

Florida Current frontal eddies and the settlement of coral reef fishes

*Su Sponaugle*¹

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

Thomas Lee and Vassiliki Kourafalou

Division of Meteorology and Physical Oceanography, Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, Florida 33149-1098

Deanna Pinkard

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

Abstract

We deployed three replicate larval light traps off the upper Florida Keys from June–September 2001 to measure the delivery of settlement-stage fish larvae to the coral reefs. Nightly measures of larval abundance were compared to water temperatures measured across the outer reef, nearby wind records, and the alongshore and cross-shelf components of the currents measured at the seaward edge of the reef. These time series, together with satellite-derived sea surface temperature and color fields indicate that a very large multi-taxa larval pulse on 20 July was directly associated with the passage of a Florida Current (FC) sub-mesoscale frontal eddy embedded within the elongated remnant of a mesoscale eddy. A second large pulse of larvae occurred when a similar mesoscale eddy passed the upper Keys in mid-June. Periods of increased tidal bore activity occurred with the passage of these eddies. Semidiurnal internal tides caused near-bottom onshore intrusions of cooler slope waters during periods of onshore meanders of the FC front when the downstream baroclinic flow and stratification increased at the reef margin. The high abundance and similarity in larval ages within taxa on 20 July indicate a Keys shelf origin, although the temporal and spatial scales of entrainment cannot be resolved. The passage of a third mesoscale eddy in September did not result in a larval pulse, possibly because of a mismatch between biological and physical criteria, several of which must be met for larval transport by mesoscale eddies to be successful.

Identification of the biological and physical mechanisms involved with the transport of the pelagic larvae of benthic

¹ Corresponding author (ssponaugle@rsmas.miami.edu).

Acknowledgments

The biological component of the research was supported by a grant from the National Science Foundation (OCE 9986359) to S.S. Collection of the current meter and hydrographic data was supported by the National Center for Caribbean Coral Reef Research through Environmental Protection Agency grant R82802001. Nearshore light trap sampling was conducted under permit 00S-524 from the Florida Fish and Wildlife Conservation Commission and permit FKNMS-2001-004 from the Florida Keys National Marine Sanctuary. Current meters were deployed under permits FKNMS-2000-018. AVHRR sea surface temperature fields were provided by the Ocean Remote Sensing Group of the Johns Hopkins University Applied Physics Laboratory. Ocean color images were prepared by K. Kilpatrick, NASA MODIS Ocean Science team, UM/RSMAS remote sensing group. Light trap deployment involved numerous participants: J. Fortuna, K. Grorud-Colvert, K. Denit, M. Paddock, M. Sullivan, and L. Buhrmaster. J. Vergara assisted with sample sorting and D. Richardson identified the larvae with the expert help of C. Paris. W. Richards kindly provided preliminary chapters of his forthcoming book on larval identification. E. Williams assisted with deployment of the current meters and processing of the physical data. Comments made by J. Leichter prompted further consideration of high-frequency tidal bore activity and, together with discussions with K. Leaman and D. Olson and the comments of R. Cowen, C. Paris, and three anonymous reviewers, substantially improved an earlier version of the manuscript.

marine animals is a topic of substantial interest to the fields of ecology, oceanography, conservation, and management. The transport and return of larvae to a suitable settlement habitat are critical to the ecology and population dynamics of marine animals with complex life histories and have important implications for population connectivity (*see* Sponaugle et al. 2002; Warner and Cowen 2002). The degree to which marine populations are open or closed clearly affects how they may be conserved and managed (Roberts 1997; Cowen et al. 2000), including the design and establishment of marine reserves (Carr and Reed 1993; Warner et al. 2000; Palumbi 2003).

Although the physical mechanisms associated with larval transport are important at all stages of pelagic larval life (*see* Cowen 2002 for review), much attention has focused on the settlement dynamics of the later stages. Temporal patterns of reef fish settlement are typically cyclic, peaking with particular lunar or tidal amplitude phases, but there is invariably an element of stochasticity superimposed on both the magnitude and timing of these events (Robertson 1992; Meekan et al. 1993; Sponaugle and Cowen 1996a). It can be difficult to identify physical mechanisms associated with episodic pulses in the delivery of late-stage larvae to reefs because concurrent measurements of the physics and biology are needed for continuous time periods and larvae must be available (*i.e.*, spawned into the water mass) for successful delivery by a physical process.

Physical processes that have been associated with the transport of late-stage larvae include wind and storm events (Shenker et al. 1993; Milicich 1994; Thorrold et al. 1994); tides (*see* Cowen 2002 for review) and internal tidal bores (Pineda 1991; Leichter et al. 1998; Findlay and Allen 2002), waves, and slicks (Shanks 1983; Kingsford and Choat 1986); and onshore flow at depth (Cowen and Castro 1994; Sponaugle and Cowen 1996a; Paris-Limouzy 2001). Recirculating features such as current eddies have been hypothesized to function both as larval retention mechanisms (e.g., Sale 1970; Hamner and Hauri 1981; Lee et al. 1994) and as onshore transport mechanisms (Limouzy-Paris et al. 1997; Yeung et al. 2001).

The Atlantic coastal waters of the Florida Keys contain a shallow reef system bordered by a major western boundary current, the Florida Current (FC). Previous studies have shown that the outer shelf region of the upper Florida Keys is strongly influenced by the FC and the transient passage of FC meanders and eddies (Lee et al. 1992, 1994). Satellite imagery has shown that frontal eddies (recirculating vortices that travel along current fronts) occur all along the boundary of the Loop Current (LC) and the FC on scales of kilometers to a few hundred kilometers in diameter (Lee et al. 1991; Fratantoni et al. 1998). The larger mesoscale eddies form where topographic constraints are weak (i.e., in this system, the Gulf of Mexico, and the southern Straits of Florida). Cold-core, cyclonic eddies with diameters of 100–200 km travel along the LC front in the Gulf of Mexico and enter the Straits of Florida near the Dry Tortugas. They move downstream along the Keys outer shelf over a period of 1–3 months with increasing forward speed and decreasing size (Lee et al. 1994; Fratantoni et al. 1998). As the width of the Straits of Florida narrows in the middle Keys, where the channel makes its turn toward the north, the topographic constraint increases (i.e., FC flow converges upon steep topography of the middle and upper Keys). Satellite imagery consistently shows that mesoscale eddies in this region begin to elongate, shear apart, and decay into smaller sub-mesoscale eddies. Recirculation within mesoscale eddies and their several months' duration in the Keys coastal zone has been proposed as a retention mechanism that may contribute to local recruitment of larvae spawned in the Dry Tortugas or along the outer reef tract (Lee et al. 1992, 1994; Lee and Williams 1999). Sub-mesoscale eddies with diameters of 10–40 km can occur anywhere along the frontal boundary as mesoscale eddies decay or as the FC meanders along the shelf edge (Lee 1975). Sub-mesoscale eddies are typically observed moving along the FC front for short periods of 1–3 weeks and are rapidly advected downstream by the background flow (Lee and Mayer 1977; Shay et al. 1998). These frontal eddies can contribute to cross-shelf larval transport (Limouzy-Paris et al. 1997).

Internal tidal bores occur frequently along the Florida Keys outer reef tract during late spring and summer (when the water column is stratified with the onset of the seasonal thermocline) and may provide an additional means of onshore transport of larvae that reside in the near-bottom slope waters offshore of the reef crest (Leichter et al. 1998, 2003). Internal tidal bores in the Straits of Florida are recognized as near-bottom intrusions of cooler slope waters generated

by semidiurnal internal tidal waves moving along the thermocline. Tidal bores of up to 10 m in height, traveling 10–20 cm s⁻¹ up the reef slope from 50–80-m depths often contain higher concentrations of nutrients as well as phytoplankton (Leichter et al. 1996, 1998, 2003). These cold intrusions have been shown to penetrate upslope to the 20-m isobath at Conch Reef (10 km upstream of our study site), causing near-bottom temperature variations of 3°C to 8°C at semidiurnal tidal periods (Leichter et al. 2003). Occasionally tidal bores are observed to extend to the 10-m isobath, but with smaller temperature changes. Larval fishes from several families have been observed within tidal bores, although most were not benthic reef fishes, nor were they settlement stage (Leichter et al. 1998). The amplitude and duration of tidal bore activity increases with depth offshore of the reef, varies somewhat inconsistently with spring and neap tides, and may be influenced by the passage of large frontal eddies (Leichter et al. 2003). Internal tidal bores are an important source of nutrient flux onto the reef (Leichter et al. 2003), but the degree to which this mechanism contributes to the settlement of reef fishes is unknown.

The upper Florida Keys region supports a diverse and abundant reef fish fauna, but the means by which populations are replenished are unknown. Pelagic distributions of larval invertebrates (Criales and Lee 1995; Stoner et al. 1997) and the influx through Keys tidal channels of postlarval invertebrates (Yeung et al. 2001; Yeung and Lee 2002; Criales et al. 2003) have been correlated with the passage of recirculating eddy features along the outer shelf of the Keys, but to date, there have been no direct correlations between actual settlement, particularly of reef fishes, and the passage of such features.

This study was designed to directly examine the physical mechanisms associated with large pulses of late-stage fish larvae to the reef. Larval light traps were deployed to provide a measure of the supply of settlement-stage larvae to the reefs, and current meters and temperature loggers were used to identify physical forcing events. Satellite-derived observations were employed to identify eddy events and to track their temporal and spatial evolution.

