Temporal patterns in the larval supply of summer-recruiting reef fishes to Lee Stocking Island, Bahamas

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ABSTRACT: Moored plankton nets were used to monitor the supply of settlement-stage reef fishes to benthic habitats on Great Bahamas Bank in the vicinity of Lee Stocking Island, Exuma Sound, Bahamas. A total of 55 771 fishes, representing 53 taxa, were captured in 79 d of sampling from June to September 1992. Reef fish larvae were extremely abundant in the samples, particularly the families Labridae, Apogonidae, Balistidae, Ophichthidae and Scaridae. Almost all fish were taken in night collections, and discrete tide sampling suggested most settlement-stage fishes were moving onshore during flood tides. Vertical distributions were taxon specific, with some taxa concentrated in surface nets while others were more abundant in mid-water collections. Larval supply of a number of taxa occurred almost entirely during several days around the new moon in early July, while other families showed more consistent, although still episodic, replenishment patterns. Time series analysis found evidence of semi-lunar cycling in the larval supply of scarids and ophichthids, lunar cycling in gobiids, bothids and apogonids, and acyclic replenishment in clupeids, blennioids, labrids and balistids. Cross-correlations between larval supply and meteorological and hydrographic variables found significant associations in the families Gobiidae, Apogonidae, Blennioidei and Labridae. Significant correlations were driven by a large pulse of replenishment of all these taxa coinciding with a relaxation of southeast trade winds. This event apparently caused a reversal in the direction of longshore currents and generated significant onshore current flow. Settlement-stage larvae may have been transported from the northern region of Exuma Sound to Lee Stocking Island. Alternatively, larvae may have been entrained from offshore waters in the southern Sound and advected across the shelf to reef areas.

KEY WORDS: Larval supply · Reef fish · Channel nets · Hydrography · Meteorology · Recruitment

INTRODUCTION

Almost all of the fishes associated with coral reefs share a bipartite life history with reef-associated demersal stages releasing pelagic eggs or larvae (Leis & Goldman 1987, Victor 1991). While a considerable amount of literature has been generated on the ecology of adult reef fishes, the larval phase has attracted comparatively little attention (Leis 1991). Tropical reef fish larvae spend little time in the plankton compared to temperate analogs (often less than 1 mo; e.g. Brothers et al. 1983, Thresher et al. 1989, Wellington & Victor 1989, Thorrold & Milicich 1990) and are notoriously difficult to sample (Choat et al. 1993). Potential for very high mortality and considerable dispersal abilities suggest, however, that survival and settlement of larvae may regulate the size of adult population (Williams 1980, Doherty 1983, Victor 1983, 1986). Extremely large inter-annual variability in the recruit-

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ment of recently settled fishes to coral reef habitats supports this contention (reviewed by Doherty & Williams 1988, Doherty 1991). More impressively, recruitment variability has been shown in at least 1 fish species to leave indelible signatures on the demographic structure of adult populations up to 10 yr later (Doherty & Fowler 1994). The number of settlement-stage fishes returning to juvenile habitats may, then, be a critical determinant of recruitment levels and ultimately stock sizes in reef fish populations.

A suite of biological and physical processes may act to generate differential supply of settlement-stage larvae to coral reefs. The most widely documented influence on intra-seasonal patterns of recruitment is the lunar cycle (Doherty 1991). Lunar replenishment may be the result of lunar spawning patterns and a relatively fixed larval duration. Indeed, this appears to be the case for a pomacentrid species in the Caribbean Sea (*Stegastes partitus*; Robertson et al. 1988) and western Pacific Ocean (*Pomacentrus amboinensis*; Meekan et al. 1993). Alternatively, larval supply may also be strongly influenced by larval behavior (Sweatman 1985, Booth 1992). Thorrold et al. (1994a) suggested that lunar periodicity in the supply of taxa such as leptocephali in the Bahamas has a considerable behavioral component. Although data were not available on the spawning patterns or larval duration of the taxa they collected, Thorrold and co-workers argued that the extended larval durations of most leptocephali should act to largely decouple spawning and recruitment. Given that the lunar patterns were not driven by similar periodicity in water movements (Thorrold et al. 1994a), it was concluded that larvae must be selectively, and actively, moving onshore over new moon periods.

Larval supply may also depend upon transport events returning settlement-stage larvae to reefs. Larval supply of several taxa of shorefish in Exuma Sound, Bahamas, has been shown to correlate with longshore or cross-shelf currents and winds (Shenker et al. 1993, Thorrold et al. 1994a). Onshore transport of settlement-stage larvae by wind-induced currents appeared to generate peaks in larval supply over several days. Several studies have examined the potential for meso-scale eddies to entrain larvae and lead to self-recruitment of isolated atolls and reefs (Sale 1970, Lobel & Robinson 1986, 1988, Boehlert et al. 1992, Williams & English 1992). While there is evidence that ichthyoplankton may accumulate in downstream eddies (Lobel & Robinson 1988, Boehlert et al. 1992), one study found no evidence of retention (Williams & English 1992). None of the above studies simultaneously measured the supply of larvae to benthic habitats, and the importance of such features to recruitment patterns remains untested.

More convincing data on the influence of hydrography on recruitment comes from studies of marine invertebrates in coastal waters. Roughgarden et al. (1991a, b) noted a correlation between low upwelling intensity and barnacle recruitment along the central coast of California, USA. Further investigation revealed that recruitment pulses were apparently driven by the movement of clear oceanic water into coastal areas (Farrell et al. 1991). Gaines & Bertness (1992) found that year-class strength of a barnacle in Narragansett Bay, Rhode Island, USA, was correlated with the estimated flushing time of water in the bay. Strong year-classes were generated by long flushing times, and presumably high rates of self recruitment within the bay.

