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S. Sponaugle · J. Fortuna · K. Grorud · T. Lee

Dynamics of larval fish assemblages over a shallow coral reef in the Florida Keys

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Abstract Few time series collections have been made of the larval ichthyofauna in waters directly above shallow coral reefs. As a result, relatively little is known regarding the composition and temporal dynamics of larval fish assemblages in shallow-reef waters, particularly those near a major western boundary current. We conducted a series of nightly net tows from a small boat over a shallow reef (Pickles Reef) along the upper Florida Keys during four new moon and three third-quarter moon periods in July (two new moons), August, and September 2000. Replicate tows were made after sunset at 0–1 m and at 4–5 m depth to measure the nightly progression in community composition, differences in depth of occurrence, and abundance and diversity with lunar phase. A total of 66 families was collected over the 3-month period, with a mean (±SE) nightly density of 23.7 ± 2.1 larvae per 100 m^3 and diversity of 24.2 ± 0.9 taxa per tow. A total of 28.8% of the catch was composed of small, schooling fishes in the families Atherinidae, Clupeidae, and Engraulidae. Of the remaining catch, the top ten most abundant families included reef fishes as well as mangrove and oceanic taxa (in descending order): Scaridae, Blennioidei (suborder), Gobiidae, Paralichthyidae, Lutjanidae, Haemulidae, Labridae, Gerreidae (mangrove), Balistidae, and Scombridae (oceanic). These near-reef larval fish assemblages differed substantially from those collected during previous offshore collections. Taxa such as the Haemulidae were collected at a range of sizes and may remain nearshore throughout their larval period. Overall, the abundance and diversity of taxa did not differ with depth (although within-night vertical migration was evident) or with lunar phase. Temporal patterns of abundance of larval fish families clustered into distinct groups that in several cases paralleled family life-history patterns. In late July, a sharp shift in larval assemblages signaled the replacement of oceanic water with inner shelf/bay water. In general, the suite and relative abundance of taxa collected each night differed from those collected on other nights, and assemblages reflected distinct nightly events as opposed to constant or cyclical patterns. Proximity to the Florida Current likely contributes to the dynamic nature of these near-reef larval assemblages. Our results emphasize the uniqueness of near-reef larval fish assemblages and point to the need for further examination of the biophysical relationships generating event-related temporal patterns in these assemblages.

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S. Sponaugle (✉) · J. Fortuna · K. Grorud
Marine Biology and Fisheries, Rosenstiel School of Marine and Atmospheric Science, University of Miami,
4600 Rickenbacker Causeway, Miami, FL 33149, USA
E-mail: ssponaugle@rsmas.miami.edu
Tel.: +1-305-3614069
Fax: +1-305-3614600

T. Lee
Meteorology and Physical Oceanography, Rosenstiel School of Marine and Atmospheric Science, University of Miami,
4600 Rickenbacker Causeway, Miami, FL 33149, USA

Introduction

The bipartite life history of most marine fishes has contributed to difficulties in understanding the relationship between the pelagic larval stage and benthic-oriented juvenile and adult phases. By necessity, sampling of each stage and environment requires different gear: benthic studies typically use SCUBA-diving-related sampling and pelagic studies revolve around plankton tows. Because it is generally logistically challenging to tow large ichthyoplankton nets in shallow waters above coral reefs at night, relatively few time series of collections have been made in these environments. This is particularly true for nearshore waters in proximity to major western boundary currents such as the Florida Current. While extensive ichthyoplankton work has been conducted in offshore waters in some of these areas (e.g. Southeast Florida and Caribbean Re-

cruitment Project, SEFCAR, in the 1980s), little is known regarding the larval ichthyofaunal assemblage(s) over coral reefs immediately inshore of these major currents.

Larval studies of coral reef fishes have focused on measuring spatial distribution patterns with respect to onshore–offshore gradients and in some cases oceanographic features (see reviews by Leis 1991a; Leis and McCormick 2002; Cowen 2002). Relatively fewer studies have examined temporal changes in near-reef assemblages (but see Kobayashi 1989; Kingsford and Finn 1997). Recently, larval purse seines and channel nets have been deployed in reef waters in the Great Barrier Reef to demonstrate that most larvae move onto the reef at night (Kingsford 2001). Also, light-trap sampling at night has become increasingly popular for intercepting late-stage larvae during settlement (Doherty 1987; Brogan 1994; Milicich 1994; Sponaugle and Cowen 1996a, 1996b; Hendriks et al. 2001; Valles et al. 2001; Wilson 2001). While this latter method can provide a relative measure of the supply of particular settlers to the reef, it is taxon and stage specific. Results of such light-trap studies suggest that the supply of late-stage larvae is often lunar cyclic (e.g. Sponaugle and Cowen 1996a, 1996b; Wilson 2001). There is also ample evidence that spawning by small reef fishes is lunar cyclic (e.g. Robertson et al. 1990, 1993). Less is known regarding the resulting temporal variation in larval assemblages (i.e. larvae of multiple ages), particularly in shallow waters over coral reefs.

The oceanographic setting of the Florida Keys is dominated by the proximity of the Florida Current (FC), a western boundary current. The FC flows northward just offshore of the upper keys, and periodic meanders of the FC enter nearshore waters. Mesoscale eddies forming in the Dry Tortugas area can result in seasonal countercurrents along the keys. It has been proposed that larvae settling to reefs along the Florida Keys are heavily influenced by the relative cross-shelf position of the FC and the frequency of spin-off eddies (Lee et al. 1992, 1994; Lee and Williams 1999). Based on data collected from current meter moorings, bottom-mounted ADCP records, and satellite-derived surface thermal patterns, Lee and colleagues described several mesoscale gyres off South Florida and the Florida Keys that may help retain organisms with varying lengths of pelagic larval duration (PLD). For example, multiple stages of penaeoid shrimp larvae and postlarvae have been found in the cyclonic Tortugas gyre and may be subjected to shoreward Ekman transport (Criales and Lee 1994). Transport of larvae to the reef also may occur with the persistent nearshore countercurrents or nearshore meandering of the FC (Yeung and Lee 2002). Late-stage *Stombus gigas* conch veligers were collected nearshore in the lower keys in association with thermal stratification and the nearshore presence of the FC (Stoner et al. 1997). The nearshore propagation of spin-off eddies provides another mechanism whereby larvae may access the reef to recruit. Limouzy-Paris et al. (1997) found that the distribution of larval fishes offshore of the Florida Keys was consistent with shoreward translocation by spin-off eddies. On a different temporal scale, Leichter et al. (1996, 1998) described semi-diurnal fluxes of nutrients and zooplankton to a Florida reef associated with breaking internal waves. An alternative to these cross-shelf transport scenarios is that fish larvae may remain near reefs during their development.

The present study was undertaken to examine the composition of the near-reef ichthyofauna, including the relative abundance of reef fish versus pelagic fish families, and the degree to which family composition changes over time (among replicates, over a night, among lunar periods, and over a 3-month sampling season). We were interested in examining how constant larval assemblages would be in waters at the dynamic interface between a large western boundary current and a reef. In a system at the fringe of a unidirectional flow field, would family composition and relative abundance remain constant over time, fluctuate with monthly spawning bouts, or respond to event-related, day-specific conditions?

Materials and methods

Biological sampling

To sample the ichthyofauna in shallow, nearshore waters over coral reefs, we towed a 1×2 m rectangular net (1.0 mm mesh) at night from a small (8 m) vessel at Pickles Reef (24°59.23′N; 80°24.86′W) in the upper Florida Keys (Fig. 1). We selected this larger net in order to maximize our catch of late-stage larvae. Late-stage larvae often have well-developed swimming abilities and can avoid standard nets (Leis 1991a). We therefore used a net with a wide opening and towed it relatively rapidly (1–2 knots) to minimize larval net evasion. Due to the shallow nature of the work, the towing had to be performed by a small vessel. The combination of these constraints required a net with a larger mesh size. The 5-min tows commenced shortly after sunset and continued to early morning hours until six replicate tows were completed. Readings were taken from a flowmeter after each tow to provide an estimate of the volume of water sampled. The mean ($\pm$SE) volume of water sampled during each tow was $1{,}707.2 \pm 29.9$ m^3. In order to minimize wake turbulence, the net was towed from a davit at the beam of the vessel in roughly circular passes over the seaward edge of the spur and groove reef formations at approximately 8 m depth. The net was towed at the surface between 0 and 1 m depth and deeper at 4–5 m depth. Tows were made twice each month, during two nights surrounding each of the third-quarter and new moon periods. These two lunar phases were selected because the settlement of reef fish larvae has been previously shown to peak during either of these periods (e.g. Sponaugle and Cowen 1996a, 1996b, 1997; Robertson 1992). Sampling began in early July and continued through September 2000, for a total of seven sampling periods.