Materials and methods

Biological sampling—Three replicate larval light traps were deployed for 41 nights from 12 June–26 September 2001 in the upper Florida Keys (Fig. 1). Attempt was made to deploy traps every other night beginning on 5 July; however, rough weather and boat engine problems resulted in three major gaps in the record. Larval light traps intercept late-stage larvae on their approach to settle on reefs located at the shelf edge (*see* Sponaugle and Cowen 1996a for trap design). Patterns of larval appearance in light traps often match settlement patterns back-calculated from recruited juveniles (Sponaugle and Cowen 1996b). Although the taxonomic composition of larvae collected in light traps is obviously limited to species that are positively phototactic, traps are useful for comparing the relative abundance of larvae among successive nights. Traps sample a radius of ~50 m and are assumed to sample equally during different flow con-

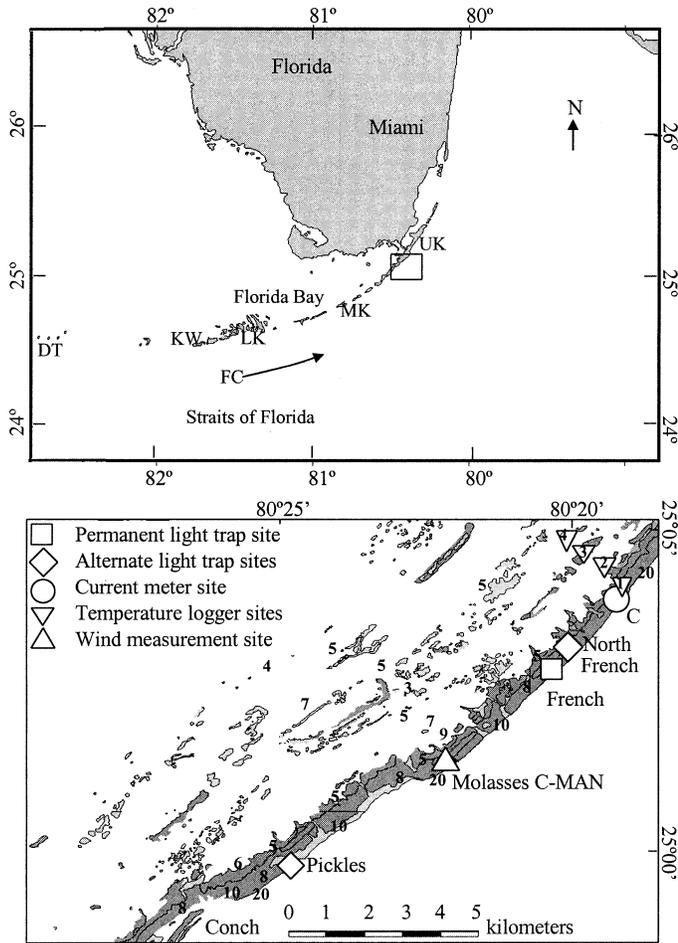


Fig. 1. Map of the upper Florida Keys study area showing sites of light trap deployment, current meter mooring (mooring C), bottom-temperature loggers (T1–4), and Molasses C-MAN station. Map was modified from the Benthic Habitats of the Florida Keys Program (unpubl. data). DT = Dry Tortugas; KW = Key West; LK = lower Keys; MK = middle Keys; UK = upper Keys; FC = Florida Current. Numbers near reefs indicate depth in meters.

ditions (e.g., traps may sample more water during high flows, but the ability of larvae to swim to the trap may be diminished). Traps were deployed 1 m below the surface at sites with depths ranging from 6–10 m by attaching each buoyant trap to a moored buoy and weighting the trap bottom (Fig. 2). Traps were deployed at dusk and retrieved the following dawn. On five occasions, traps were retrieved after 5–6 h of fishing as a result of attempts to calibrate light trap collections with plankton net tows (12, 13, 20, and 22 June) or because of boat engine problems (12 July). Because settlement likely occurs primarily during the first half of each night (Sponaugle unpubl. data), we did not standardize these samples to reflect the shortened fishing period. We include them in the time series for reference, although overall fishing effort was not entirely comparable to other nights.

On most nights, three replicate traps were deployed parallel to shore approximately 150–200 m apart at French Reef (25°02.06'N, 80°21.00'W; Fig. 1; Table 1). During four lunar periods (two new moons, 20–22 June and 18–19 August;

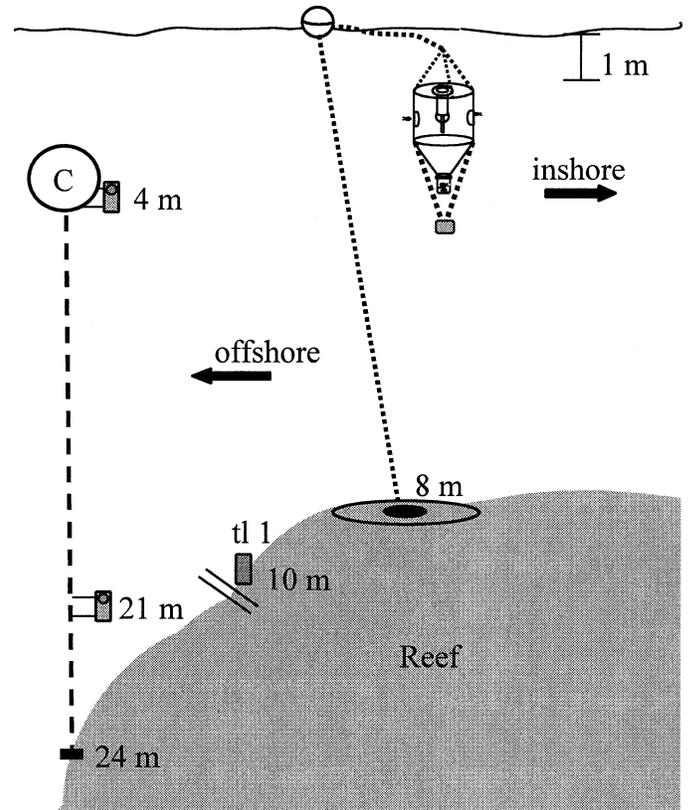


Fig. 2. Schematic of instrument configuration. Light traps were attached to permanent moorings anchored just seaward of the high-relief portion of the reef. A weight suspended off the bottom of the trap served to orient the traps vertically and position them approximately 1 m below the surface. Mooring C was positioned seaward of the reef crest and consisted of a current meter and temperature logger (attached boxes) at 4 and 21 m. The 10-m bottom temperature logger (tl) is included for reference. Schematic view is looking alongshore to the south, into the Florida Current.

and two third-quarter moons, 10–11 August and 9–10 September), three replicate traps were deployed at two nearby sites each night: Molasses Reef (25°00.74'N, 80°22.40'W) and Pickles Reef (24°59.23'N, 80°24.88'W), or French Reef and North French Reef (25°01.23'N, 80°26.52'W). This sampling design was part of another study examining differences in larval supply to protected and unprotected areas (Grouud-Colvert and Sponaugle unpubl. data). As a result of general long-term concordance and specific concordance during the study period of samples among sites along the upper Keys reef tract (D'Alessandro and Sponaugle unpubl. data), collections from neighboring sites were averaged for each night and plotted together with samples from French Reef.

Upon trap retrieval each morning, samples were preserved in 95% ethanol and returned to the lab for processing. Samples were sorted for fish larvae under a dissecting microscope. Larvae were identified to the lowest feasible taxonomic level using the NOAA-NMFS Southeast Fisheries Science Center Larval Fish Identification Guide (Richards unpubl. data), but for the purposes of this study, patterns of larval supply were analyzed by family. All small, silvery, mid-water reef fishes were grouped into an Atherinidae/Clu-

Table 1. Type, location, and depth of deployment of all physical sampling equipment deployed during the study period 20 June–30 September 2001. TL refers to temperature logger. MLRF-1 refers to a NOAA data buoy station at Molasses Reef.

| Station | Depth (m) | Instrument type | Latitude | Longitude |
|-----------|--------------------|---|------------|------------|
| Mooring C | 21.0 (bottom) | Sontek acoustic current meter/TKSA temperature logger | 25°04.04'N | 80°19.10'W |
| Mooring C | 4.0 (top) | Sontek acoustic current meter/TKSA temperature logger | 25°04.04'N | 80°19.10'W |
| TL 1 | 9.8 | TKSA temperature logger | 25°04.14'N | 80°19.17'W |
| TL 2 | 7.0 | TKSA temperature logger | 25°04.43'N | 80°19.47'W |
| TL 3 | 4.0 | TKSA temperature logger | 25°04.77'N | 80°20.06'W |
| TL 4 | 5.6 | TKSA temperature logger | 25°05.27'N | 80°20.83'W |
| MLRF-1 | 10 m above surface | Wind data logger | 25°00.36'N | 80°22.48'W |

peidae/Engraulidae (ACE) complex. Further, all Blenniidae, Clinidae, Labrisomidae, and Tripterygiidae were grouped together under the suborder Blennioidei. The majority of larvae were late-stage and near settlement, with several taxa in the process of undergoing metamorphosis.

The age of a selected number of larval fish taxa was obtained by examination of fish otolith increments. Most reef fishes have otoliths (ear stones) that are deposited on a daily basis, providing a daily record of age and transitional events, such as settlement. Ten randomly selected individuals per species or larval type from each of the 10 most abundant families collected on a single night of the largest larval pulse (20 July) were aged using standard procedures (Brothers 1987). The otoliths of two of these species that also settled during an earlier large pulse on 13 June were examined for comparison. The number of daily increments provided a measure of how long each individual had been in the water column prior to collection.

Physical sampling—To identify and describe oceanographic processes influencing settlement, a moored array of current and temperature loggers was maintained across the shelf at the study site for the duration of the study period: 19 June–30 September 2001. In this study, we used data from bottom temperature loggers (made by TSKA) positioned across the outer reef crest at depths of 9.8, 7.0, 4.0, and 5.6 m, and from mooring C, which was positioned just seaward of the reef crest at the 24-m isobath, where FC influences are expected to be significant (Fig. 1; Table 1). Mooring C was equipped with Sontek Argonaut-MD single point measuring acoustic current meters and temperature loggers at depths of 4 and 21 m; the data were recorded every 10 min in UTC. Mean hourly wind data were obtained from the NOAA-NDBC SEAKEYS/C-MAN Station MLRF1 at nearby Molasses Reef. To help identify and track the movement of frontal eddies and meanders into and through the Straits of Florida, satellite AVHRR sea surface temperature (SST) images from the study period were downloaded from the Ocean Remote Sensing Group website at Johns Hopkins University Applied Physics Lab (<http://fermi.jhuapl.edu/avhrr/>). Chlorophyll *a* (Chl *a*) data were obtained from the Distributed Active Archive Center of the Goddard Earth Sciences Data and Information Services Center (<http://daac.gsfc.nasa.gov/>).