Lunar relationships and hydrographic forcing may both play a major role in regulating larval supply of coral reef fishes. Examining the relative importance of these factors requires monitoring the supply of larvae and hydrodynamic variability on daily time scales. In earlier papers, we have reported the use of channel nets to quantify larval supply of shorefishes to shallow-water habitats during winter months of December to February at Lee Stocking Island, Bahamas (Shenker et al. 1993, Thorrold et al. 1994a, b). While large numbers of settlement-stage shorefishes were captured, a number of reef fish taxa were conspicuously rare or absent in these collections. In this communication, patterns in larval replenishment of reef fishes to Lee Stocking Island are examined for the summer months of June to September 1992. Analyses of daily time series of larval supply allows quantitative assessment of semi-lunar and lunar cycling patterns. Detailed meteorological and hydrographic monitoring also allow the influence of both wind and hydrodynamic forcing events on temporal patterns of larval supply to be determined.

MATERIALS AND METHODS

Settlement-stage reef fishes were captured in large nets permanently moored in tidal channels at 3 stations around Lee Stocking Island (23° 46' N, 76° 06' W), at the southern end of the Exuma Cays, Bahamas. Sampling was conducted from 25 June to 11 September 1992. Net design and location of stations are described in Shenker et al. (1993). Briefly, at each of 3 stations (corresponding to Stns 1, 2 and 3 in Shenker et al. 1993) a single surface (1 × 2 m) and sub-surface (2 × 2 m) net was moored. All nets had 2 mm mesh and were equipped with General Oceanics model 2030R flow meters and low speed rotor blades. Samples were collected from the nets at approximately 08:00 and 16:00 h. Fish were separated from macro-algae and flotsam within 1 h of collection, fixed in a 5% formalin

solution and transferred to 50% isopropanol after 24 to 48 h for storage and subsequent identification. Identification of larvae was truncated at the family level, as taxonomic information on most families is lacking beyond this level of resolution. To examine larval supply during discrete flood tides, nets were sampled at each tide change during 8 nights. These nights were chosen so that a slack tide (either high or low) occurred around sunset.

Meteorological and current data were monitored throughout the sampling period. Wind speed and direction were recorded every 30 min by a Campbell Scientific weather station situated at the Lee Stocking Island airstrip. These values were then averaged over a 24 h period (12:00 to 12:00 h). Current data was recorded with a General Oceanics Mark II current meter moored at 10 m, in approximately 30 m of water, on the shelf edge approximately 1.5 km from the coast of Lee Stocking Island (see Fig. 1 in Shenker et al. 1993). Currents were logged every 30 min, and converted to 24 h means as for weather data. Longshore and cross-shelf vectors were then calculated from the 24 h mean values, and these components were then used for subsequent statistical analyses.

Statistical analyses. Multivariate cluster analysis was used to examine temporal patterns of larval supply among taxa. A total of 22 families were chosen for the cluster analysis; these represented families for which more than 200 specimens were collected throughout the sampling period. A data matrix was constructed by summing the number of fish across all 6 surface and sub-surface nets to give a single value of larval supply on each sampling date. The matrix was standardized by family maxima to give a scale-independent measure of larval supply for each family (Belbin 1987). Cluster analysis of the standardized matrix followed using a Euclidean distance measure and Ward's minimum variance cluster strategy. An inverse cluster using families as attributes was also performed as outlined above. Results of these analyses were displayed by plotting 2-way table summaries (Smith et al. 1989). The 'bubbles' in the summary plots represent the percentages of the family groups upon summing the mean proportion of each family group either across columns or down rows.

To examine cycling in larval supply, time series were constructed by summing the number of fish collected across all 6 surface and sub-surface nets within a given night. Day samples were eliminated, as 97% of all fish were collected at night. Fish numbers were then converted to concentrations (ind. 100 000 m^{-3}) using the volumes of water sampled as measured by the flow meters. The use of larval concentrations allowed any lunar or semi-lunar periodicity in water volumes moving through the cuts to be removed from the analy-

sis. Cycling in the larval supply time series could therefore be attributed unambiguously to periodicities in the availability of settlement-stage larvae. Larval concentrations were $\log_{10}(x+1)$-transformed to reduce the influence of large, but rare, peaks in the data.

The resulting 79 d time series was examined for both semi-lunar and lunar cycles. Methods based on spectral analysis (Robertson et al. 1988, Milicich 1992, Thorrold et al. 1994a) could not be used, as the time series was not long enough to give accurate estimates at periods greater than 20 d (approximately ¼ the length of the entire series; Chatfield 1979). Instead we used a seasonal modelling approach to the data to determine if there were significant semi-lunar and/or lunar cycling within the time series. We fitted additive seasonal models with periods of 14 and 28 d using a least squares technique for parameter estimations. If significant semi-lunar or lunar seasonal components were detected, the cycles were centered on the lunar cycle by cross-correlating the larval supply time series with a 28 d sine curve (Robertson et al. 1988).

Cross-correlation techniques were used to examine the relationship between larval supply and wind and current vectors (Thorrold et al. 1994a). Raw time series were constructed by summing the number of larvae for each family collected at all 3 stations in both surface and sub-surface nets taken in any given night; day samples were again eliminated. These series were cross-correlated with longshore and cross-shelf components of both winds and currents. Significant autocorrelations were present in both the biological and physical time series. ARIMA models were fitted to the raw data to remove both short-term autocorrelations and longer term cyclic activity. The residuals from these models were then used in the cross-correlation analyses. Model choice was based on examination of autocorrelation plots of the model residuals, and a number of diagnostic statistics including a χ^2 test for white noise and the Durban-Watson statistic. Only significant correlations between time series where wind or current data preceded larval supply at lags less than 6 d are presented. No biological interpretation could be given to lags in which larval replenishment preceded meteorological or hydrographic events, or to longer time lags between the physical variables and larval supply. All analyses were conducted using the statistical time series package Mesosaur (Kuznetsov & Khalileev 1991).