Samples were preserved in 90% ethanol and returned to the laboratory for sorting. Fish larvae were sorted from the samples under a dissecting scope and identified to the lowest feasible taxonomic level using currently available identification keys (NOAA-NMFS SEFSC larval fish identification key; W. Richards (in preparation) and at http://www4.cookman.edu/noaa/). Most identifications were made to the family level, or, in a few cases, to the generic (three scarid genera; four labrid genera) or species level (e.g. *Thalassoma bifasciatum*). All small, silvery, mid-water reef fish larvae were grouped into an Atherinidae/Clupeidae/Engraulidae complex (except for the morphologically distinct clupeid, *Jenkinsia* sp.), and all Blenniidae, Clinidae, Labrisomidae, and Tripterygiidae were grouped together under the suborder, Blennioidei. Due to the

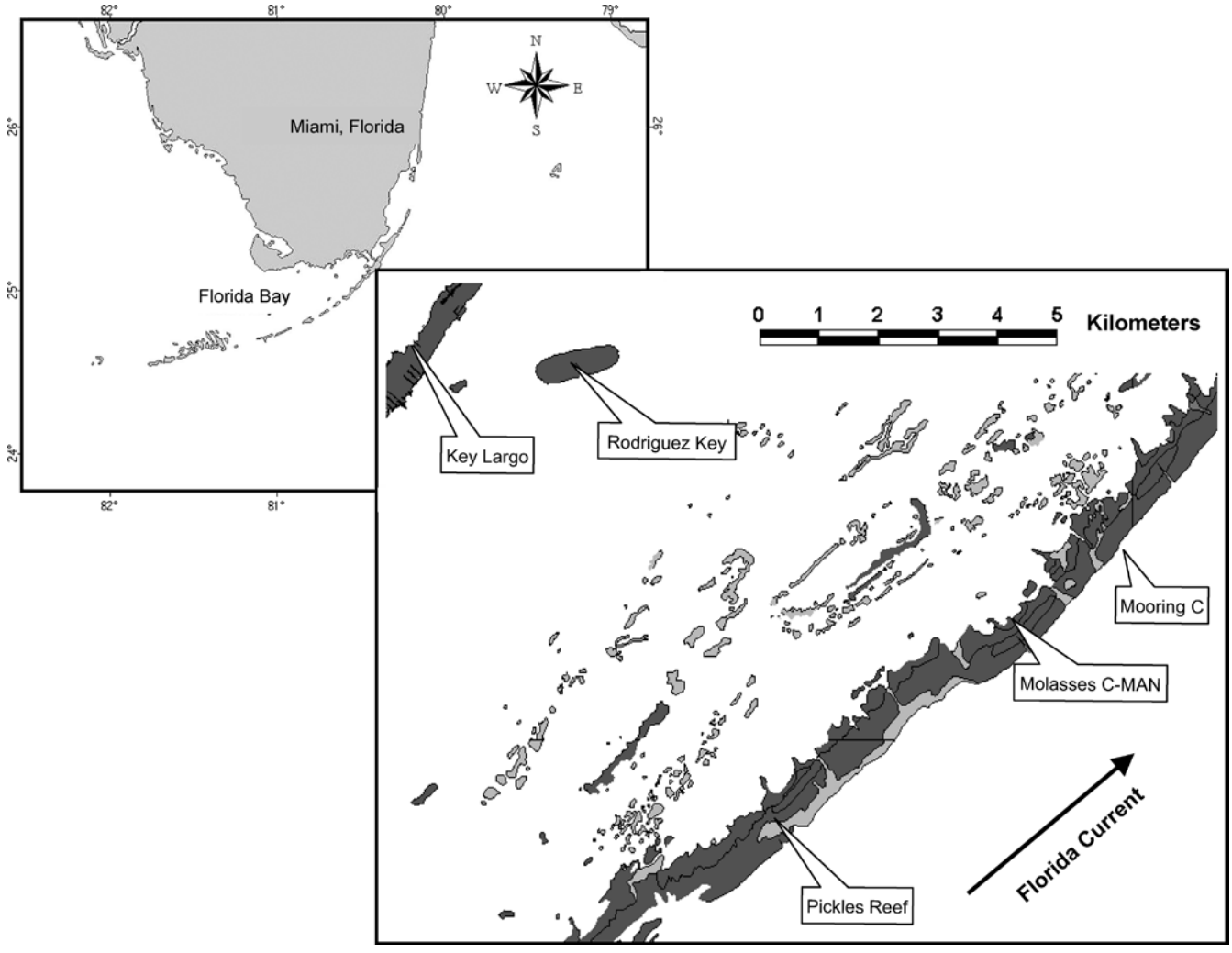


Fig. 1 Map of sampling site and mooring locations off Key Largo, upper Florida Keys. Reef map was modified from the ''Benthic Habitats of the Florida Keys Program''. Nightly ichthyoplankton sampling occurred just seaward of Pickles Reef. Concurrent hydrographic measurements were made at mooring C, and wind measurements, at the Molasses C-MAN station

relatively large mesh size of the neuston net, we collected almost entirely post-flexion larvae. The few preflexion larvae collected were included in the analysis of predominantly post-flexion larvae. The degree to which collected larvae were nearing settlement varied by taxa. For example, the labrids and scarids were often near settlement (based on size); the pomacentrids were never near settlement. The number of larvae per sample was recorded and later converted to density of larvae per 100 m^3 for data analysis (see below).

Biological data analysis

While sampling was initially designed to orthogonally test the influence of depth and lunar phase on catch, weather and other environmental conditions (presence of large amounts of *Sargassum* or jellies in surface waters) prevented balanced sampling throughout the study period. As a result, both variables could not be tested simultaneously. To examine whether samples collected in two depth layers (0–1 m and 4–5 m) differed, we analyzed two collection periods in which at least three replicate tows were made at each depth (July third-quarter moon and August new moon). We used a two-way ANOVA to examine the influence of depth and sampling period (Sokal and Rohlf 1995; SYSTAT version 8.0). To examine the influence of lunar phase on overall larval density and diversity, we analyzed only those samples where both the third-quarter and new moon were sampled in a given month (three periods: late July, August and September). Because there was no detectable depth-related difference in overall larval density (see ''Results''), we pooled all samples from each sampling period for this analysis and used a two-way ANOVA. Prior to all tests, the raw data were $\log_{10}$ transformed to meet assumptions of normality and homogeneous variances. Variances were examined with Bartlett's test (Sokal and Rohlf 1995). The Atherinidae/Clupeidae/Engraulidae (ACE) complex was excluded from analysis of trends in overall larval density because these catches were dominant (see Table 1) and highly variable. Their inclusion would have introduced heteroscedasticity and may have hidden any depth-related or temporal patterns in reef fish larvae. The ACE complex was retained in measures of overall diversity, because they were present in every sample.