Data analysis—Calculations of the mean nightly larval abundance per trap and larval family diversity each night were made to identify general temporal patterns of larval supply. In order to examine the degree to which different families of larvae exhibited similar temporal patterns of larval supply, the mean nightly abundance of individual families over all sampling days was clustered with other families. To avoid weighting apparent gaps in the data due to lack of sampling, sampling days were collapsed from actual dates to a series of sampled days (i.e., from day 1–41). Families were clustered using standard cluster analysis techniques and average Euclidean distances (SYSTAT 8.0). The ACE complex was removed prior to analysis because these are non-benthic schooling fishes that are not returning to the reef to settle. To be included in the analysis, the mean nightly abundance of other families had to exceed one fish/trap on at least one night. One exception was made: Serranidae was retained in the analysis because of its significant ecological and commercial importance and relative paucity of settlement and recruitment data. As a result, 23 fish families were included in the analysis. Fish families were grouped according to a Euclidean distance of 0.06.

Current and wind data were converted into an along-shelf (*v*-component) and cross-shelf (*u*-component) coordinate system, rotated 40° clockwise from true north, with *v* positive downstream (northeastward) toward 40° and *u* positive offshore toward 130°. The raw, unfiltered (10-min) current and temperature records were used to examine high-frequency physical processes. High-frequency decreases in bottom water temperatures at semidiurnal tidal periods indicate the onshore movement of internal tidal bores. In order to examine low-frequency physical processes, the raw data were filtered with a 3-h low-pass filter to apply some initial smoothing to the data, and then a 40-h low-pass filter was applied to remove tidal and higher frequency fluctuations, resulting in subtidal time series. These filtered data were used to identify low-frequency events such as the passage of frontal eddies. Mesoscale eddies pass along the Florida Keys reef tract every few months on their downstream march through the Straits of Florida. Their cyclonic circulation entrains warm-water streamers from the FC and causes reversals in the typical downstream alongshore currents. Thus, the passage of eddies through the coastal waters is indicated by a sharp increase in near-bottom water temperature occurring simultaneously with a current reversal at subtidal periods.

Time-series analysis techniques were applied only to the physical data as a result of gaps in the light trap sampling time series. In order to more explicitly examine the relationship between physical forcing and larval fish abundance, the subtidal filtered current data were separated into wind- and FC-influenced time series with a linear multiple-regression technique "REGRESS," a MATLAB routine that incorporates least-squares methods to minimize the residual variance with 95% confidence intervals. Alongshore currents were regressed against both alongshore and cross-shore wind components to construct a time series of alongshore flow due to wind forcing only (modeled v). This modeled wind-forced current was then subtracted from the observed flow to yield a time series of alongshore current attributable solely to FC influences (i.e., meanders and frontal eddies), defined as residual v . The residual current was then compared to nightly larval abundances.

The SST imagery was examined to track the progress of the frontal eddies along the FC front. Speed of movement was estimated for each feature based on the distance traveled between successive images. The ocean color (Chl a) data were archived from the Moderate Resolution Imaging Spectroradiometer (MODIS, Terra satellite) Level 3 and 4 ocean color global data on 4 km resolution and processed for the domain of interest. The daily and weekly ocean color files from 1 June 2001 to 30 September 2001 were analyzed and used to compliment the SST satellite images.

Results

In total, 7,892 larvae from at least 42 families were collected over the 41 nights of light trap deployment. Catches were dominated by the ACE complex (comprising 41% of the overall catch). Once the ACE complex was excluded, the top three most abundant reef fish families collected in the light traps were the damselfishes (Pomacentridae), parrotfishes (Scaridae), and gobies (Gobiidae; Table 2). Not all collected fish were settling to the reef. Groups such as the Sphyraenidae (barracudas) and Carangidae (jacks) comprise mid-water fish that remain associated with reefs as adults, but others, such as the Scombridae, remain wholly pelagic as juveniles and adults. Families such as the Haemulidae (grunts) and Gerreidae (mojarra) may be moving over the reefs to settle in the seagrass beds or mangroves landward of the reefs.

The mean nightly larval supply varied in magnitude from zero to nearly 400 fish larvae per trap (Fig. 3). Settlement did not appear to be lunar cyclic; however, this perception is likely biased by the gaps in the record. Most notable was a pulse on 20 July that was at least twice as large as the next highest pulse (13 June) and five times greater than the mean nightly collection. This peak was a multi-taxa pulse composed of at least 29 families, including (in decreasing order of abundance) Scaridae, Apogonidae, Monacanthidae, Sphyraenidae, Pomacentridae, Scorpaenidae, Pomacentridae, Gobiidae, Labridae, and Gerreidae. A second multi-taxa pulse occurred on 13 June and consisted primarily of Gobiidae, Blennioidei, Scaridae, Pomacentridae, Haemulidae, and Labridae.

Table 2. Composition, relative abundance, and mean proportion of fish families collected in nightly light traps deployed off French Reef in the upper Florida Keys. Mean proportion was calculated without the Atherinidae-Clupeidae-Engraulidae (ACE) complex.

| Family | Total No. | % of non-ACE total* |
|-----------------|-----------|---------------------|
| ACE complex | 3,253 | N/A |
| Pomacentridae | 1,178 | 25.39 |
| Scaridae | 787 | 16.96 |
| Gobiidae | 473 | 10.20 |
| Sphyraenidae | 359 | 7.74 |
| Blennioidei | 336 | 7.24 |
| Apogonidae | 334 | 7.20 |
| Labridae | 213 | 4.59 |
| Monacanthidae | 197 | 4.25 |
| Lutjanidae | 114 | 2.46 |
| Gerreidae | 94 | 2.03 |
| Scombridae | 86 | 1.85 |
| Scorpaenidae | 77 | 1.66 |
| Unknown | 64 | 1.38 |
| Haemulidae | 62 | 1.34 |
| Pomacanthidae | 52 | 1.12 |
| Bothidae | 37 | 0.80 |
| Synodontidae | 28 | 0.60 |
| Tetraodontidae | 23 | 0.50 |
| Syngnathidae | 17 | 0.37 |
| Ophichthidae | 14 | 0.30 |
| Muraenidae | 14 | 0.30 |
| Microdesmidae | 12 | 0.26 |
| Carapidae | 10 | 0.22 |
| Holocentridae | 9 | 0.19 |
| Serranidae | 7 | 0.15 |
| Dactyloscopidae | 7 | 0.15 |
| Carangidae | 6 | 0.13 |
| Paralichthyidae | 6 | 0.13 |
| Dactylopteridae | 4 | 0.09 |
| Acanthuridae | 3 | 0.06 |
| Priacanthidae | 2 | 0.04 |
| Ostraciidae | 2 | 0.04 |
| Cynoglossidae | 2 | 0.04 |
| Opistognathidae | 2 | 0.04 |
| Exocoetidae | 2 | 0.04 |
| Callionymidae | 2 | 0.04 |
| Mugilidae | 1 | 0.02 |
| Chaetodontidae | 1 | 0.02 |
| Gempylidae | 1 | 0.02 |
| Triglidae | 1 | 0.02 |
| Non-ACE total | 4,639 | N/A |
| Grand total | 7,892 | N/A |

* N/A, not applicable.

Family-specific patterns clustered into seven groups (Figs. 4, 5). Group A, consisting of only Holocentridae, exhibited a single peak on day 27 (19 August). Group B, Haemulidae, Gobiidae, Microdesmidae, and Blennioidei, exhibited a large pulse on day 2 (13 June). Group C, Scombridae, Labridae, and Synodontidae, exhibited a large pulse on day 7 (9 July) as well as on day 13 (20 July). Group D, Muraenidae, Scorpaenidae, Sphyraenidae, Gerreidae, and Bothidae, had its largest peak on day 13 (20 July) but pulsed on many other days as well. Group E consisted of only Pomacentridae, which appeared in pulses on several days (2, 8, 9, 14, and 25). Group F, Lutjanidae and Serranidae, exhibited pulses on

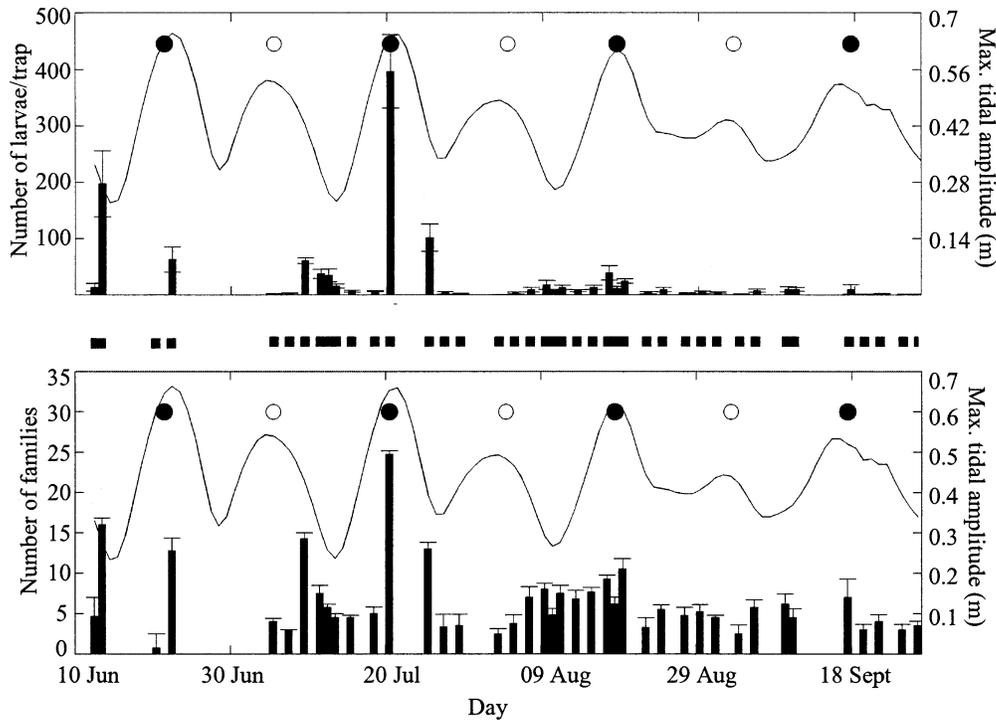


Fig. 3. Mean (± 1 standard error [SE]) (top panel) abundance and (bottom panel) diversity of fish families collected each night of light trap deployment. Sampling days are indicated by the black bars between the panels. Black circles are new moons and open circles are full moons. Predicted maximum tidal amplitude is plotted below the moons. Fish from the Atherinidae-Clupeidae-Engraulidae complex were excluded from the analysis. Note that sampling during 12, 13, 20, and 22 June and 12 July was conducted for only the first 5–6 h each night. See text for details.