RESULTS

A total of 55 771 fishes, representing 53 taxa, were collected over 79 sampling days (Table 1). Dominant taxa included the Clupeidae, Labridae, Apogonidae,

Table 1. Total numbers, % taken in night samples, and % taken in surface samples, for all larval fish families collected in surface and mid-water channel nets fished in tidal cuts in the vicinity of Lee Stocking Island, Bahamas, during June to September 1992

Family	Total	% Night	% Surface
Acanthuridae	23	96	70
Albulidae	1102	98	90
Antennariidae	63	98	56
Apogonidae	3680	98	47
Atherinidae	594	99	59
Aulostomidae	14	93	82
Balistidae	3459	87	68
Belonidae	25	80	98
Blennioidei	2087	99	39
Bothidae	1759	96	66
Callionymidae	403	97	48
Carangidae	128	78	66
Carapidae	4	75	84
Chaetodontidae	37	92	75
Chlopsidae	343	91	36
Clupeidae	13887	99	22
Congridae	400	97	72
Coryphaenidae	4	100	84
Elopidae	38	95	83
Elver	143	99	48
Exocoetidae	15	100	100
Fistulariidae	2	50	0
Gerreidae	43	84	81
Gobiesocidae	40	100	38
Gobiidae	2316	99	46
Holocentridae	3	67	0
Istiophoridae	19	95	57
Kyphosidae	10	90	88
Labridae	12403	98	35
Leptocephalus	90	94	80
Lutjanidae	941	95	57
Malacanthidae	1	100	0
Megalopidae	17	100	89
Microdesmidae	18	100	64
Moringuidae	807	97	80
Mugilidae	5	100	100
Muraenidae	157	99	72
Ogcocephalidae	127	98	62
Ophichthidae	2605	98	70
Ophidiidae	1202	99	24
Opistognathidae	3	100	78
Pomacanthidae	55	95	79
Pomacentridae	561	96	65
Scaridae	2561	99	64
Scombridae	71	92	62
Scorpaenidae	985	99	65
Serranidae	528	99	39
Soleidae	100	98	49
Sphyraenidae	307	77	63
Syngnathidae	163	93	86
Synodontidae	189	98	45
Tetraodontidae	277	97	73
Trichiuridae	6	83	26
Unidentified	951	94	44
Total	55771	97	46

Balistidae, Ophichthidae and Scaridae. Over 97 % of the total number of fish taken were collected in night-time samples; almost all families showed a similar pattern. Depth distribution patterns were, however, taxon-specific. A number of families were concentrated in surface layers, including albulids, balistids, bothids, congrids, moringuids, ophichthids, scarids and tetraodontids. Other families were more evenly distributed across nets, or distributed away from the surface layer, including clupeids, blennioids, gobiids, labrids, lutjanids, ophidiids and serranids.

Discrete tidal sampling was conducted on a total of 8 occasions during the sampling period. Movement of reef fishes through the channels occurred predominantly during flood tides (Fig. 1). The only exception was on 3 August, when apogonids, gobiids and scarids were all taken in higher numbers during the ebb tide. Clupeids dominated the catch on this occasion, and were also taken in high numbers on the ebb tide. On both occasions that the family Atherinidae contributed significant numbers to the total catch, ebb tide catches were higher than those on the flood tide.

Cluster analysis detected 3 major sample groupings (Fig. 2). The first cluster contained samples from the latter part of the study, and predominantly over full moon and third quarter moon phases. The second cluster was composed of samples from the new moon and first quarter phase in late July to early August. The final cluster contained samples from the new moon and first quarter in late June to early July, along with a small number of samples from the late August to early September new moon period. Cluster analysis using families as attributes also found 3 distinct clusters within the data (Fig. 3). The first family grouping contained representatives of both reef (Congridae, Scaridae and Gobiidae) and pelagic (Atherinidae and Clupeidae) families. The second grouping consisted entirely of reef fish families; Apogonidae, Pomacentridae, Blennioidei, Lutjanidae, Tetraodontidae, Labridae, Serranidae, Scorpaenidae and Ophidiidae. The final grouping contained the reef fish families Ophichthidae, Chlopsidae, Bothidae, Moringuidae, Balistidae and Albulidae, along with a single pelagic family (the Sphyraenidae).