We examined patterns of association among families by comparing the mean density of each family from each sampling period to other families using standard cluster analysis techniques. A Bray–Curtis matrix was created from the data, and this was analyzed using average Euclidean distances (SYSTAT 8.0). To be included in the analysis, families had to occur during at least four sampling periods and contain at least a seasonal total of 35 individuals. Using these criteria and an average Euclidean distance of 0.4, we clustered 29 taxa (2 suborders or complexes; 22 families, 5 genera). Temporal patterns of abundance of clustered taxa then

Table 1 Families of fish larvae collected at night in surface (0–5 m) waters off of the upper Florida Keys. Results are presented for replicate 5-min tows conducted with a neuston net between 1900 and 0200 hours during the third-quarter and new moon periods of July, August, and September 2000

Family	Total number
Atherinidae/Clupeidae/Engraulidae complex	4,774
Scaridae	2,389
Blennioidei	2,157
Gobiidae	1,687
Paralichthyidae	736
Lutjanidae	680
Haemulidae	520
Labridae	478
Gerreidae	377
Balistidae	282
Scombridae	276
Callionymidae	239
Sphyraenidae	233
Carangidae	196
Serranidae	194
Apogonidae	187
Ophichthidae	160
Unknown	143
Exocoetidae	98
Muraenidae	68
Scorpaenidae	64
Eleotridae	60
Pomacentridae	44
Tetraodontidae	42
Myctophidae	42
Bothidae	38
Istiophoridae	36
Sygnathidae	31
Ophidiidae	31
Caproidae	28
Cynoglossidae	26
Priacanthidae	24
Congridae	24
Clupeidae (*Jenkinsia*)	22
Opistognathidae	21
Diodontidae	20
Monacanthidae	18
Gempylidae	14
Microdesmidae	12
Coryphaenidae	12
Gobiosocidae	10
Nomeidae	10
Ostraciidae	9
Synodontidae	8
Holocentridae	7
Elopidae	7
Dactylopteridae	7
Hemiramphidae	5
Pomacanthidae	4
Antennariidae	3
Carapidae	3
Ogcocephalidae	3
Mugilidae	3
Sciaenidae	2
Triglidae	2
Ephippidae	2
Paralepididae	2
Pleuronectidae	1
Malacanthidae	1
Mullidae	1
Echeneidae	1
Lophidae	1
Chaetodontidae	1
Fistulariidae	1
Grand total	16,577

were compared to concurrently collected wind and hydrographic data.

We further clustered the family composition of individual samples (using above methods; average Euclidean distance of 0.5) to examine temporal patterns of larval assemblages within coastal waters (within night as well as among lunar periods and across the sampling season). Because there was some indication that sample composition changed over the course of each night (see "Results"), we grouped samples by time of collection (standardized to hours after sunset), and plotted mean larval density and diversity over time. The samples were insufficiently balanced for statistical analysis, so these data are presented qualitatively.

Larval sizes were examined in detail for the family Haemulidae. This group has one of the shortest larval durations (14–20 days; Brothers and McFarland 1981; Lindeman 1997) and previously has been suggested to spend most of their larval period nearshore (Lindeman et al. 2001). To examine the sizes of larvae collected over nearshore reefs, we randomly selected at least 20% of each sample for measurement of standard length. Individuals were measured at ×20 magnification through a Leica microscope with an attached digital camera. Their standard length was measured digitally using Image-Pro Plus 4.5 image analysis software.

Physical data collection and analysis

A mooring equipped with two Sontek Argonaut acoustic current and temperature recorders was deployed during the same period (1 July–30 September) at 25°04′N; 80°19′W, at a water depth of 26.8 m (Fig. 1). The two current meters were mounted at 4 and 21 m depths. An additional temperature logger was mounted at 12 m depth. Mean hourly data on winds were obtained from the NOAA-NDBC SEAKEYS/C-MAN station MLRF1 at Molasses Reef (25°01′N; 80°38′W). The raw wind and current time-series data were rotated into isobath coordinates, with v positive downstream toward 40° and u positive offshore toward 130°. All data were filtered with a 40-h, low-pass Lancos filter, to remove tidal variations and more clearly present the low-frequency fluctuations due to wind and FC influences.

Satellite images were examined for the sampling period to identify the presence of frontal eddies or inner shelf/bay water in the sampling region. Sea surface temperature (SST) data from the advanced very high resolution radiometer (AVHRR) were examined, but found to be uninformative for the period of interest due to spatially uniform surface water temperatures (signatures of features could not be distinguished). Ocean color data derived from the sea-viewing wide field-of-view sensor (SeaWiFS) also were examined, and a single image collected on 31 July 2000 was found to be useful (image provided by C. Hu, Institute for Marine Remote Sensing, College of Marine Science, University of South Florida).

Results

Larval assemblages

Over the seven sampling periods, a total of 16,577 larvae was collected, representing more than 66 families (Table 1; $n = 41$ tows). Mean ($\pm$SE) density was 23.7 ± 3.9 larvae per 100 m^3 (or 16.9 per 100 m^3 without the ACE complex); mean ($\pm$SE) diversity was 24.2 ± 0.9 taxa per tow. Catches were dominated by the ACE complex (28.8%), Scaridae (14.4%), Blennioidei (12.9%), and Gobiidae (10.2%). At least 47 families comprised $< 1.0\%$ of the overall catch (Fig. 2). Highly abundant families generally occurred frequently: the top four most abundant families occurred most frequently. Similarly, a majority of families comprised $< 1\%$ of the

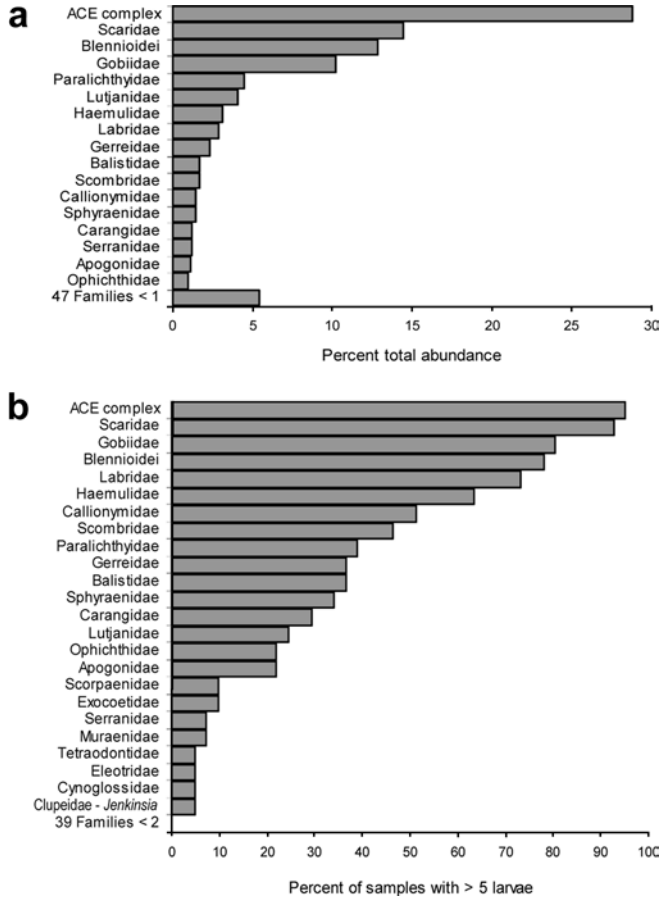


Fig. 2a, b Composition of nightly plankton catches in the upper Florida Keys over 3 months. Family proportions are plotted as: **a** total abundance and **b** frequency of occurrence of five or more larvae in a sample

total catch and occurred $<2\%$ of the time (Fig. 2). However, some relatively less abundant families occurred at a consistent low level such that they appeared more frequently in the catch than would be predicted based on their total abundance (e.g. Callionymidae and Scombridae). The Lutjanidae was one of the few taxa that was relatively abundant but was caught less frequently (i.e. occurred in a few very large pulses).

There was no significant difference in total larval density or diversity between depths (Fig. 3; Table 2). While there was a consistent trend for larval density to be higher on the new moon relative to the third-quarter moon (Fig. 3), this was not significant (Table 2). There also was no significant effect of lunar phase on larval diversity (Fig. 3; Table 2).

Based on mean nightly density over the sampling period, families could be clustered into seven characteristic groups (Figs. 4, 5; Table 3). In several cases these groupings represented families with clear life-history similarities. For example, the reef fishes Serranidae and Lutjanidae, which include species that form large temporally and spatially distinct spawning aggregations, exhibited almost identical patterns of relative abundance (density). Most of these larvae occurred in a single pulse early in the season. They were almost always present in the samples during the remainder of the season, but at much lower levels (Fig. 5). Similarly, the pelagic families Scombridae and Carangidae, exhibited comparable patterns of larval abundance. Their density decreased over the sampling period, exhibiting a sharp drop during the new moon in late July. This pattern was the reverse for several taxa that typically inhabit inshore lagoon waters (i.e. Florida Bay) as juveniles and adults. The ACE complex, Gerreidae, and *Cryptotomus roseus* (Scaridae) all exhibited a single seasonal peak during the same new moon period in late July (Fig. 5).

Assemblages of individual samples were most similar within nights, regardless of depth (Fig. 6). For example, group A consisted primarily of samples from the late-July new moon period, and the early-July new moon samples grouped separately from the others (group D). However, there was some within-moon grouping: group B consisted of primarily third-quarter moon deep samples from all sampling periods. Group C was a mix of new and third-quarter moon periods as well as deep and shallow samples. A few of the outliers were the very first samples collected on two different nights during the July third-quarter moon, while the single August new moon sample differed from the others in having relatively high densities of Blennioidei and Apogonidae, and lower numbers of Paralichthyidae.