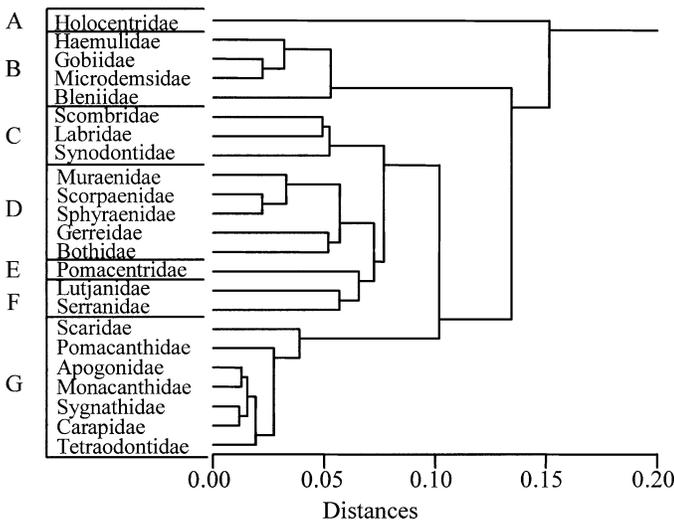


Fig. 4. Results of cluster analysis of larval fish families collected in the light traps over 41 d of sampling. See text for criteria for family inclusion. Average Euclidean distances reflect degree of similarity, and families were clustered into seven groups (A–G) according to an average Euclidean distance of 0.06.

days 13 and 20. Group G, with the largest constituency, Scaridae, Pomacanthidae, Apogonidae, Monacanthidae, Syngnathidae, Carapidae, and Tetraodontidae, exhibited a single large peak on day 13 (20 July; Fig. 5).

The mean larval ages of 10 species/types from the most abundant families on 20 July ranged from 15–46 d (Table 3). These are comparable to estimates of the pelagic larval duration for several of the species or closely related species (Victor 1986; Rogers et al. 2001). There was generally little variation in age within taxa, except for the labrid *Xyriethys* sp., which, like several other wrasses, has a highly variable length of larval life. As a comparison, 10 individuals of two species from the second largest larval pulse (13 June) were aged. During the 13 June pulse, both *Stegastes partitus* and *Sparisoma* type A were an average of 2–4 d older than settlers on 20 July (*S. partitus*: mean pelagic larval duration [PLD] = 28.1 d; range = 25–31 d, mean standard length [SL] = 10.1 mm; *Sparisoma* A: mean PLD = 42 d; range = 34–51 d; mean SL = 9.3 mm; see Table 3 for ages of fish from 20 July).

The subtidal time series of alongshore and cross-shore currents and temperatures from depths of 4 and 21 m at mooring C and winds measured at nearby Molasses Reef reflect the dominance of the northward-flowing baroclinic FC (positive v ; Fig. 6). The strong downstream sheared flow at the outer shelf was interrupted on occasion by periods of current reversals. We first examined whether these reversals were wind driven, and we found that wind-induced currents

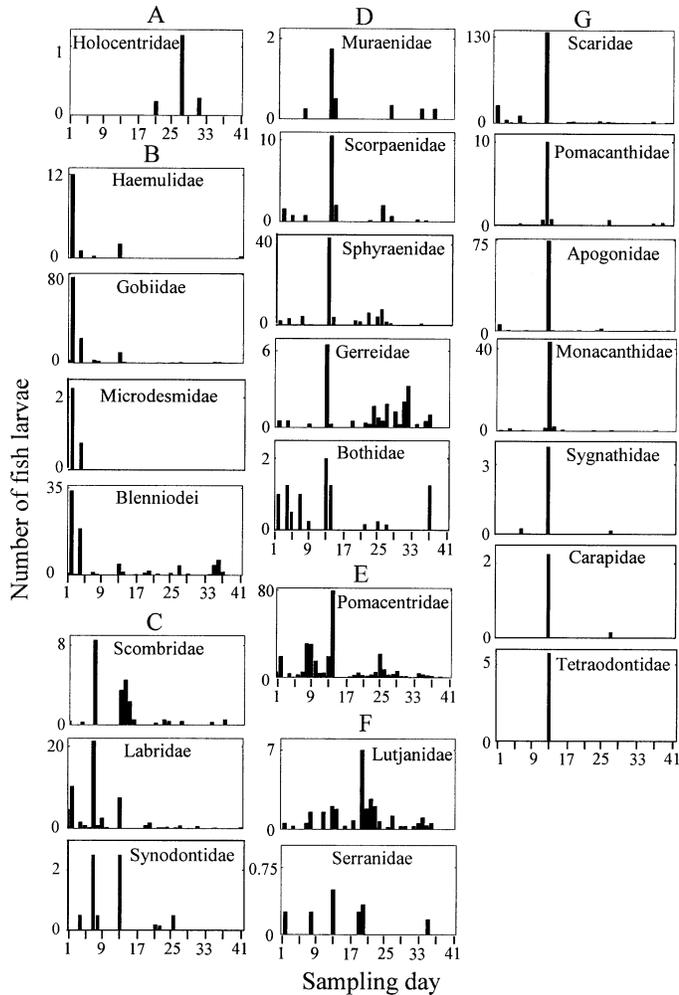


Fig. 5. Family-specific patterns of larval supply. Results of cluster analysis were used to group families exhibiting similar patterns of nightly abundance. The raw time series was concatenated in order to compare abundance on only those 41 nights that were sampled.

were weak during this period (as is typical of summer periods). Results of the multiple regression demonstrated that the residual current accounted for approximately 92% of the total variance of the subtidal alongshore current, indicating that wind-driven currents were weak in comparison to changes produced by FC variations. Wind directions were primarily onshore, which is not conducive to coastal upwelling, and only two significant wind events occurred, on 23 July and 14–16 September, when positive alongshore winds reached 10 m s^{-1} . These northeastward wind events were in a direction counter to that which would have caused the observed current reversals (Fig. 6). These results directed our data analysis toward the other primary mechanism that can cause such reversals in the study area, namely Florida Current eddies (e.g., Lee 1975; Lee and Mayer 1977; Lee and Williams 1999).

The increase in bottom-water temperatures that occurred simultaneously with a cyclonic current reversal around 20 July (Fig. 6) is indicative of the passage of a frontal eddy. Alongshore current reversals occur when the swirl velocity within the eddy exceeds the downstream eddy advection speed. Entrainment of a warm streamer from the FC around the shoreward side of the eddy results in warming of the shallow waters. To evaluate the effects of FC variations and internal tidal bores on reef fish recruitment, the larval abundance time series was plotted together with alongshore residual currents (wind effects removed, *see* previous section) from 4 m at mooring C and raw time series of near-bottom temperature (Fig. 7). The passage of three mesoscale eddies (ME 1–3) identified from persistent decreases or reversals of downstream currents is designated on Fig. 7; sub-mesoscale eddies (SME 2 and 3) are also identified on the enlarged inset. Reversals of residual currents indicate that sub-mesoscale frontal eddies moved through the study area during the periods 22–25 June (SME 1); 18–21 July (SME 2) and 25–28 July (SME 3); 31 July–3 August (SME 4); and every few days during the second half of September (Fig. 7). These frontal eddies were identified as sub-mesoscale eddies based on their size (20–40-km diameters), the time duration of their passage (3–4 d), and the typical downstream advection rates ($8\text{--}9 \text{ km d}^{-1}$).

Comparison of larval abundance with the residual currents

Table 3. Mean ages of selected fish larvae from the 10 most abundant families collected on 20 July 2001. Ages were determined from analysis of larval otoliths.

| Family | Type/species | Mean standard length (mm) | Mean PLD* (d) | PLD range (d) |
|---------------|-----------------------------|---------------------------|---------------|---------------|
| Scorpaenidae | <i>Scorpaena calcarata</i> | 7.61 | 19.4 | 17–24 |
| Apogonidae | <i>Phaeoptyx</i> type A | 8.27 | 24.8 | 19–30 |
| Gerreidae | <i>Euconostomus</i> type A | 8.33 | 14.7 | 12–18 |
| Pomacentridae | <i>Stegastes partitus</i> | 9.23 | 24.3 | 21–28 |
| Labridae | <i>Xyrichtys</i> type B | 11.69 | 46.1 | 19–75 |
| Scaridae | <i>Cryptotomus roseus</i> | 8.61 | 29.5 | 24–38 |
| Scaridae | <i>Sparisoma</i> type A | 8.88 | 39.9 | 32–44 |
| Gobiidae | <i>Coryphopterus</i> type A | 9.09 | 32.1 | 27–43 |
| Pomacanthidae | <i>Pomacanthus paru</i> | 8.07 | 17.8 | 14–19 |
| Sphyraenidae | <i>Sphyraena barracuda</i> | 14.91 | 17.6 | 15–21 |
| Monacanthidae | <i>Aluterus schoepfi</i> | 9.00 | 17.5 | 13–24 |

* PLD, pelagic larval duration.