Summary tables were used to display relationships between the sample clusters and family groupings. While all 3 family clusters were found in sample cluster 1, this cluster was characterised by low numbers for each of the family groups (Fig. 3). Sample cluster 2 was dominated by taxa from family cluster 1, although all 3 family groups were represented. Numbers were generally higher than for sample cluster 1, especially within family group 1. Finally, sample cluster 3 was evenly represented across all 3 family groups, and dominated numerically in all 3 family groupings.
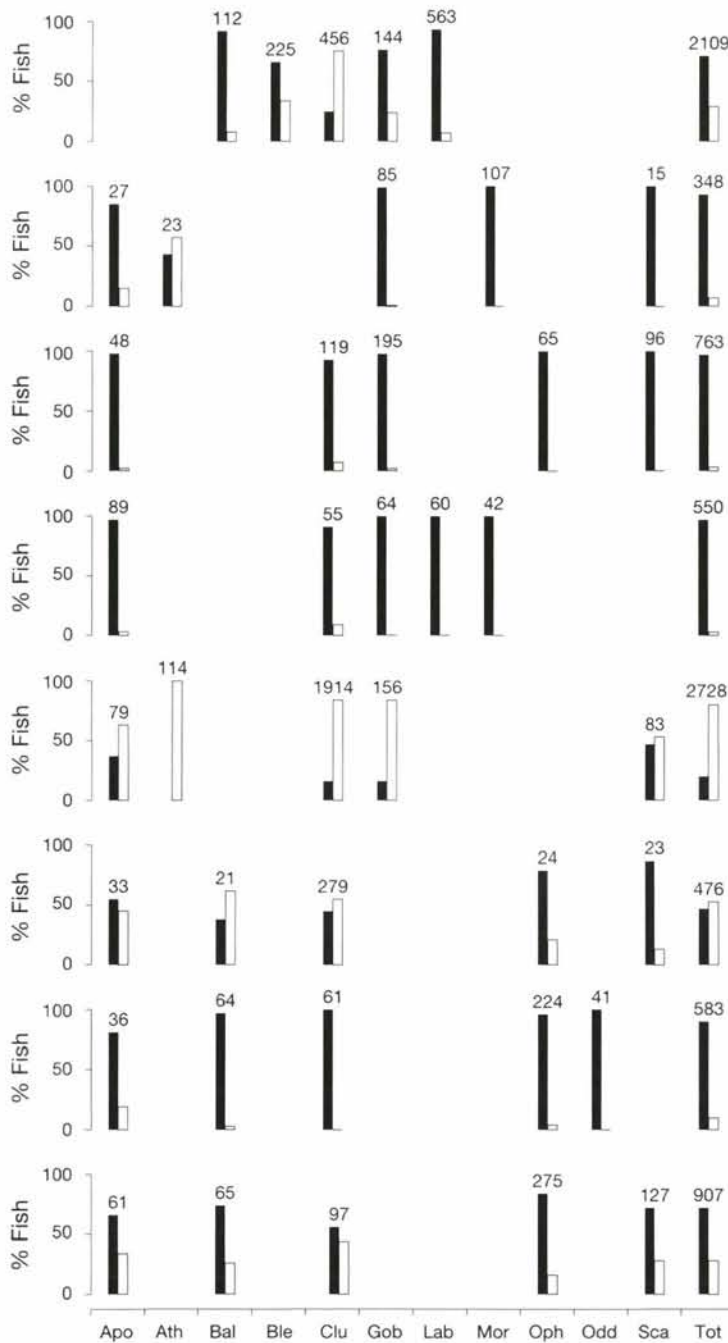
Fig. 1. Percent frequency of 11 abundant families, and total fish, on flood (solid bars) and ebb (open bars) tides during 8 nights of sampling (from top: 5, 12, 21 and 26 July, 3 August, 1, 3 and 4 September). Ebb tide in early evening on 12 and 26 July, otherwise flood tide in early evening. Numbers above bars indicate number of fish collected; family not plotted if number collected < 10 for that night. Ath: Atherinidae; Apo: Apogonidae; Bal: Balistidae; Ble: Blennioidei; Clu: Clupeidae; Gob: Gobiidae; Mor: Moringuidae; Lab: Labridae; Odd: Ophidiidae; Oph: Ophichthidae; Sca: Scaridae; Tot: total larvae

A general overview of larval supply during the sampling period can be obtained by combining data from the proceeding analyses. Sample cluster 1 was made

up of low numbers of most taxa around full moon and third quarter periods of the lunar cycle. Sample cluster 2 contained those taxa making up the first family grouping that recruited during the second new moon period. Numbers were generally lower during this period than during the first new moon. Finally, the third sample cluster contained those samples from the first new moon and first quarter, distributed evenly among all family groupings.

Time series of the 3 most abundant taxa in each of the family clusters showed several distinct patterns in the timing of larval supply (Table 2, Fig. 4). Within the first cluster grouping, scarids displayed significant semi-lunar periodicity centered 2 to 4 d after the new moon, gobiids showed lunar cycling centered around the new moon, while no evidence was found for either semi-lunar or lunar peaks in larval supply of the clupeids. The apogonids were the only family to display significant cycling from cluster 2. Activity was lunar-cyclic and centered on the new moon. In the final cluster, the family Ophichthidae showed semi-lunar activity centered 0 to 1 d after the new and full moons, bothids displayed lunar cycling centered around the first quarter, and balistids showed no evidence of either semi-lunar or lunar cycling.

Correlations between larval supply and wind and current data revealed a number of significant relationships (Table 3, Fig. 5). Scarids showed no detectable relationships between larval supply and longshore winds, cross-shelf winds or longshore currents. A significant correlation was found between larval replenishment and offshore currents. Clupeids and ophichthids showed no significant correlations with any of the physical variables. Gobiids, apogonids, blennioids and labrids all showed similar relationships between larval supply and wind and current data. Significant correlations were found with the northwest wind component (with the exception of blennioids and labrids), and with current vectors from the northwest, and onshore, at 0 to 2 d lags. Finally, larval supply in the Balistidae was significantly correlated with the southeast wind vector at a lag of 2 d, with offshore winds at a lag of 1 d, and offshore currents at a lag of 1 d.

To examine the relationships between larval supply and physical variables in more detail, scatter plots were generated between larval replenishment and
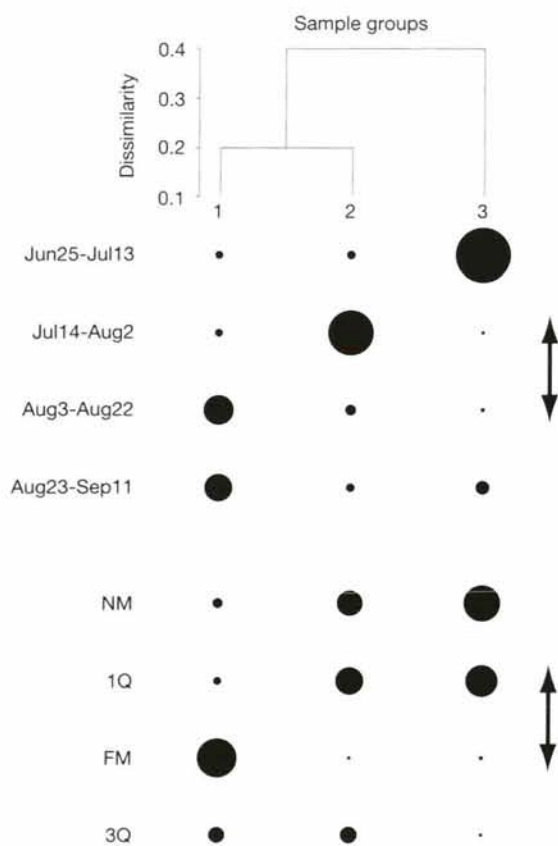
Fig. 2. Summary of cluster analysis for channel net data, showing relationship of sampling time and lunar phase on cluster groupings. Area of the symbols represents the percentage of a sample group which occurs in each of the 4 time periods, and each of the 4 moon phases. Percentages within the time periods and moon phases sum to 100 %, in direction indicated by arrows

shore. However replenishment was also high on 2 d with high longshore flows from the southeast and net offshore transport.