Samples were not sufficiently balanced to rigorously test for faunal changes over the course of a sampling night; however, qualitatively there appeared to be several trends in the mean density and diversity of larvae collected each night. Mean larval diversity tended to be relatively low in the early samples, peaking around 4 h after sunset in both surface and deeper samples (Fig. 7). The ACE complex was most abundant in the first samples of a given night (at 5 m depth, within 1–2 h after sunset), with densities dropping off over time (Fig. 7). Higher densities of non-ACE complex larvae also tended to be collected at deeper depths early in the night, with a low at 3–4 h after sunset. There were relatively few surface tows and no tows were made between 2 and 3 h after sunset; however, a somewhat opposite trend is exhibited in the surface waters: densities peaked at 3–4 h after sunset, with lows at either end (Fig. 7).

The size frequency of Haemulidae was examined in detail to determine which larvae were collected over nearshore reefs. The standard length (SL) of collected haemulids ranged from 1.5 to 11.2 mm, and was roughly normal about a mode of 3.5–4.5 mm for the majority of the collection periods (Fig. 8). On two occasions (July new moon and September third-quarter moon) the size frequency was shifted up to a mode of 6.0 mm. On any given sampling night the size range encompassed (i.e. between minimum and maximum size) 4 mm to a maximum of 11 mm. Based on Brothers and McFarland (1981), these sizes would correspond to ages 0–25 days for *Haemulon flavolineatum*.

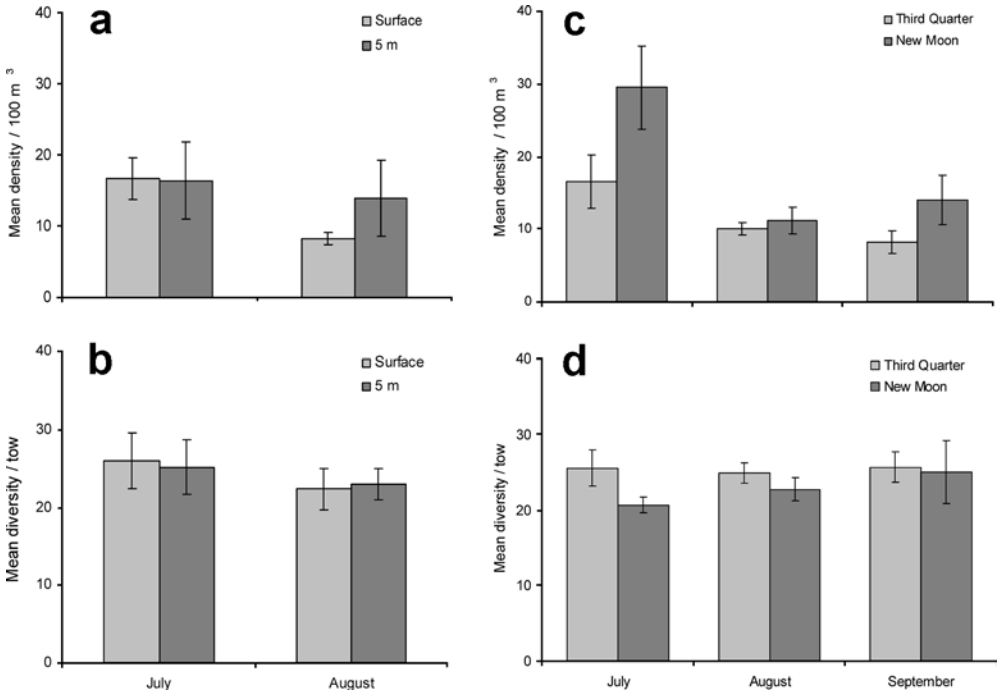


Fig. 3 Mean (±SE) density and diversity of families of fish larvae collected in nightly tows in the upper Florida Keys as a function of depth (**a**, **b**) and lunar phase (**c**, **d**). The Atherinidae/Clupeidae/Engraulidae complex was excluded from the density comparisons

Table 2 Results of two-way ANOVA for overall catch of fish larvae ($\log_{10}$ transformed density and diversity) between two depth layers (0–1.5 m and 4–5 m) and between two lunar phases (third-quarter and new moon) (*NS* not significant)

Sources	SS	*df*	MS	*F*	*P*	
Density of fish larvae with depth						
Period	0.080	1	0.080	0.596	0.453	NS
Depth	0.006	1	0.006	0.044	0.838	NS
Interaction	0.019	1	0.019	0.141	0.713	NS
Error	1.870	14	0.134			
Diversity of fish larvae (families) with depth						
Period	33.432	1	33.432	0.555	0.469	NS
Depth	2.781	1	2.781	0.046	0.833	NS
Interaction	2.300	1	2.300	0.038	0.848	NS
Error	843.524	14	60.252			
Density of fish larvae with lunar phase						
Period	0.628	2	0.314	2.824	0.073	NS
Moon	0.410	1	0.410	3.693	0.063	NS
Interaction	0.449	2	0.224	2.019	0.148	NS
Error	3.890	35	0.111			
Diversity of fish larvae with lunar phase						
Period	46.242	2	23.121	0.470	0.629	NS
Moon	11.471	1	11.471	0.233	0.632	NS
Interaction	4.606	2	2.303	0.047	0.954	NS
Error	1,721.922	35	49.198			

Physical oceanography

There was a persistent northward and onshore flow of nearshore waters along the upper Florida Keys during the entire sampling period. Downstream currents reached speeds near 40 cm s^{-1} and averaged 11 cm s^{-1}. The downstream flow was interrupted on occasion by short-duration (1–3 days) current reversals, with speeds of 5–10 cm s^{-1} (Fig. 9). Onshore flow in the upper layer ranged from 1–5 cm s^{-1} over the sampling period. This strong northward flow is typical for summer months as the FC undergoes its seasonal maximum volume transport (Niiler and Richardson 1973; Lee and Williams 1988; Schott et al. 1988) and the shoreward frontal boundary remains close to the shelf edge. The proximity of the FC to shore can increase water stratification at the shelf edge, elevating the isotherms of the main thermocline on the western side of the FC. Decreased stratification occurred in August and September as the FC transport declined toward the fall minimum. The general increase in water temperature through July reflects the proximity of the FC as well as seasonal warming. With the FC located close to the shelf edge, only small meanders along the western boundary of the FC are apparent as short-duration, small-amplitude current reversals. These reversals occurred as cyclonic frontal eddies were advected down-

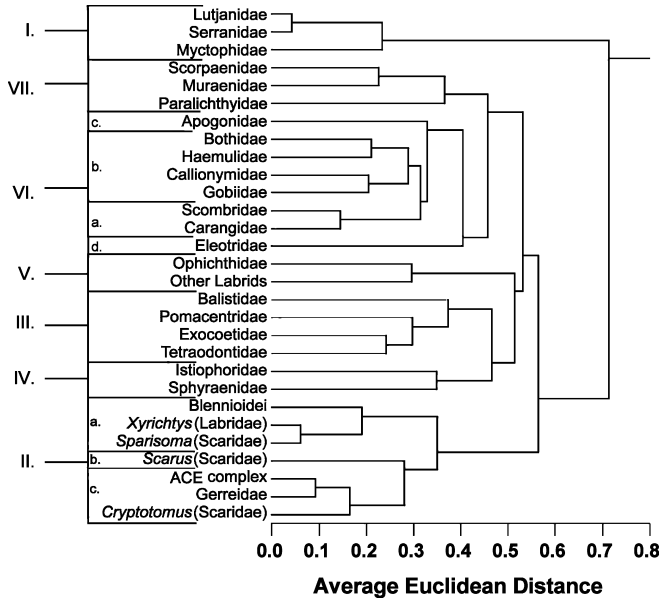


Fig. 4 Results of cluster analysis on taxon-specific nightly mean densities. A Bray–Curtis matrix was created with data for families of which more than 35 individuals were collected over at least four nights. Average Euclidean distances reflect degree of similarity and groups were clustered according to an average Euclidean distance of 0.4 (*ACE complex* Atherinidae/Clupeidae/Engraulidae complex; *group numbering* follows order in Table 3)

stream past the study site by the background flow of the FC (Lee and Mayer 1977; Lee et al. 1992). The frequency of meanders and eddy occurrence ranges from 7 to 10 days during the study, which is typical for this time of year (Lee et al. 1994). There is no evidence during this period of larger eddies that occasionally migrate from the Tortugas to the upper Florida Keys. Off the upper keys, these larger eddies can have diameters of 15–30 m and cause the FC front to be displaced much farther offshore from the shelf edge.