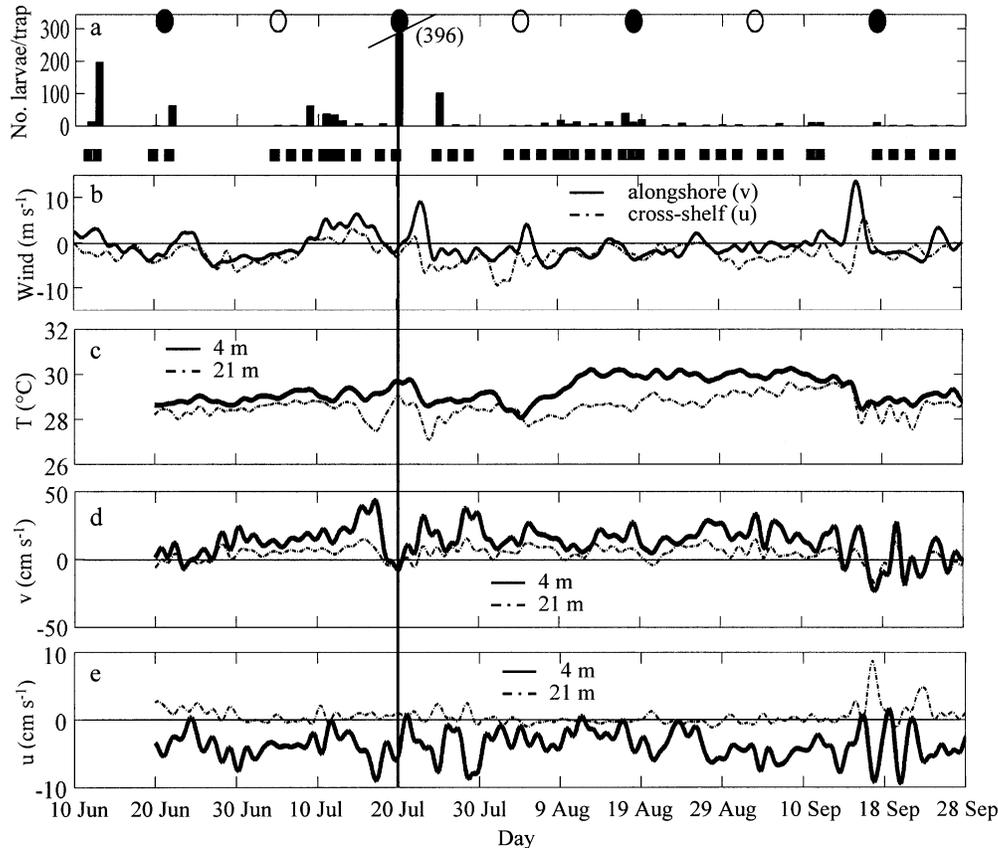


Fig. 6. Subtidal time series of physical measurements for the upper Florida Keys for 10 June–28 September 2001 plotted with (a) non-Atherinidae-Clupeidae-Engraulidae (ACE) larval abundance. (b) Wind data from the Molasses C-MAN station divided into alongshore and cross-shelf components. (c) Water temperature and (d, e) current meter data from the top instrument (4 m) and bottom instrument (21 m) at Mooring C (see Fig. 1). The raw data were low-pass filtered and rotated into isobath coordinates (positive v = downstream, alongshore toward 40° ; positive u = offshore toward 130° ; see text for full description). A vertical line is drawn on 20 July 2001, the night during which the largest number of late-stage larvae was collected in the light traps. Black bars below panel a indicate the nights that light traps were deployed.

shows that increased larval abundances occurred with each of the three sub-mesoscale eddies that caused strong current reversals (SME 1–3); larval sampling was not conducted during SME 4. In contrast, the sub-mesoscale eddies of ME 3 in September did not result in large larval pulses. The highest larval abundance (night of 20 July) occurred near the end of sub-mesoscale eddy 2 (SME 2) of 18–21 July (Fig. 7, enlargement). The subtidal current and temperature records for this event show that onshore flow of warmer FC water occurred as the leading edge of the eddy approached and alongshore currents began to shift from strong downstream to upstream flow (Figs. 6, 7). The trailing portion of the eddy occurred with offshore or weaker onshore flow of a cooler mix of shelf and FC waters. The cold-core of this cyclonic, sub-mesoscale eddy was likely located farther offshore, and the cold upwelled water within the eddy's center did not extend to the shallow depths (<25 m) of the reef tract. The 20 July larval settlement pulse occurred toward the end of the eddy event as the residual flow shifted from southwestward back to northeastward (Fig. 7).

The original 10-min temperature records from the near-

bottom (21 m) current meter at mooring C (Fig. 7) show that high-frequency bottom-temperature variability increased seaward of the reef edge during three periods—mid-June, mid-July, and mid-September—that correspond to the time periods during which mesoscale eddies were passing the study area. High-frequency temperature fluctuations are evident toward the start and end of ME 2, but not at the time of the large peak in larval supply. The relationship between this activity and the passage of mesoscale eddies (e.g., ME 2) can be examined in an enlargement of the high-frequency temperature data from mooring C and the bottom-temperature loggers positioned across the outer reef crest (Figs. 8, 9). Figures 8 and 9 also contain the high-frequency cross-shore and alongshore currents from 4 and 21 m at mooring C, as well as the larval supply data. The thin vertical event lines identify the sudden onset of cooler bottom-water intrusions, which are highly correlated with pulses of onshore flow at the near-bottom instrument, indicative of upslope internal tidal bore behavior. Similar high-frequency temperature changes did not occur in the upper layer. High-frequency current variability in the upper layer had a significant

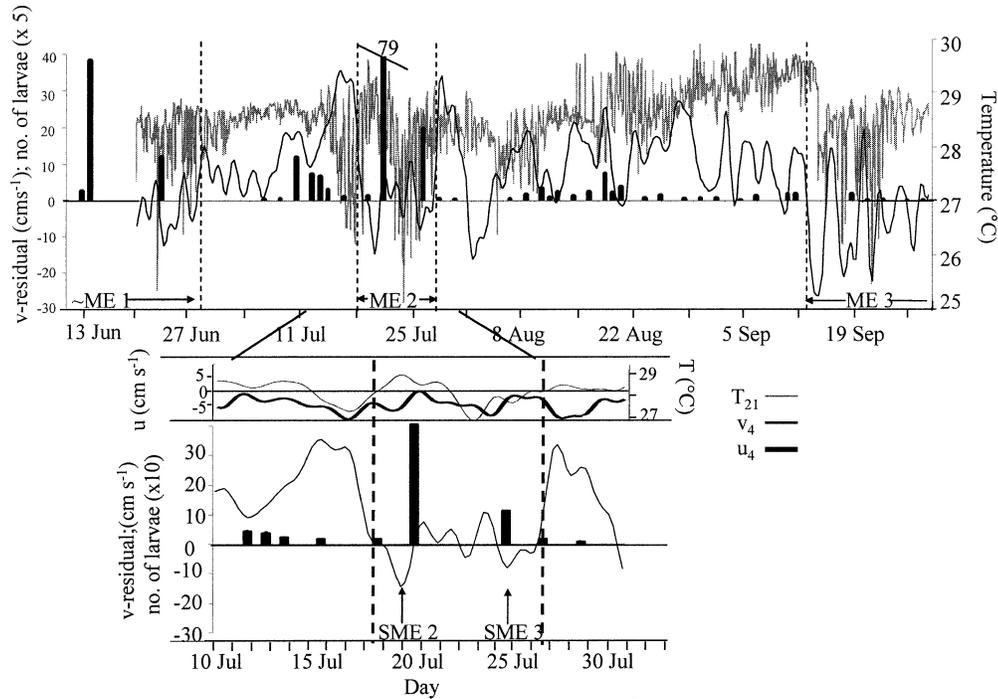


Fig. 7. Mean (non-ACE) larval abundance ($\times 5$) in replicate light traps plotted with residual alongshore currents (v_4) from the 4-m current meter at mooring C (i.e., currents that were not forced by wind) and high-frequency temperature data (T_{21}) from the 21-m temperature logger at mooring C. Residual current reversals ($< 0 \text{ cm s}^{-1}$) indicate sub-mesoscale eddies; sharp decreases in bottom-water temperatures (decrease of $2\text{--}3^\circ\text{C}$; e.g., $< 27^\circ\text{C}$) indicate tidal bore activity. Peak larval collection occurred during the passage of a sub-mesoscale eddy (SME 2) embedded within a mesoscale eddy (ME 2; boundaries indicated by dashed line); a secondary larval peak occurred with SME 3. Satellite imagery indicates mesoscale eddy 1 (ME 1) passed the site during mid-June, when the second highest larval peak occurred. No larval pulses were associated with the movement of a mesoscale eddy through the area in September (ME 3; start marked by dashed line). Period encompassing ME 2 is enlarged and included with low-pass filtered cross-shelf currents at 4 m (u_4) and smoothed near-bottom (21 m) temperature data.

semidiurnal component in both the cross-shelf and along-shore directions as a result of the local M2 barotropic tide, causing near-uniform tidal current variations in the upper and lower layers. Diurnal tidal changes were primarily in the alongshore direction because of the diurnal standing wave joining the Atlantic and the Gulf of Mexico (Zetler and Hansen 1970; Lee and Williams 1999).

In July, there were two periods when sudden near-bottom temperature drops ($2\text{--}3^\circ\text{C}$) occurred simultaneously with near-bottom surges of onshore flow at semidiurnal tidal periods, indicating tidal bore activity: 15–19 July and 23–26 July. The first case was associated with the leading edge of ME 2, when the FC front was in an onshore position, the water column was strongly stratified, and intense downstream baroclinic flow was occurring (Figs. 7, 8). The second case was also associated with an onshore meander of the FC front that occurred between the two sub-mesoscale eddies embedded within ME 2 (SME 2 and SME 3), when the downstream baroclinic flow and stratification once again increased (Figs. 7, 9). At times these cold intrusions reached the 10-m isobath near the reef crest. Tidal bore activity was not significant during the large larval peak of 20 July that occurred toward the upstream end of SME 2, as the subtidal

flow shifted back toward the northeast and temperature stratification decreased. However, tidal bore activity was still significant during the smaller larval peak of 25 July, which occurred during the countercurrent flow of SME 3 (Figs. 7, 9).