DISCUSSION

Channel net collections from summer months at Lee Stocking Island, Bahamas, provided samples with similar taxonomic diversity to those from winter collections at the same sites (Shenker et al. 1993, Thorrold et al. 1994b). Relative contributions of the taxa were, however, very different. Winter samples were domi-

each of the 4 wind and current vectors for 3 families (Fig. 6). The families chosen were the most abundant reef fish taxa in each of the 3 family groupings detected in the cluster analysis: the families Scaridae, Labridae and Ophichthidae. No pattern was obvious between larval supply and any of physical variables for the family Scaridae. Scatter plots for the labrids showed considerably more pattern. Larval supply was high during periods of calm winds when both long-shore and cross-shelf wind vectors were low. More striking relationships were observed between larval supply and current vectors, with high alongshore flows from the northwest, and high onshore flows, being associated with strong replenishment peaks. Larval supply of the ophichthids showed some of the associations with physical variables exhibited by the labrids, although there was considerably more scatter. Plots with longshore and cross-shelf winds showed little structure. Replenishment was high on occasions of strong longshore currents from the northwest and on-
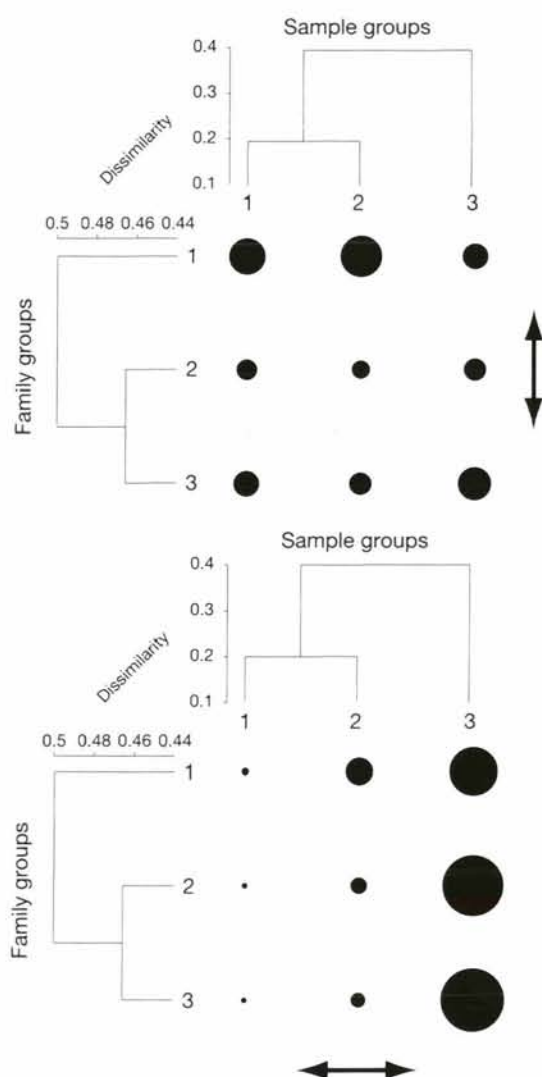

Fig. 3. Two-way summary table of cluster analyses of sample and family groups for channel net data. The upper table displays the distribution of sample groups within family groups (columns sum to 100 % in direction of arrows), while the lower table shows the distribution of family groups within sample groups (rows sum to 100 % in direction of arrows)
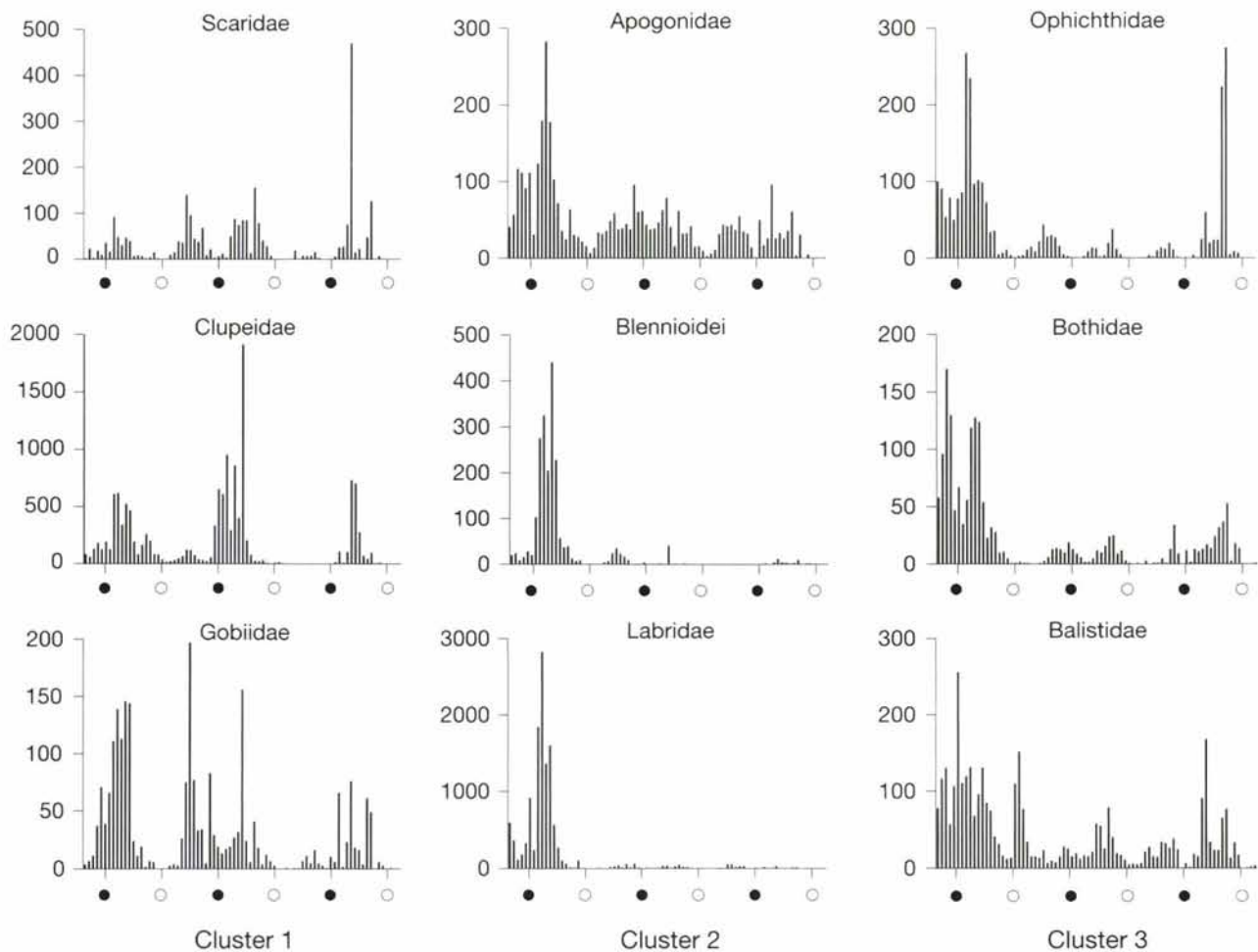
Fig. 4. Time series of larval abundance in channel nets, for the 3 most abundant families in each of 3 groupings identified by cluster analysis, from 25 Jun to 11 Sep 1992. (●) New moon; (○) full moon