The wind record reflects typically weak SE winds during July, with some stronger easterly events reaching speeds of 7 m s^{-1} during August and September. Local winds bore no relation to the observed currents at the study site. There are few available records on coastal flushing of Florida Bay waters through the Keys' inlets. Most of the volume of water transported from the bay occurs through inlets in the middle and lower Florida Keys. For example, typically there are large net movements of bay water through the Seven-Mile Bridge and Long Key Channels toward the reef tract (Lee and Smith 2002). Small movement through the channels in the upper Keys occurs with tides and strong wind events, but net flows are weak. During July, the winds were favorable for flushing waters out of the bay in the middle Keys to the reef tract. These discharged bay waters would be carried northeastward with the prevailing northward alongshore flow of nearshore waters at that time. Due to seasonally high and uniform water temperatures, SST satellite thermal images of the FC for the month of July were not useful for distinguishing the presence of FC eddies or meanders, but a SeaWiFS RGB true color composite image from 31 July 2000 showed a plume of turbidity moving out of Florida Bay through the Seven-Mile Bridge Channel and along the Keys east- and westward. The image further confirms the nearshore location of the FC and the lack of any major eddies in the study area. Patchy cloud cover over the region resulted in an image that is best viewed in full color (http://imars.usf.edu/~hu/river/florida_bay/S2000213170926.fbay.gif).

Discussion

Comparisons of the mean density of larval fishes collected in near-reef waters of the upper Florida Keys with other regional studies are difficult since few such collections have been made and, where they have been made, substantially different gear has been used. For example, offshore SEFCAR cruises used MOCNESS nets fitted with 0.33 mm mesh; tows by McGowan (1985) in near-reef areas in the Flower Garden Banks in the Gulf of Mexico were made with bongo nets also fitted with 0.33 mm mesh; other recent collections do not report the nets used (Vásquez-Yeomans et al. 1998). Our neuston net was fitted with 1.0 mm mesh; thus, many small (pre-flexion) larvae were not retained. In addition, recent near-reef collections have tended to use larval light traps that not only select for late-stage, phototaxic larvae, but also sample volumes of water that cannot be quantified other than relative to other within-study collections (e.g. Choat et al. 1993; Brogan 1994; Milicich 1994; Sponaugle and Cowen 1996a; Hendriks et al. 2001; Meekan et al. 2001; Valles et al. 2001; Wilson 2001). Clearly, such gear differences preclude regional or spatial comparisons of relative larval densities; however, by cautiously examining relative abundances of taxa collected within tow-based ichthyoplankton studies, we can make some rough comparisons of overall larval ichthyofaunal compositions.

The family composition of larval fishes in near-reef waters of the Florida Keys differed substantially from those collected previously in waters offshore of the Keys: our catches were dominated by the ACE complex (28.8%), Scaridae (14.4%), Blennioidei (12.9%), and Gobiidae (10.2%), while offshore SEFCAR samples were dominated by Bregmacerotidae (18.7%), Myctophidae (16.3%), Gobiidae (9.3%) and Gonostomatidae (7.9%; Limouzy-Paris et al. 1994). While the gobiids are prominent in both collections, deep-water taxa such as the Myctophidae and Bregmacerotidae, which have been shown to be distributed farther offshore (Limouzy-Paris et al. 1997), were rare to entirely absent in our shallow-water collections. Elsewhere, the nearshore presence of myctophids has been shown to indicate the proximity of a large western boundary current (i.e. shoreward intrusions of the Agulhas Current off the southeast coast of Africa; Olivar and Beckley 1994; Harris et al. 1999). The pulsed nature of the appearance of myctophids in our

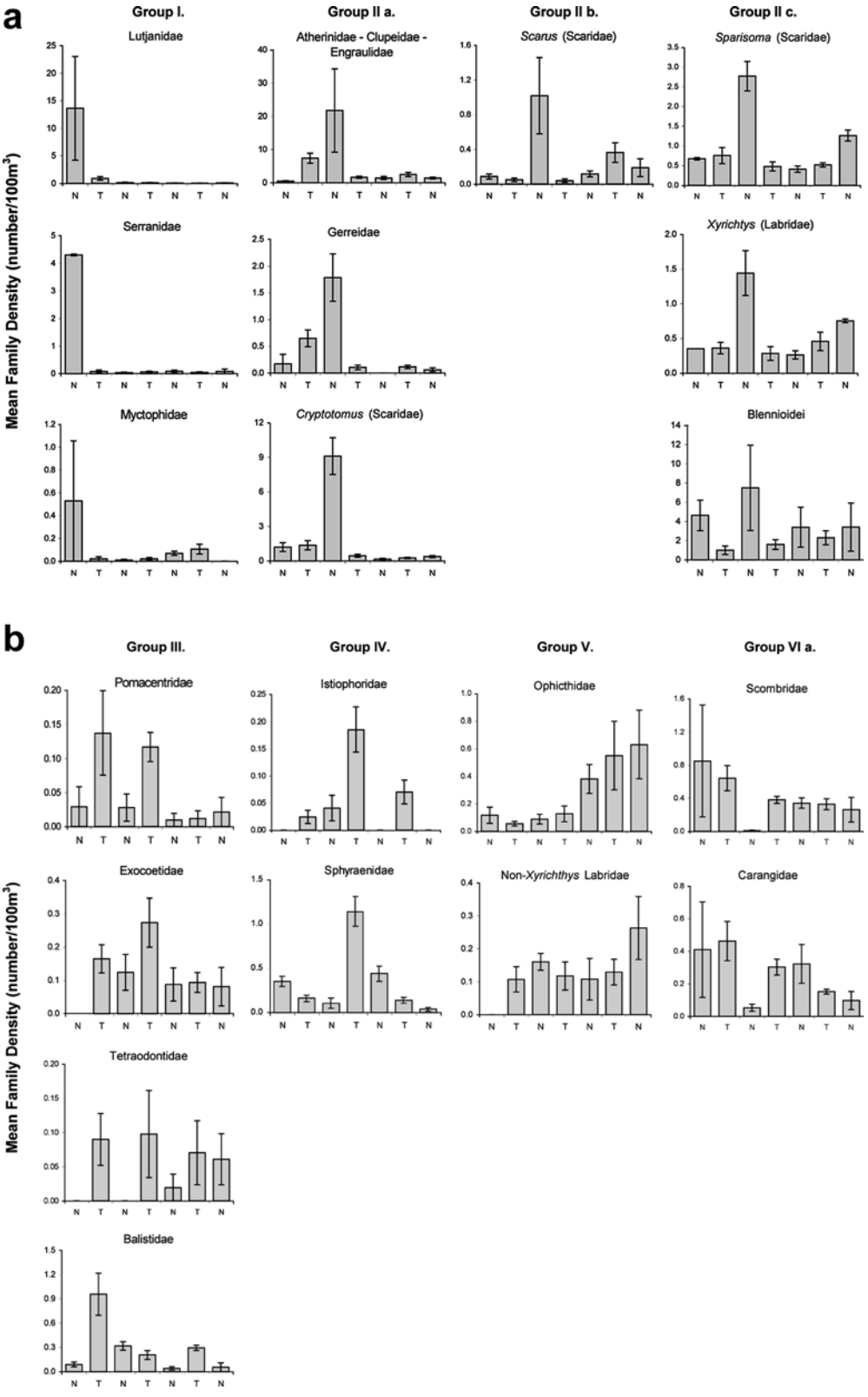
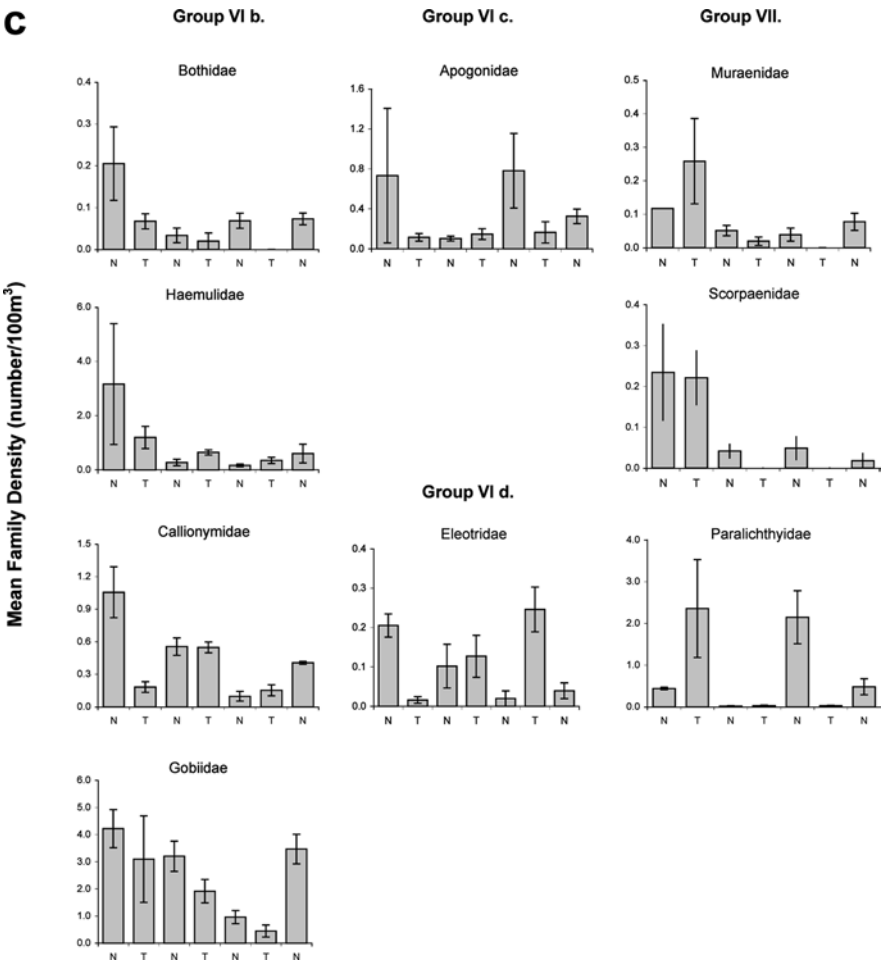