SST and ocean color (Chl *a*) images help explain the origin, arrival, and dimensions of the three mesoscale eddies observed during the study period. Three-day and weekly composite images were examined for several months leading up to and including the study period. A subset of the available imagery (Fig. 10) demonstrates that a progression of mesoscale eddies was moving along the LC front and into the Straits of Florida throughout the spring and summer of 2001. During 21–23 March (Fig. 10a), ME 2 (ultimately associated with the 20 July sub-mesoscale event in the upper Keys) is clearly identified about halfway along the east side of the LC, trailing a similar mesoscale feature (ME 1) located west of the Tortugas at the entrance to the Straits of Florida. Both cyclonic eddies were positioned within offshore meanders of the LC front and entrained warm streamers from their leading onshore meander wave crests that wrapped into the cold eddy centers. Both eddies had similar dimensions with diameters of approximately 160 km (ME

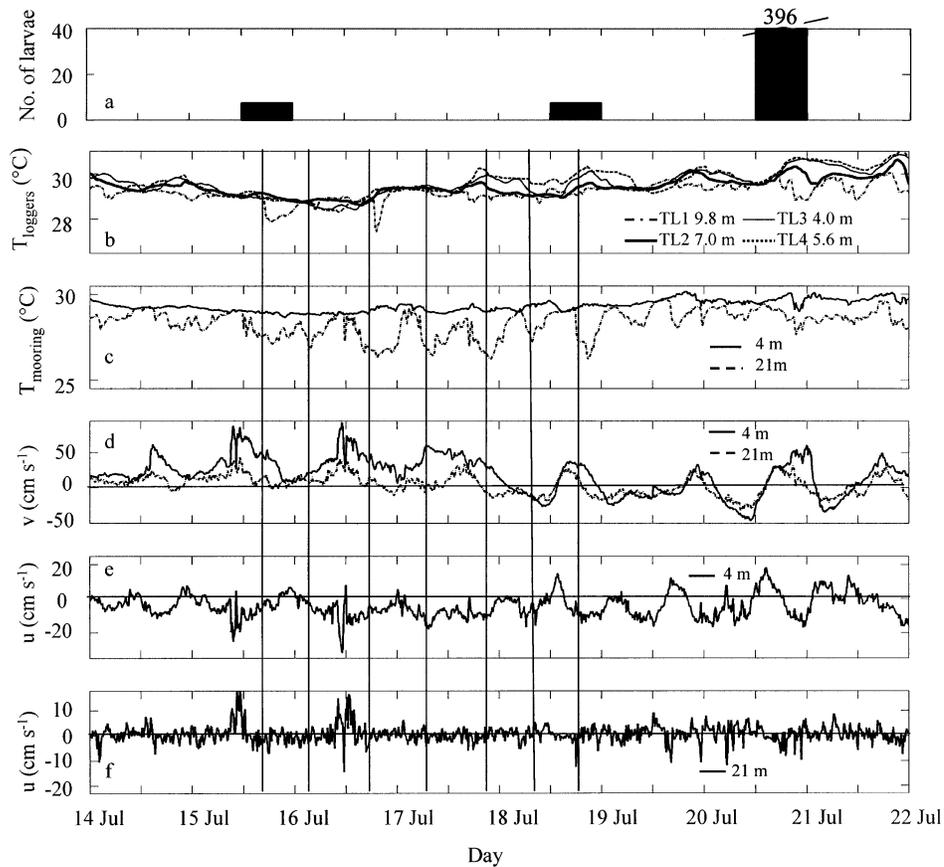


Fig. 8. Expansion of raw (10-min) current and temperature data from mooring C and cross-shelf temperature loggers for the period (14–21 July) before, during, and after the passage of ME 2. (a) Mean number of non-Atherinidae-Clupeidae-Engraulidae (ACE) larvae collected in the light traps; (b) raw (10-min) bottom-water temperature from the four temperature loggers; (c) water temperature from the 4-m and 21-m temperature loggers on mooring C (24-m depth); (d) alongshore currents measured at the 4-m and 21-m current meters at the mooring; (e) cross-shelf current measured at 21 m (note that scales differ between two plots of u); and (f) cross-shelf current measured at 21 m. Thin vertical event lines identify the sudden onset of cooler bottom-water intrusions, correlated with pulses of onshore flow at the near-bottom instrument, indicative of upslope internal tidal bore behavior. See Fig. 1 and Table 1 for current meter mooring and temperature logger locations. Along bottom of plots dates are marked at 0 h UTC.

1) and 110 km (ME 2). During 26–28 April (Fig. 10b), ME 1 was located offshore of the Dry Tortugas and ME 2 was approaching from the northwest. Neither had undergone significant change in size. During 19–21 May (Fig. 10c), ME 1 was located offshore of the lower Keys and had elongated and decreased in size, with new dimensions of 90 km alongshore and 60 km cross shore. ME 2 was positioned southwest of the Dry Tortugas without much change in size, but with a shift in the major axis to more of a north–south orientation. By summer, the SST gradients were typically weak, but an offshore meander of the FC front is discernable in the upper to middle Florida Keys, and a large offshore meander is observable off the Dry Tortugas at the same time. By 12–14 June (Fig. 10d), encompassing the day of the second largest larval settlement event (200 larvae per trap; Figs. 3, 6), ME 1 was weakly identified as an elongated band of cooler temperatures and elevated Chl a that stretched along the upper Keys, ME 2 was located off the Dry Tortugas and

had become elongated to approximately 150 km alongshore and 90 km offshore, and a third mesoscale eddy (ME 3) was evident on the east side of the LC. The SST images after this time were not informative because of weaker thermal gradients, so we turned to a sequence of weekly ocean color composites with stronger pigment gradients (although still reduced in summer). In two images from the week before and after 20 July, the LC is evident as water that is low in Chl a and the eddies as areas with mid-range values of Chl a . The 12–19 July image (Fig. 10e) clearly shows a large eddy in the Tortugas area, which corresponds to ME 3 in Fig. 10a–d. ME 2 was elongated and in the vicinity of the upper Keys, similar to the findings from the SST imagery and the moored current records. The presence of ME 2 caused a seaward displacement of the FC front to 20–30 km off the upper Keys shelf. No clear color images were available for the week of 20 July, but by 1–2 weeks later (Fig. 10f), ME 2 had passed through the Keys area, ME 3 was

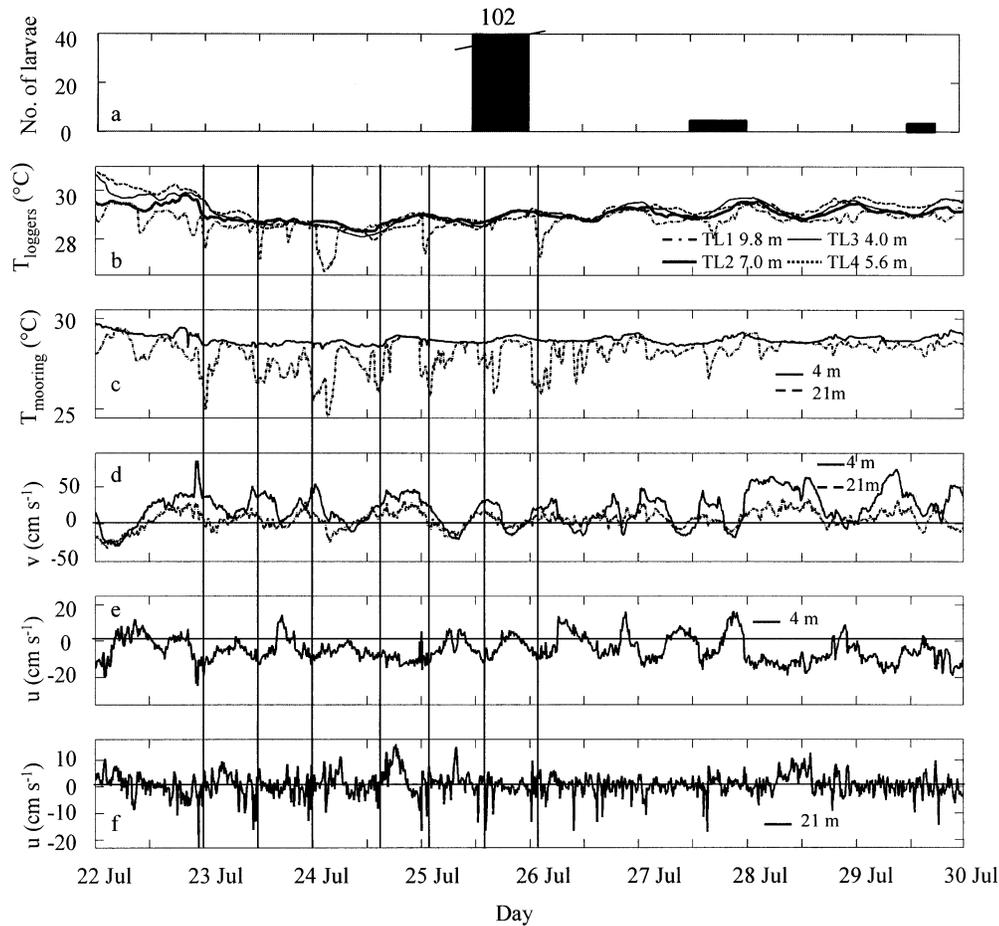


Fig. 9. Expansion of raw (10-min) current and temperature data from mooring C and cross-shelf temperature loggers for 22–29 July, after the passage of ME 2. (a) Mean number of non-Atherinidae-Clupeidae-Engraulidae (ACE) larvae collected in the light traps; (b) raw (10-min) bottom-water temperature from the four temperature loggers; (c) water temperature from the 4-m and 21-m temperature loggers on mooring C (24-m depth); (d) alongshore currents measured at the 4-m and 21-m current meters at the mooring; (e) cross-shelf current measured at 4 m; and (f) cross-shelf current measured at 21 m (note that scales differ between two plots of u). Thin vertical event lines identify the sudden onset of cooler bottom-water intrusions, correlated with pulses of onshore flow at the near-bottom instrument, indicative of upslope internal tidal bore behavior. See Fig. 1 and Table 1 for current meter mooring and temperature logger locations. Along bottom of plots dates are marked at 0 h UTC.

located southwest of Key West, and the FC was in a southward (offshore) position, particularly in the vicinity of the lower Keys, but also considerably detached from the upper Keys (about 40–60 km). Later images confirm the passage of ME 3 past the study site in September.

Current meter data indicate that it took approximately 10 d (from 18 to 28 July) for the elongated offshore meander (remnant of ME 2) to pass the study site, as determined from the time separating the two strong downstream velocity peaks that occurred when the FC front was in an onshore position at the site (Fig. 7). From the SST imagery, downstream advection rates for ME 2 were roughly 8 km d^{-1} from the LC to the Tortugas region, slowing to 3 km d^{-1} past the Dry Tortugas, and then accelerating to 8 km d^{-1} for the passage from the Dry Tortugas to the upper Keys. ME 1 moved slightly faster, at $\sim 4 \text{ km d}^{-1}$, from 23 March to 28

April around the Dry Tortugas, increasing to $\sim 9 \text{ km d}^{-1}$ from 28 April to 21 May toward the upper Keys. ME 3 was moving at the same rate as ME 2, or at about 8 km d^{-1} from the LC to the Tortugas. Within the ME 2 offshore meander, there were three separate current reversals with durations of 4, 2, and 3 d that appear to be sub-mesoscale eddies with spatial dimensions of tens of kilometers (~ 32 , 16, and 24 km, respectively; using 8 km d^{-1} downstream speed).