nated by leptocephali, bothids, ophidiids, serranids and clupeids. Scarids, pomacentrids and lutjanids were all rare in their collections, but were taken frequently in the present study. While labrids, clupeids and apogonids made significant contributions to the total numbers collected in each season, they were an order of magnitude more abundant in the summer collections than in the winter ones. These differences may reflect strong seasonality of spawning patterns in the Bahamas or, alternatively, that there is considerable inter-seasonal variability in larval survivorship. Greater taxonomic resolution from samples collected in the channel nets, and more information on spawning patterns, will be required to test between these hypotheses in the study area.

Relationships between day/night and flood tide/ebb tide catches were very similar to the results of Shenker et al. (1993). Samples from flood tides caught considerably more fish. Interestingly, this did not appear to be influenced by the time of the tide, as high tides both

early in the night and during morning hours showed this pattern. This provided strong circumstantial evidence, when combined with lack of specimens collected during the day, that larvae are actively timing their movement through cuts. Bank waters on the ebb tide form easily identifiable jets as they pass through the narrow cuts and out into Exuma Sound. It is possible, therefore, that larvae may aggregate in slicks forming along the edge of the out-going tidal jet (Wolanski & Hamner 1988) and then get swept through the cuts and onto the bank as the jet reverses direction on the change of tide.

The time series constructed in this study were comparatively short to rigorously examine lunar cycling (Chatfield 1979). However, of the 9 taxa analysed, 3 showed significant cycling at a period of 28 d (the families Gobiidae, Apogonidae and Bothidae). Bothids also showed strong lunar cycling in larval supply during winter months (Thorrold et al. 1994a). Lunar periodicity in larval supply or settlement has been found in studies

Table 2. Results of fitting semi-lunar (14 d) and lunar (28 d) seasonal models to time series of larval supply for the 3 most abundant families in each of 3 family groupings identified by cluster analysis. If there was a significant lunar or semi-lunar periodicity, time series were cross-correlated with a 14 or 28 d sine curve to center the time series according to lunar phase (NM: new moon, 1stQ: first quarter, FM: full moon)

Family	df	MS	F	p	Timing
Cluster 1					
Scaridae					
14 d	13	0.682	2.50	0.008	NM
Residual	65	0.276			FM
28 d	27	0.509	2.01	0.016	
Residual	51	0.253			
Clupeidae					
14 d	13	0.318	0.46	0.935	
Residual	65	0.679			
28 d	27	0.813	1.57	0.081	
Residual	51	0.517			
Gobiidae					
14 d	13	0.330	1.08	0.393	
Residual	65	0.306			
28 d	27	0.511	2.50	0.002	NM
Residual	51	0.204			
Cluster 2					
Apogonidae					
14 d	13	0.248	1.24	0.271	
Residual	65	0.199			
28 d	27	0.293	1.81	0.034	NM
Residual	51	0.162			
Blennioidei					
14 d	13	0.269	0.723	0.734	
Residual	65	0.372			
28 d	27	0.280	0.710	0.830	
Residual	51	0.394			
Labridae					
14 d	13	0.393	0.612	0.835	
Residual	65	0.643			
28 d	27	0.633	1.08	0.392	
Residual	51	0.584			
Cluster 3					
Ophichthidae					
14 d	13	0.672	2.33	0.013	NM
Residual	65	0.288			FM
28 d	27	0.446	1.47	0.115	
Residual	51	0.302			
Bothidae					
14 d	13	0.360	1.43	0.171	
Residual	65	0.252			
28 d	27	0.471	2.87	0.006	1stQ
Residual	51	0.164			
Balistidae					
14 d	13	0.150	0.69	0.765	
Residual	65	0.217		0.926	
28 d	27	0.142	0.59		
Residual	51	0.239			

Table 3. Results of cross-correlation analyses between numbers of fish collected overnight in the channel nets and longshore and cross-shelf wind and current vectors, June to September 1992. Values in table indicate lag (in d) with associated correlations (in parentheses) when significant ($\alpha = 0.05$). Positive correlations for longshore components indicate relationships with transport to the northwest; positive correlations for cross-shelf components indicate relationships with transport to the offshore (to the northeast)