Fig. 5a–c Taxon-specific seasonal patterns of larval density. Groups are defined by the cluster analysis. Mean (± 1 SE) family density (number of larvae per 100 m^3) are plotted for each collection period beginning with the early-July new moon and continuing through the September new moon (*N* new moon; *T* third-quarter moon). Note that the *y*-axis scales differ among taxa

reef-based samples also likely reflects the relative influence of offshore waters.

Another taxon occurring in very different proportions onshore and offshore was Haemulidae (grunts). Haemulidae was our seventh most abundant taxon, but this family was not collected at all during the first SEFCAR cruise (133 net tows; 29 stations; a total of 20,619 fish larvae collected; Limouzy-Paris et al. 1994). During later cruises, a very small number of haemulids was collected (e.g. fall 1989 cruise: 6 haemulids out of a

Fig. 5a–c (Contd.)



total of 12,506 collected larvae from 179 net tows; spring 1990 cruise: 16 haemulids out of a total of 19,274 collected larvae from 133 net tows; Limouzy-Paris et al., unpublished data). Based on their abbreviated larval period, haemulids have been hypothesized to spend a large portion of their larval period nearshore (Lindeman et al. 2001). Not only were very few haemulids collected offshore during the SEFCAR cruises, but collected individuals were all very small (2–3 mm SL) pre-flexion larvae (Limouzy-Paris et al., unpublished data) that were probably simply lost to the system. The haemulids we collected ranged in size from 1.5 to 11.2 mm and were generally normally distributed around 4 mm (five collection periods) or 6 mm (two collection periods). Based on a published length–age relationship for *Haemulon flavolineatum*, these sizes correspond to age 0- to 25-day-old larvae and postlarvae. The age of the largest size collected also agrees with length–age relationships calculated for four other haemulids (Lindeman 1997). Settlement is considered to occur after 14–20 days in the plankton (Brothers and McFarland 1981; Lindeman 1997), and most of the smallest demersal *Haemulon* sp. collected in a separate study in South Florida were 7–8 mm SL (Lindeman 1997). Thus, not only are all larval sizes represented in our collections, but small numbers of postlarvae were likely collected. Our near-reef collection of relatively high numbers of haemulids in a range of sizes is consistent with the idea that haemulids remain nearshore throughout their larval period. Such a life-history strategy would have important implications for population connectivity (Sponaugle et al. 2002; Swearer et al. 2002).

Onshore–offshore gradients in larval densities previously have been reported for a number of reef fish taxa (Leis 1982, 1991a; Leis and Goldman 1987; Kingsford and Choat 1989; Kobayashi 1989; Franco-Gordo et al. 2002). Unpublished SEFCAR results comparing inshore to offshore stations in the Straits of Florida suggest that taxa such as the Scaridae, Gerreidae, Blenniidae, and, to a lesser extent, Apogonidae, Balistidae, and Tetraodontidae tend to occur in higher densities nearshore (Limouzy-Paris et al., unpublished data). Kobayashi (1989) demonstrated that gobiid larvae were most concentrated in near-reef waters of Kaneohe Bay, Hawaii, and this distribution was maintained during daylight and bright, moonlit nights. This pattern broke down during dark, moonless nights, suggesting that near-reef distributions were actively maintained using visual cues. Similarly, larvae of families with demersal eggs were most abundant near reefs off New Zealand (Gobies-

Table 3 Summary of temporal patterns of abundance exhibited by families of fish larvae collected in reef waters of Pickles Reef, Florida Keys. Similarity based on cluster analysis (see "Materials and methods")

Group, subgroup	Taxon
Group I: early-July new moon peak in density	
	Lujanidae
	Serranidae
	Myctophidae
Group II: late-July new moon peak in density	
a	Atherinidae/Clupeidae/ Engraulidae
	Gerreidae
	Cryptotomus (Scaridae)
b	*Scarus* (Scaridae)
c	*Sparisoma* (Scaridae)
	Xyrichtys (Labridae)
	Blennioidei
Group III: July and August third-quarter moon peaks in density	
	Pomacentridae
	Tetradontidae
	Balistidae
	Exocoetidae
Group IV: single August third-quarter moon peak in density	
	Istiophoridae
	Sphyraenidae
Group V: seasonal increase in density (peak at September new moon)	
	Ophicthyidae
	Non-*Xyrichtys* Labridae
Group VI: seasonal decrease in density	
a	Scombridae
	Carangidae
b	Bothidae
	Haemulidae
	Callionymidae
	Gobiidae
c	Apogonidae
d	Eleotridae
Group VII: July third-quarter moon peak with lows at other third-quarter moons	
	Scorpaenidae
	Muraenidae
	Paralichthyidae

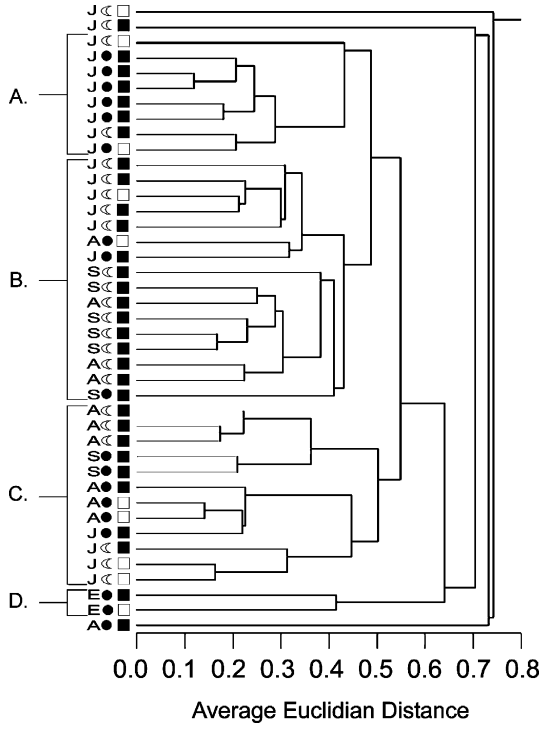


Fig. 6 Results of cluster analysis of larval fish assemblages based on individual samples. A Bray–Curtis matrix was created with data for families of which more than 35 individuals were collected over at least four nights. Average Euclidean distances reflect degree of similarity and groups A–D were clustered according to an average Euclidean distance of 0.5. Samples were identified by three variables: sampling period, moon phase and depth (*E* early July; *J* July; *A* August; *S* September; *filled circle* new moon; *open sickle-shaped symbol* third-quarter moon; *open box* 0–1 m depth; *filled box* 4–5 m depth)