Discussion

The largest pulse of late-stage larvae collected in the upper Florida Keys during 2001 (as well as over 170 nights of sampling in 2002 and 2003; D'Alessandro and Sponaugle unpubl. data) occurred on the night a Florida Current sub-mesoscale eddy embedded in a mesoscale Tortugas eddy im-

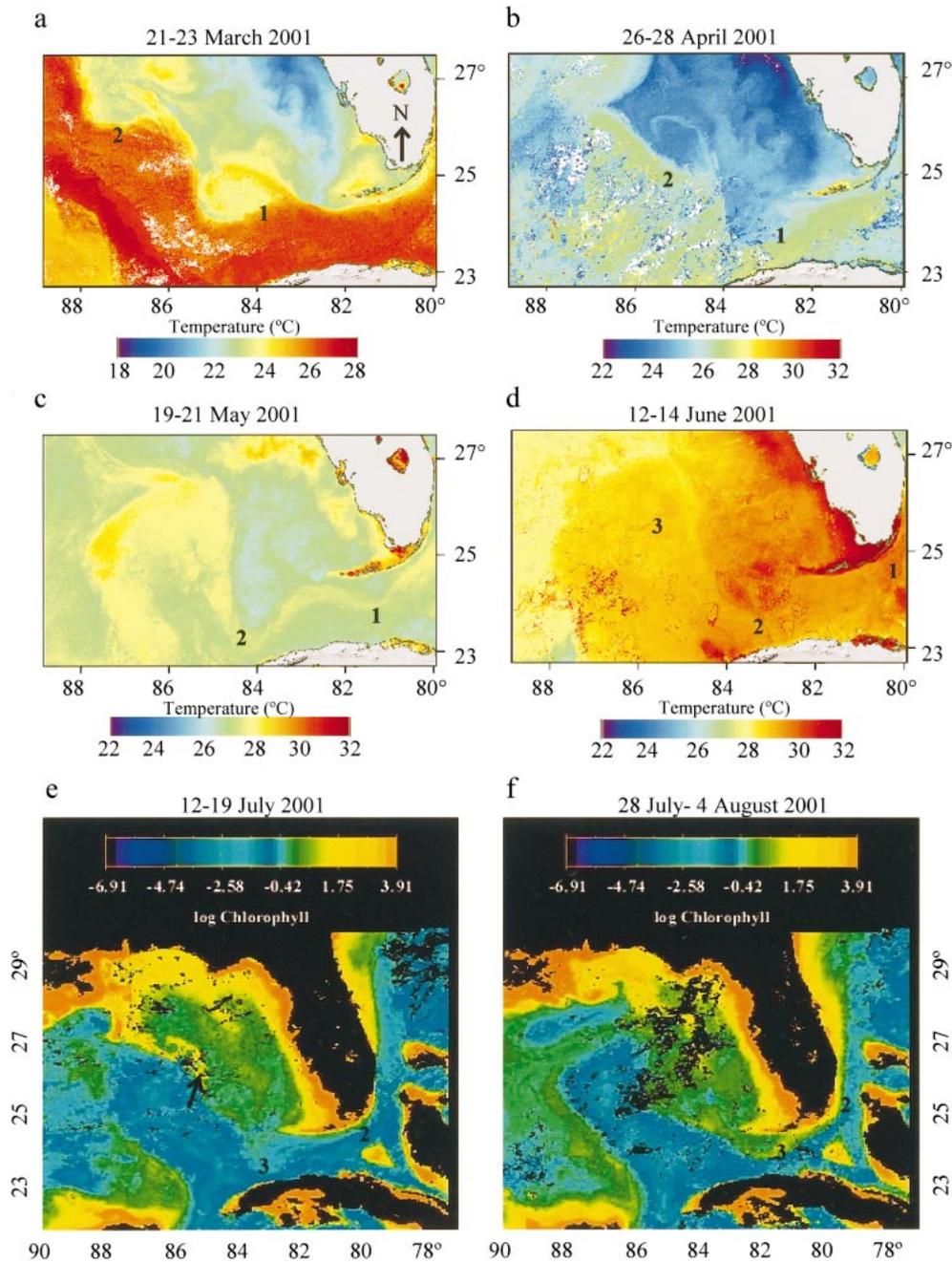


Fig. 10. The evolution and progression of three cold, cyclonic Florida Current frontal eddies through the southern Straits of Florida during spring and summer 2001 is visualized in (a-d) AVHRR satellite imagery of 3-d composite SST fields and (e-f) Chl *a* weekly composites derived from the MODIS Ocean Color data. Mesoscale eddy 1 (ME 1; for clarity, all mesoscale eddies are abbreviated in images with number only) passed the upper Keys study site in mid-June 2001; ME 2 passed in mid-July and ME 3 in September. Note that the SST color scales are different to clarify details in temperature gradients and that the ocean color scale is logarithmic. Also evident in (e) is a filament of enhanced Chl *a* water of possible Mississippi River origin entrained into the Loop Current (black arrow).

pinged on the reef tract. The pulse not only consisted of high numbers of individual taxa but also included larvae from at least 29 fish families. This observation is the first definitive demonstration of settlement in conjunction with such large recirculating features.

Satellite imagery and current meter records demonstrate the movement and passage of a mesoscale Tortugas eddy (ME 2) through the upper Keys study site, with several embedded sub-mesoscale frontal eddies, one of which (SME 2) occurred simultaneously with the 20 July larval pulse. Sat-

ellite imagery further indicates that a similar mesoscale Tortugas eddy (ME 1) moved through the upper Keys during mid-June, corresponding to the second largest larval pulse. Our findings indicate that this passage of mesoscale eddies was the most likely physical mechanism delivering the observed large larval pulses to the upper Florida Keys. Winds were weak during the study period, and wind-driven transport played a minor role in the alongshore current variability. Although tidal bores occurred in association with the passage of mesoscale eddies, several lines of evidence support eddies as the primary larval delivery mechanism for the events observed during our study: in particular, the specific timing of the largest larval pulse was coupled most tightly with the passage of a sub-mesoscale eddy (SME 2) and, more specifically, with the convergence zone formed by the merging of upstream flows in the shoreward side of the eddy, with downstream flows in the trailing onshore meander wave crest. Internal tidal bores occurred with the leading onshore meander crest just prior to ME 2 and the imbedded SME 2; they did not occur during the largest 20 July larval peak. Furthermore, during the period of enhanced tidal bore activity, 2 d and 5 d prior to the large 20 July larval pulse, very few larvae were collected in the traps. It is noteworthy that all eddy-induced current reversals that were sampled during the summer had relatively large larval pulses. Finally, late-stage reef fish larvae occur predominantly in the upper layer of the ocean, and our traps were set in the upper 2 m with this in mind. For example, preliminary data from vertically stratified (to 100 m) ichthyoplankton collections offshore of the study site demonstrate that at the stations closest to shore, 13 of the 14 most abundant reef fish families from the 20 July pulse occur almost exclusively above 40 m (Richardson and Cowen, RSMAS, unpubl. data; no larvae of the 14th family were collected nearshore). Internal tidal bores can transport deep water up onto the reef, and it is certainly possible that deep-water taxa utilize this cross-shelf process. However, with regard to the very large, multi-taxa pulses that occurred during eddy passage, late-stage larvae of a diversity of reef fishes would have to be concentrated in deep layers for this to be a viable larval transport mechanism.

Internal tidal bore activity appears to increase as onshore meanders of the FC front that lead and trail the passage of frontal eddies cause the strong downstream baroclinic flow with increased stratification to converge on the steep bottom slope seaward of the outer reefs. Bottom boundary layer adjustment to this increased downstream flow can cause an onshore flow in the bottom layer and strengthen stratification, thus allowing propagation of internal tides into shallower waters of the uplifted pycnocline. The only times during our sampling period during which bottom-water temperatures dropped sharply (e.g., below 27°C) occurred around the times of mesoscale eddy passage. In fact, our estimation of the timing of the passage of ME 1, based on satellite imagery, agrees well with the occurrence of large-amplitude tidal bore activity recorded during the same period at a location ~10 km south of our study site (see fig. 2 in Leichter et al. 2003).

Although it is more likely that near-surface cross-shelf transport processes associated with eddy passage are directly

related to larval delivery, our biological sampling effort was not at a sufficient temporal or spatial resolution to truly examine the role of high-frequency internal tidal bores in delivery of reef fish larvae to the reef. The greater sampling rate of the physical data shows that internal tidal bores generally occurred prior to or just after large eddy-induced current reversals. However, on one occasion (25 July), bores continued during a current reversal when larval abundance was high. Thus, it remains possible that the delivery mechanism could involve both frontal eddies and tidal bores. For example, frontal eddies may concentrate and transport larvae to the shelf edge, where their onshore movement is enhanced by eddy-induced cross-shelf currents in the water column and internal tidal bores near bottom. The physical interaction between eddy passage and tidal bores clearly warrants further study.

During times when pulses of larvae settled and no mesoscale eddies or internal tidal bores were present, additional physical mechanisms may be operating. On several occasions (e.g., 11–13 July and 19 August), smaller larval pulses occurred when the FC front was close to the shelf break, causing strong downstream flow with a persistent onshore component in the upper layer. The front provides a convergent mechanism to concentrate larvae (e.g., Stoner et al. 1997; Yeung and Lee 2002) and the shoreward movement can transport larvae to the offshore edge of the reef tract. Alternatively, some larvae may be retained on the shelf for the duration of their larval period (Lindeman et al. 2001; Sponaugle et al. 2003) and not require transport by physical processes to reach a suitable settlement habitat. The settlement of such species may be less episodic and more constant or lunar cyclic (i.e., organisms may be more able to respond to periodic settlement cues).

Further support of our hypothesis that eddies are important mechanisms of larval transport and delivery would include measures of high concentrations of late-stage larvae within the mesoscale eddy. Unfortunately, no ichthyoplankton samples were collected during this time period. A few ichthyo- and zooplankton studies have shown higher concentrations of some larval fishes and invertebrates within mesoscale eddies of the FC (Lee et al. 1992; Criales and Lee 1995; Yeung and Lee 2002) and other western boundary currents (Okazaki et al. 2002). There is little evidence of late-stage reef fish larvae within such eddies because of the difficulties in sampling these larvae. Late-stage reef fish larvae have strong swimming and sensory abilities that enable them to evade traditional ichthyoplankton nets (Leis and McCormick 2002).