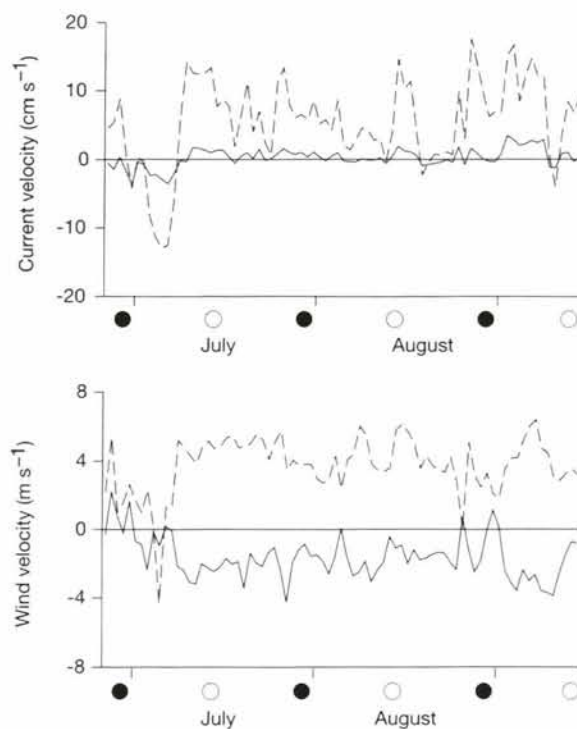| Family	Long-shore wind	Cross-shelf wind	Long-shore current	Cross-shelf current
Cluster 1				
Scaridae	ns	ns	ns	0 (0.24)
Clupeidae	ns	ns	ns	ns
Gobiidae	2 (0.27)	0 (0.22)	0 (−0.31)	0 (−0.24)
Cluster 2				
Apogonidae	0 (−0.44)	ns	0 (−0.24) 1 (−0.24)	1 (−0.22) 5 (−0.23)
Blennioidei	ns	ns	0 (−0.34)	0 (−0.30) 5 (0.25)
Labridae	ns	4 (0.29)	0 (−0.25)	1 (−0.24) 4 (0.35)
Cluster 3				
Ophichthidae	ns	ns	ns	ns
Bothidae	ns	4 (0.24)	ns	ns
Balistidae	2 (0.28)	1 (0.29)	ns	1 (0.34)

Fig. 5. Cross-shelf (——) and longshore (– – –) components of currents at 10 m on the shelf edge offshore of Lee Stocking Island (upper) and winds at the Lee Stocking Island airstrip (lower) averaged over 24 h during the study period (25 Jun through 11 Sep 1992). (●) New moon; (○) full moon

from the Indo-west (Milicich 1992) and south Pacific Ocean (Dufour 1991), Caribbean Sea (e.g. Victor 1986, Robertson et al. 1988, Robertson 1992) and Bahamas (Thorrold et al. 1994a). The prevalence of lunar cycling in a wide range of taxa across oceans suggests that such a strategy confers a degree of selective advantage to those fish. Perhaps the most obvious explanation is that settlement over new moon periods will lessen the likelihood of predation immediately before, or sometime after, settlement. There have yet to be any direct tests of the assumption that predation on settlement-stage fishes entering nearshore waters, or on newly settled

juveniles, is higher during the full moon than on new moon nights. Alternatively, lunar supply of settlement-stage larvae may be caused by lunar spawning and a relatively fixed larval duration (Robertson et al. 1990). While spawning does appear to drive temporal patterns of recruitment in at least 2 species of damselfish (Robertson et al. 1988, Meekan et al. 1993), it has not been possible to determine if this is due to constraints of adult biology while spawning or larval biology at the time of settlement (Robertson et al. 1990).

Multivariate analyses identified 3 major family groupings. The first grouping consisted of families that were
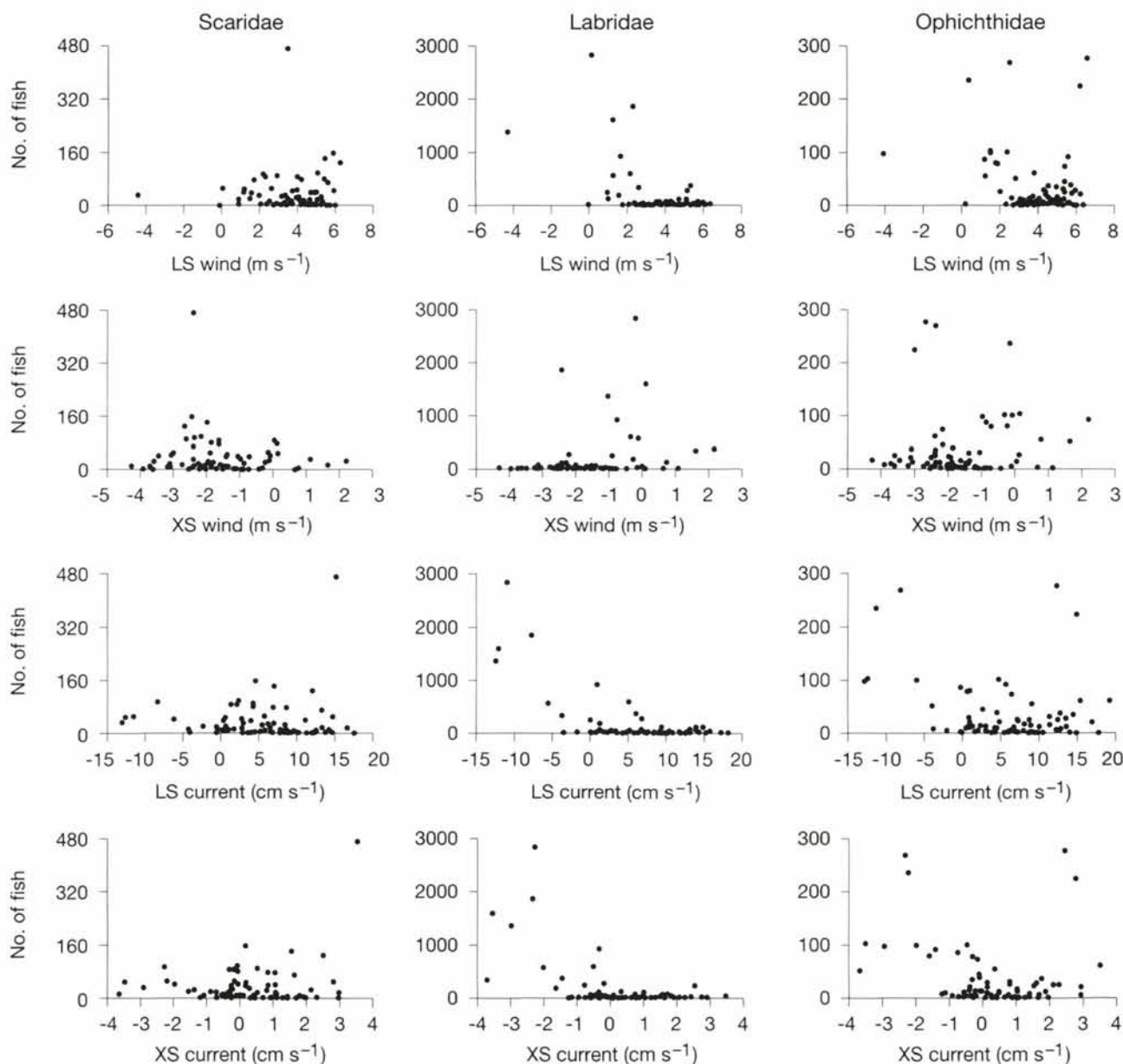