cocidae, Acanthoclinidae, Tripterygiidae, Eleotridae, and Gobiidae; Kingsford and Choat 1989) and Mexico (Tripterygiidae and Gobiidae; Vásquez-Yeomans et al. 1998), and dominated catches near reefs and within an atoll lagoon in the Great Barrier Reef (Gobiidae, Pomacentridae, and Apogonidae; Leis and Goldman 1987). Larvae hatching from benthic eggs typically are more developmentally advanced than larvae hatching from pelagically spawned eggs such as scarids and haemulids (see Cowen and Sponaugle 1997, for review); thus, they may be more able to actively swim to maintain their position in the water column (e.g. Brietburg 1989; Stobutski and Bellwood 1994; Leis and Carson-Ewart 1997; Fisher et al. 2000). The means by which presumably more weakly swimming larvae of haemulids and scarids remain near-reef during their early larval period is less clear.

Interestingly, and in contrast to the above predictions, our collection of benthic-spawning pomacentrids was very low. Pomacentrids are a conspicuous constituent of the nearshore reefs of South Florida and late-stage larvae appear regularly in light traps deployed in the upper Florida Keys (Sponaugle, unpublished data). During the same sampling period, new settlers of the most common pomacentrid, *Stegastes partitus*, were collected from the reef (Sponaugle, unpublished data). Therefore, the fact that we did not collect many in our tows suggests that either larvae do not remain nearshore during development, that they occupy a different (i.e. deeper) portion of the nearshore water column, or that they were able to evade our nets. As discussed above, the swimming abilities of this group may be relatively advanced at an early age; thus, any of these options may be possible. Recent larval otolith tagging efforts demonstrated that a significant portion of a pomacentrid population at Lizard Island in the Great Barrier Reef may be self-recruited (Jones et al. 1999). The mechanisms by which such larvae remain near or return to their natal population are yet unknown (e.g. Sponaugle et al. 2002).

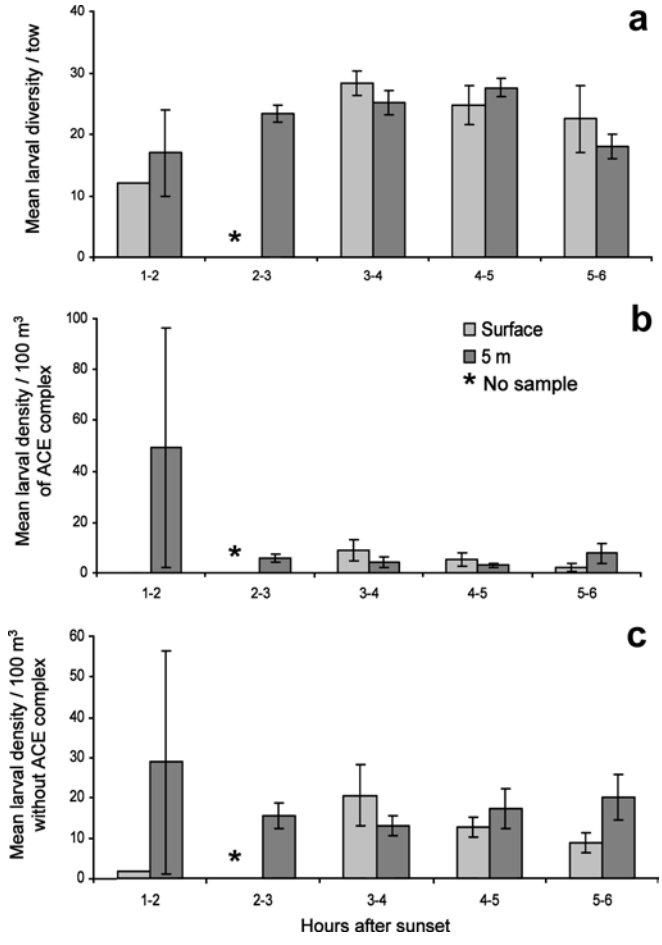


Fig. 7 Mean (±SE) diversity of all larvae (**a**) by depth over a sampling night off the Florida Keys. Mean (±SE) density of the Atherinidae/Clupeidae/Engraulidae (*ACE*) complex (**b**) and other larvae (**c**) by depth over a sampling night. Time is relative to sunset. Note that there was only one surface sample collected within 1–2 h after sunset

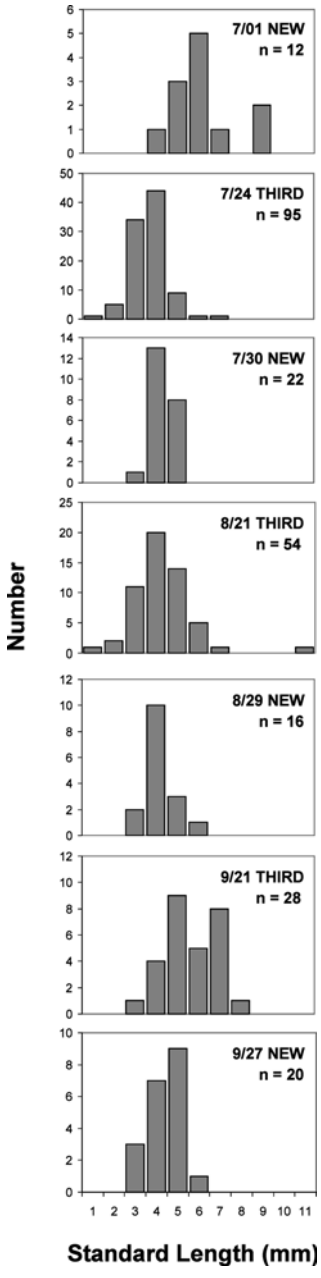


Fig. 8 Size frequency of randomly selected Haemulidae collected during each sampling period

Most of the abundant taxa (e.g. ACE complex, Scaridae, Blennioidei, and Gobiidae) collected in our near-reef samples occurred frequently over the 3.5 months of sampling. In addition, several of the less abundant taxa (e.g. Callionymidae, Scombridae) occurred regularly, but at lower levels. While all of these taxa exhibited some periodicity, their presence in the samples reflects regular spawning activity. For other taxa, spawning events are likely more discrete. The lutjanids and serranids, for example, occurred in one large pulse in early July. These two families have been shown to undertake migrations to spatially and temporally distinct locations to spawn in large aggregations (see review by Domeier and Colin 1997). Lindeman et al. (2000) report that commercial fishermen have identified at least 22 potential spawning sites for lutjanids near the Dry Tortugas and Key West. Riley's Hump in the Dry Tortugas is likely one of the most important sites, where at least five lutjanid and several serranid species have been found in spawning aggregations (Lindeman et al. 2000). The finding that larval abundance patterns in near-reef waters are similar for these two groups suggests that they also may be subjected to or utilize the same oceanographic transport mechanisms as they move up the Keys. Further testing of this concept would require aging the collected larvae to determine similarity in birthdates. Lutjanids and serranids may differ somewhat with regard to the length of their larval life (or pelagic larval duration). Most lutjanids from Floridian have PLDs between 25 and 40 days, and serranids, between 30 and 45 days (see Lindeman et al. 2000, for compilation of PLDs; Cowen and Sponaugle 1997, for review of PLD). But as PLD has been shown to vary with temperature in another coral reef fish (*Thalassoma bifasci-*

