current rings observed from TOPEX/POSEIDON altimetry: 1992–1998. Geophys Res Lett 28:1–4

Harrison PL, Babcock RC, Oliver JK, Bull GD, Wallace CC, Willis BL (1984) Mass spawning in the tropical reef corals. Science 223:1186–1189

Hayashibara T, Shimoike K, Kimura T, Hosaka S, Heyward A, Harrison P, Kudo K, Omori M (1993) Patterns of coral spawning at Akajima Island, Okinawa, Japan. Mar Ecol Prog Ser 101:253–262

Hensley DA, Appeldoorn RS, Shapiro DY, Ray M, Turingan RG (1994) Egg dispersal in a Caribbean coral reef fish, *Thalassoma bifasciatum*. I. Dispersal over the reef platform. Bull Mar Sci 54:256–270

Hernandez-Leon S (1988) Gradients of mesozooplankton biomass and ETS activity in the wind-shear area as evidence of an island mass effect in the Canary Island Waters. J Plankton Res 10:1141–1154

Hunt von Herbing I, Hunte W (1991) Spawning and recruitment of the bluehead wrasse *Thalassoma bifasciatum* in Barbados, West Indies. Mar Ecol Prog Ser 72:49–58

Jassby AD, Powell TM (1990) Detecting changes in ecological time series. Ecology 71:2044–2052

Kelly PS, Lwiza KMM, Cowen RK, Goni G (2000) Low-salinity pools at Barbados West Indies: their origin frequency and variability. J Geophys Res 105 (C8):19 699–19 708

Kingsford M, Finn M (1997) The influence of phase of the moon and physical processes on the input of presettlement fishes to coral reefs. J Fish Biol 51:176–205

Krauss W (1999) Internal tides resulting from the passage of surface tides through an eddy field. J Geophys Res 104 (C8):18 323–18 331

Leis JM, McCormick MI (2002) The biology, behavior and ecology of the pelagic larval stage of coral reef fishes. In: Sale PS (ed) Coral reef fishes: dynamics and diversity in a complex ecosystem. Academic Press, San Diego, p 171–199

Lessios HA (1991) Presence and absence of monthly reproductive rhythms among eight Caribbean echinoids off the coast of Panama. J Exp Mar Biol Ecol 153:27–47

Marconato A, Shapiro DY, Petersen CW, Warner RR, Yoshikawa T (1997) Methodological analysis of fertilization rate in the bluehead wrasse *Thalassoma bifasciatum*: pair versus group spawns. Mar Ecol Prog Ser 161:61–70

McCormick MI, Molony BW (1992) Effects of feeding history on the growth characteristics of a reef fish at settlement. Mar Biol 114:165–173

McIlwain JL (2002) Link between reproductive output and larval supply of a common damselfish species, with evidence of replenishment from outside the local population. Mar Ecol Prog Ser 236:219–232

Meekan MG, Milicich MJ, Doherty PJ (1993) Larval production drives temporal patterns of larval supply and

recruitment of a coral reef damselfish. Mar Ecol Prog Ser 93:217–225
Morgan SG (1995) The timing of larval release. In: McEdward L (ed) The ecology of marine invertebrate larvae. CRC Press, Boca Raton, FL, p 157–191
Pearse JS (1990) Lunar reproductive rhythms in marine invertebrates: maximizing fertilization? In: Hosin M, Yamashita O (eds) Advances in invertebrate reproduction. Elsevier, Oxford, p 311–316
Petersen CW, Warner RR, Shapiro DY, Marconato A (2001) Components of fertilization success in the bluehead wrasse, *Thalassoma bifasciatum*. Behav Ecol 12:237–245
Pineda J (1995) An internal tidal bore regime at nearshore stations along western USA: predictable upwelling within the lunar cycle. Cont Shelf Res 15:1023–1041
Reyns N, Sponaugle S (1999) Patterns and processes of brachyuran crab settlement to Caribbean coral reefs. Mar Ecol Prog Ser 185:155–170
Richardson PL, Hufford GE, Limeburner R, Brown WS (1994) North Brazil Current retroflexion eddies. J Geophys Res 99:5081–5093
Rissik D, Suthers IM, Taggart CT (1997) Enhanced zooplankton abundance in the lee of an isolated reef in the South Coral Sea: the role of flow disturbance. J Plankton Res 19:1347–1368
Robertson DR (1992) Patterns of lunar settlement and early recruitment in Caribbean reef fishes at Panama. Mar Biol 114:527–537
Robertson DR, Green DG, Victor BC (1988) Temporal coupling of production and recruitment of larvae of a Caribbean reef fish. Ecology 69:370–381
Robertson DR, Petersen CW, Brawn JD (1990) Lunar reproductive cycles of benthic-brooding reef fishes: reflections of larval biology or adult biology? Ecol Monogr 60:311–329
Robertson DR, Swearer SE, Kaufmann K, Brothers EB (1999) Settlement vs environmental dynamics in a pelagic-spawning reef fish at Caribbean Panama. Ecol Monogr 69: 195–216
Sancho G, Solow AR, Lobel PS (2000) Environmental influences on the diel timing of spawning in coral reef fishes. Mar Ecol Prog Ser 206:193–212
Searcy S, Sponaugle S (2000) Variable larval growth in a coral reef fish. Mar Ecol Prog Ser 206:213–226
Searcy S, Sponaugle S (2001) Selective mortality during the larval-juvenile transition in 2 coral reef fishes. Ecology 82: 2452–2470
Shapiro DY, Marconato A, Yoshikawa T (1994) Sperm economy in a coral reef fish, *Thalassoma bifasciatum*. Ecology 75:1334–1344
Sogard SM (1997) Size-selective mortality in the juvenile stage of teleost fishes: a review. Bull Mar Sci 60: 1129–1157
Sponaugle S, Cowen RK (1994) Larval duration and recruitment patterns of two Caribbean gobies (Gobiidae): contrasting early life histories in demersal spawners. Mar Biol 120:133–143
Sponaugle S, Cowen RK (1996) Nearshore patterns of coral reef fish larval supply to Barbados West Indies. Mar Ecol Prog Ser 133:13–28
Sponaugle S, Cowen RK (1997) Early life history traits and recruitment patterns of Caribbean wrasses (Labridae). Ecol Monogr 67:177–202
Sponaugle S, Pinkard DR (2004) Impact of variable pelagic environments on natural larval growth and recruitment of a reef fish. J Fish Biol 64:34–54
Thorrold SR, Shenker JM, Maddox ED, Mojica R, Wishinski E (1994) Larval supply of shorefishes to nursery habitats around Lee Stocking Island, Bahamas. II. Lunar and oceanographic influences. Mar Biol 118:567–578
Victor BC (1982) Daily otolith increments and recruitment in two coral-reef wrasses *Thalassoma bifasciatum* and *Halichoeres bivittatus.* Mar Biol 71:203–208
Victor BC (1983) Settlement and larval metamorphosis produce distinct marks on the otoliths of the slippery dick *Halichoeres bivittatus.* In: Reaka ML (ed) The ecology of deep and shallow coral reefs. Symposium Series on Underwater Research, Vol. 1, National Oceanic and Atmospheric Administration, Rockville, MA, p 47–51
Warner R (1988) Traditionality of mating-site preferences in a coral reef fish. Nature 335:719–721
Wilkinson L (1992) SYSTAT: the system for statistics. SYSTAT, Evanston, IL

Editorial responsibility: Otto Kinne (Editor), Oldendorf/Luhe, Germany

Submitted: June 30, 2003; Accepted: September 30, 2003
Proofs received from author(s): February 9, 2004