Fig. 6. Scatter plots of larval supply of 3 reef fish taxa and longshore (LS) and cross-shelf (XS) components of currents and wind during the study period (25 June through 11 September 1992)

captured episodically but consistently throughout the summer, and whose peak catches were associated with the second or third new moon. The consistency of larval supply throughout the sampling period implies that, at least for these taxa, there is a relatively constant supply of settlement-stage larvae within Exuma Sound. This may be related to the distributions of younger larvae within the plankton. Clupeids and gobiids were both part of a near-reef larval fish fauna in the Caribbean (Powles 1977, Smith et al. 1987). Indeed gobiids show inshore affinities in most coastal regions of both temperate (e.g. Jenkins 1986) and tropical oceans (Kobayashi 1989, Thorrold 1993). While scarids have been taken in oceanic collections considerable distances from land (Richards 1984), at least some species settle at very small sizes, and presumably young ages (Victor 1991). Scarids that settle at small sizes may, then, be restricted to waters adjacent to the coast.

The second and third family clusters identified by the cluster analysis all displayed a large peak in abundance during the first 2 weeks of the sampling period. This coherency among taxa may be interpreted as indicating the fortuitous arrival of a large, multi-specific larval patch in the vicinity of Lee Stocking Island. Several authors have speculated that reef fish larvae may be distributed in meso-scale patches (Victor 1984, Williams 1986, Doherty 1987), although the existence of patches of reef fish larvae in open waters has only recently been verified (Thorrold 1993, in press, Williams & English 1992). A more pressing question is to identify the mechanisms leading to patch formation. Thorrold (1992) noted that reef fish larvae within a patch detected in the central Great Barrier Reef lagoon comprised both pelagic and benthic spawning families. He argued that a synchronous spawning event was, therefore, unlikely to have generated the patch and suggested instead that larvae may have aggregated in the vicinity of a coastal front. Williams & English (1992) detected water temperature anomalies that may have indicated the presence of a cold-core eddy associated with a patch of larval reef fish on the shelf break off Townsville, in the Great Barrier Reef. Meso-scale eddies have been shown to aggregate pelagic (Thomson et al. 1992) and meso-pelagic (Olson & Backus 1985) fishes, and the convergence associated with such structures may also act to entrain or aggregate fish larvae (Kingsford 1990). However, as there were no current measurements to substantiate the claim, the hypothesis remains speculatory only.

While hydrographic phenomena may influence the distribution patterns of larvae in marine environments, these interactions appear complex and taxon, as well as size, specific (Thorrold 1993, in press). Strong correlations were found between meteorological and hydrographic variables and the families in cluster 2. However

no such relationships were detected for the families in either clusters 1 and 3. Apogonids, blennioids and labrids were all significantly correlated with longshore and cross-shelf currents. These relationships were driven by extremely high replenishment during the first 2 weeks of sampling associated with a reversal in the direction of longshore currents. Wind data indicated that this reversal was caused, at least in part, by a relaxation of longshore wind stress as the southeasterly trades died for several days. We suspect that the prevailing southeasterly winds and longshore current flows from the southeast act to concentrate larvae in northern Exuma Sound. The pulse of replenishment may, then, have been generated by large numbers of settlement-stage larvae from the northern Sound being delivered to the southern Sound by the longshore current reversal. Larvae were, however, also correlated with onshore current flows. Reversal of longshore currents was correlated with an increase in onshore current flow, which may have entrained larvae from offshore waters in the southern Sound. The fact, however, that larval concentrations, along with total numbers, increased at this time demonstrates that the pulse was not due simply to an increase in the volume of water moving through the cuts.

The influence of oceanographic conditions on larval survivorship has been addressed in a number of studies in temperate environments (e.g. Lasker 1981, Sinclair et al. 1985, Checkley et al. 1988, Maillet & Checkley 1991). Stochastic or chaotic mortality probabilities within the plankton may lead to highly variable larval survival which would be manifested in variable recruitment patterns. Workers in coral reef systems have largely accepted this model as the explanation for the highly episodic recruitment typical of reef fish populations (Robertson 1990, Robertson et al. 1993). Indeed, Doherty & Williams (1988) suggest that the dynamics of tropical reef fish populations were not qualitatively different to those of temperate counterparts. Within this framework, environmental variability is seen as the dominant source of short-term fluctuations in recruitment, due to differential survival of larvae (Fogarty et al. 1991). There has, however, been very little research designed to address this question (Thorrold 1993). While we concur that climatic variations driving regional hydrographic conditions may generate recruitment variability, such hypotheses cannot be tested without direct sampling of tropical reef fish larvae and their environment over the relevant spatio-temporal scales.

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