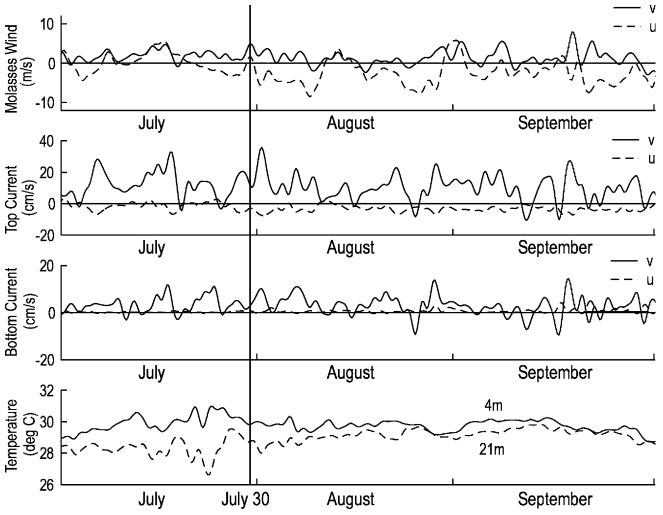


Fig. 9 Subtidal time series of wind components from Molasses C-MAN station, and current components and temperature from mooring C located at the shelf edge near Molasses Reef (see Fig. 1). Top mooring instrument was located at 4 m depth and the bottom instrument at 21 m depth. The raw data were low-pass filtered and rotated into isobath coordinates (*positive v* downstream, alongshore to 40°; *positive u* offshore to 130°; see "Materials and methods" for full description). For reference, a *vertical line* is drawn at 30 July, the night when oceanic taxa in the samples were replaced by inner shelf/bay taxa

atum; Sponaugle, unpublished data), these estimates may vary seasonally. Despite the fact that lutjanids and serranids are among the top predators on Florida reefs, that they are major constituents of commercial and recreational fishing, and that they are managed together, we know relatively little about larval transport pathways and population connectivity. Their parallel appearance in near-reef waters suggests the possibility that there are commonalties in their early life-history strategies.

There was no clear pattern in overall larval density or diversity between the two sampled depths. This may be due to several reasons. First, the strata were rather finely divided due to the shallow depth of the water column. Both of our strata are typically included in the first sampling strata (0–25 m) of most ichthyoplankton studies (but see Leis 1991b). Second, the strata were not discretely sampled, since we did not have an opening–closing net; thus, there was likely some integration between the two depths. Third, there is a suggestion that there is less overall vertical structure in the distribution of larval fishes at night than during the day (reviewed in Leis 1991a, 1991b). Finally, there may have been some fine-scale vertical migration occurring over the course of the night that may have blurred any differences. Plots of mean larval density (without the ACE complex) suggest that larval densities peaked at the 4–5 m depth immediately after and 5–6 h after sunset, while the reverse was true for densities at the surface. Mean larval densities in surface waters increased after sunset to a peak 3–4 h after sunset. This suggests that larvae may undergo vertical migration from depth during the day to surface waters 3–4 h after sunset, and then reverse the migration in the early morning. Such migrations may be linked to vertical migration of zooplankton prey or utilization of physical mechanisms to remain in proximity to reefs or other nearshore structures. It is well documented that zooplankton in many oceans undergo a diel vertical migration, whereby populations move up from depth during the day to occupy shallower waters at night (e.g. Haney 1988; Hays et al. 1996; Thompson and Allen 2000). Off Barbados, larval fishes migrate vertically, but whether they move up or down at night is taxon specific (Paris and Cowen, unpublished data). Leis (1986) demonstrated that, with some exceptions, larval fishes at Lizard Island in the Great Barrier Reef (GBR) generally move upwards at night. Similarly, larval fishes at One Tree Island, GBR, appear to avoid surface waters during the day (Kingsford 2001). Position in the water column also may influence horizontal larval transport if deep and shallow waters move in different directions (e.g. Cowen 2002).

There was a non-significant trend for total catches during the new moon to be higher, but less diverse, than catches during the third-quarter moon. While some temporal patterns of larval abundance in near-reef waters may not be evident due to our examination of larval abundance and diversity at the family level, several taxa at the genus level reflect family-wide patterns of abundance in the plankton. For example, while the relative abundance of *Cryptotomus* and *Sparisoma* shifted over the course of the sampling season, all three scarid genera peaked on 30 July. The lack of lunar cycling in our near-reef collections is apparent at the family and genus level. The only evidence suggestive of some lunar cyclic fluxes in density was for group III taxa. When comparing the third-quarter moon and new moon of a particular month, catches during the third-quarter moon were somewhat higher for the Pomacentridae, Exocoetidae, Tetraodontidae, and Balistidae, but even here patterns were not distinct (i.e. high SE). The lack of significant lunar cycling in the ichthyoplankton suggests that either there are relatively few taxa that exhibit lunar-cyclic spawning patterns, or lunar-cyclic spawning patterns are dampened by variable oceanographic conditions.

Most families of larvae exhibited event-specific pulses. Even where there were seasonal increases or decreases over time, event-related signals were evident. For example, Scombridae and Carangidae had noticeably reduced densities during the late-July new moon. There was similar episodic temporal variation in the densities of most of the other taxa, except for Ophicthyidae and, to a lesser degree, the non-*Xyrichtys* labrids (group V taxa), both of which exhibited a smooth seasonal increase.

Event-related patterns in larval assemblages also are apparent in the cluster analysis of individual samples. The tightest clustering of samples occurred within particular nights, regardless of sample depth. Beyond individual nights, a few samples clustered by lunar phase, particularly the third-quarter moons. Other groups consisted of an even mix of new and third-quarter moon

nights. Two nights were particularly distinct from the others. The 1 July new moon samples clustered together, apart from the rest of the nights. These samples were characterized by especially large volumes of group I and VIb taxa and noticeably low volumes of group IIa, IIb, and III taxa. Interestingly, the 30 July new moon samples also clustered apart from the other nights. These samples were characterized by large pulses of group II and particularly low volumes of group I and VIa taxa. It appears as though there may have been a significant change in water masses at this time. Oceanic taxa such as the scombroids and carangids disappeared from the samples, and inner shelf/bay taxa such as the ACE complex, Gerreidae, and *Cryptotomus* (Scaridae) appeared in large numbers. The shift in larval assemblages is likely due to the flushing of Florida Bay waters out of channels in the middle Florida Keys and entrainment of that water mass northeastward with the FC. Concurrently measured currents throughout the sampling period reflect the nearshore proximity of the FC. Nearshore waters were largely flowing alongshore to the north as they were entrained by the FC, and a SEAWIF image from the following day shows the movement of a turbidity plume northward from the middle Florida Keys. On a very different scale and in a different system, Smith and Suthers (1999) documented the offshore displacement of shelf-spawned larvae during an upwelling event. Similarly, large changes in larval fish distributions over short time-scales were associated with changes in the position of the shelf-slope front in the NW Mediterranean (Sabates and Olivar 1996). Distinct larval fish assemblages can effectively function as biological tracers of physical phenomena (Smith and Suthers 1999; Smith et al. 1999).

Lee and Williams (1999) describe the upper Florida Keys system as being dominated by the proximal FC and associated meanders and frontal eddies. Cyclonic eddies can spin off the western edge of the FC and enter coastal waters on a regular basis (Lee 1975), entraining warmer streamers around the western side of each eddy (see Zantopp et al. 1987). Such gyres, frontal eddies, and meanders have been suggested to play an important role in the transport of offshore larvae to benthic marine populations along the Keys (Lee et al. 1992, 1994; Lee and Williams 1999). Field evidence of offshore larval distributions and results of modeling efforts are consistent with this hypothesis (Criales and Lee 1994; Limouzy-Paris et al. 1997; Stoner et al. 1997; Yeung and Lee 2002), but direct correlations between the presence of such physical features and settlement pulses to the reef are needed. Our study was not designed to measure settlement pulses, and there were no large meanders or frontal eddies during the course of our study. However, results of this study have shed light on the nearshore dynamics of larval fish assemblages and have contributed to our understanding of population replenishment in the Florida Keys. First, there are nearshore assemblages of larvae immediately over reefs, and these differ substantially from offshore larval assemblages. Second, these assemblages are not constant, but change significantly over time. There is little evidence of lunar cyclic behavior. Instead, groups of larvae appear and disappear from the water episodically according to particular nights or times of the season. Sharp changes in assemblages can reflect patterns in adult spawning (e.g. lutjanids and serranids) or changes in water masses (replacement of oceanic water with inner shelf/bay water). Third, changes in water masses and their associated larval assemblages can occur in a seemingly unidirectional flow field in the absence of major oceanographic features such as frontal eddies. The proximity of reefs to a major western boundary current likely contributes to the dynamic nature of the larval assemblages, but some taxa may be able to remain in nearshore waters throughout the duration of their larval period (e.g. haemulids). Clearly, the biological and physical mechanisms associated with larval retention and transport to nearshore reefs are complex and warrant further study.

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