While the larvae of many fish families were influenced by the passage of mesoscale eddies, not all families were similarly affected. The composition of major fish taxa delivered to the upper Keys during the June and July eddy events differed. The majority of all fish families exhibited a large pulse on 20 July, and for many of these taxa, this was the primary settlement pulse over the 41 sampling days. The second highest larval pulse occurred on 13 June and comprised larvae from 20 different families. Four families (Haemulidae, Gobiidae, Microdesmidae, and Blenniodei) clustered into Group B based on their single large pulse on 13

June. A single family, Holocentridae, pulsed during times when neither mesoscale eddy occurred.

Clearly the timing of taxon-specific spawning relative to the proximity of an eddy will contribute to larval compositions, and there are insufficient data on spawning patterns to examine this in greater detail at this time. Also, the match between the timing of eddy passage and the age and developmental stage of larvae may need to be more precise in some species than in others. For two of the families that appeared during both events, larvae from 13 June were an average of 2–4 d older than larvae collected on 20 July. Many factors could contribute to differences in PLD. For example, differences in water temperatures in the Florida Keys can influence the growth rate and larval duration of a coral reef fish (Sponaugle and Pinkard unpubl. data), and warm-core eddies in other systems have been shown to reduce larval reef fish growth and increase larval durations (Sponaugle and Pinkard 2004). The reverse may be true with the FC cold-core cyclonic eddies, where upwelling in the core may enhance productivity and, potentially, the growth of larvae. The degree to which larvae near settlement age can settle upon approaching suitable settlement habitat (i.e., the specific timing and length of the competency period) is unknown. Additional detailed examination of larvae from multiple eddies is needed to examine the relationship between larval composition, age and growth, and the passage of eddies.

Fishes exhibit a diversity of spawning strategies ranging from pair spawning within small reef territories to long-distance migration to mass spawning sites. During particular times of the year, lutjanid and serranid species (snappers and groupers) undertake spawning migrations to upstream promontories in the lower Keys and Dry Tortugas (Lindeman et al. 2000). Interestingly, temporal patterns of abundance of young (i.e., non-settlement stage) larvae of these two families in waters directly over the upper Keys reefs were similar (Sponaugle et al. 2003), as were their settlement patterns in this study. Larvae of these two families were likely transported by the same physical mechanisms as transported other larvae on 20 July, although these two species also pulsed on 9 August (near the third-quarter moon, during a time when no eddies were present; Fig. 5). Delivery of larvae to settlement habitat will only be successful if the larvae are of a sufficient age and developmental stage (i.e., competent) to settle and undergo metamorphosis.

The age range of all the larvae collected on 20 July was broad, with the mean larval age of different families ranging from 15–46 d. These taxa were clearly spawned at different times, which complicates our ability to back-calculate potential sources. Larval ages together with satellite imagery and the general structure of the frontal eddies indicate that larvae could have been entrained into the eddy at any point along the reef tract from the Tortugas to the middle Keys. Larvae could have entered the eddy progressively during its passage from the lower Keys to the upper Keys, or they could have been entrained at a single source as part of a water mass containing larvae of a variety of young ages. The youngest larvae were about 2 weeks old, which, coupled with the rate of eddy movement, indicates that at least these larvae could not have entered the eddy in the Dry Tortugas.

The farthest away these larvae could have been spawned is in the vicinity of Key West (distance = 150 km). The oldest larvae were over 2 months old, which means that numerous sources are possible. These larvae may have been entrained into the Tortugas eddy shortly after they were spawned (ME 2 was in contact with shallow reef communities for up to 60 d before reaching the study site), or older larvae could have been entrained during the movement of the eddy along the Keys. High abundances of a diversity of fish larvae occur in nearshore surface waters directly over upper Keys reefs (Sponaugle et al. 2003). It is most likely that larvae were entrained from shelf waters, because the highest concentration of larvae generally occurs nearshore over reef spawning sites (for review of onshore–offshore gradients of fish larvae, see Leis 1991). While it is possible that larvae were entrained from LC water and thus were sourced from upstream locations (see Hare and Cowen [1991] for example of transport of *Xyrichtys* to the Middle Atlantic Bight), larvae entrained from distant sources would occur in more diffuse concentrations (Cowen et al. 2000), particularly since the nearest upstream reef source in the LC pathway is the Yucatan (~1,500 km away via the LC). The entrainment of Mississippi River water along the eastern boundary of the LC (Fig. 10e) is not a likely source of larvae, since there are few reefs in this area of the Gulf of Mexico. Depending on the size and position of the FC mesoscale eddies, the northern coast of Cuba is another possible source region, but satellite imagery during ME 2 indicates that the eddy did extend sufficiently close to that shore.

Successful transport by eddies of reef fish larvae to their settlement habitat requires (1) successful spawning by adults (i.e., availability of larvae on the outer shelf); (2) a mechanism for larvae to enter the recirculating feature; (3) a transport time that corresponds to time to competency (i.e., PLD, or shorter if larvae are entrained at older ages); (4) feature characteristics that concentrate larvae in a favorable environment (e.g., convergent fronts within eddies); and (5) impingement of the eddy on suitable settlement habitat. By definition, FC mesoscale eddies satisfy the second and fifth criteria by moving along the outer shelf and interacting with shelf water masses over reef habitats. The cyclonic circulation within an eddy, eddy interaction with the encompassing boundary of the FC front, and development of sub-mesoscale vortices along the frontal boundary provide the conditions necessary to potentially satisfy the third and fourth criteria. Coincidence of all five criteria can result in the successful retention and delivery of diverse reef fish larvae to Keys reefs by large recirculating frontal eddies. In theory, the fifth criterion could be bypassed by actively orienting and swimming larvae that may be able to traverse large distances to reach suitable settlement habitat (reviewed in Leis and McCormick 2002). However, the simultaneous arrival of such a diverse group of fishes with varying swimming abilities (Stobutski and Bellwood 1997) indicates that larval delivery was more influenced by physical transport induced by the eddy.

Interestingly, the fall passage of a series of sub-mesoscale eddies associated with the ME 3 did not result in similar pulses of larvae to the reef. Because of the lack of well-resolved satellite imagery during the fall, it is not possible

to determine if the fall eddies were somehow physically different from those we observed during the spring and early summer. However, multiple years of satellite imagery and long-term moored current observations from the Keys indicate that there are no significant seasonal differences in frontal eddy evolution patterns. As with earlier mesoscale eddies, internal tidal bores were also present. Assuming that the physical structure and movement of the eddies were similar, the lack of settlement events may be more related to a biological cause, such as the timing or reduced magnitude of spawning events (i.e., reproductive seasonality; criterion 1), or to a mismatch between eddy passage and larval age (i.e., criterion 3).

The specific timing of eddy impingement on the shelf edge is clearly important relative to larval ages and their ability to settle, and related to this is the particular lunar phase during which impingement occurs. Settlement of many reef organisms to a variety of locations has been shown to be lunar cyclic, often peaking during new and third-quarter moons (e.g., Robertson 1992; Sponaugle and Cowen 1996a; Reyns and Sponaugle 1999). It is worth noting that the 20 July eddy passed over the upper Keys reefs during a new moon, and the 13 June eddy occurred during a third-quarter moon. However, ME 3 passed the upper Keys in September during a new moon and did not deliver larvae, so other factors must be playing a role. More work is needed to determine the degree to which the specific lunar timing of eddy passage influences the size of the settlement event.

In conclusion, the combined biological and physical records of this study demonstrate for the first time that large pulses of multi-taxa settlement-stage reef fish larvae can be delivered to reef settlement habitats during the passage of cyclonic mesoscale and sub-mesoscale frontal eddies moving downstream along the reef tract between the outer reefs and the FC front. Increased internal tidal bore activity was found to be associated with the passage of onshore meanders of the FC front, both leading and trailing frontal eddies, and this interaction warrants further examination. The data provide some sense of the boundaries of these events but do not yet allow for the determination of larval sources. Successful transport and settlement of reef fish larvae will depend on the coincidence of a number of biological and physical criteria.

References

- BROTHERS, E. 1987. Methodological approaches to the examination of otoliths in aging studies, p. 319–330. *In* G. E. Hall [ed.], *Age and growth of fish*. Iowa State Univ.
- CARR, M. H., AND D. C. REED. 1993. Conceptual issues relevant to marine harvest refuges: Examples from temperate reef fishes. *Can J. Fish Aquat. Sci.* **50**: 2019–2028.
- COWEN, R. K. 2002. Larval dispersal and retention and consequences for population connectivity, p. 149–170. *In* P. F. Sale [ed.], *Coral reef fishes: Dynamics and diversity in a complex ecosystem*. Academic.
- , AND L. R. CASTRO. 1994. Relation of coral reef fish larval distributions to island scale circulation around Barbados, West Indies. *Bull. Mar. Sci.* **54**: 228–244.
- , K. M. M. LWIZA, S. SPONAUAGLE, C. PARIS, AND D. OLSON. 2000. Connectivity of marine populations: Open or closed? *Science* **287**: 857–859.
- CRIALES, M. M., AND T. N. LEE. 1995. Larval distribution and transport of penaeoid shrimps during the presence of the Tortugas Gyre in May–June 1991. *Fish. Bull.* **93**: 471–482.
- , C. YEUNG, D. L. JONES, T. L. JACKSON, AND W. J. RICHARDS. 2003. Variation of oceanographic processes affecting the size of pink shrimp (*Farfantepenaeus duorarum*) postlarvae and their supply to Florida Bay. *Estuar. Coast. Shelf Sci.* **57**: 457–468.
- FINDLAY, A. M., AND L. G. ALLEN. 2002. Temporal patterns of settlement in the temperate reef fish *Paralabrax clathratus*. *Mar. Ecol. Prog. Ser.* **238**: 237–248.
- FRATANTONI, P. S., T. N. LEE, G. P. PODESTA, AND F. MULLER-KARGER. 1998. The influence of Loop Current perturbations on the formation and evolution of Tortugas eddies in the southern Straits of Florida. *J. Geophys. Res.* **103**: 24759–24799.
- HAMNER, W. M., AND I. R. HAURI. 1981. Effects of island mass: Water flow and plankton pattern around a reef in the Great Barrier Reef lagoon, Australia. *Limnol. Oceanogr.* **26**: 1084–1102.
- HARE, J. A., AND R. K. COWEN. 1991. Expatriation of *Xyrichtys novacula* (Pisces: Labridae) larvae: Evidence of rapid cross-slope exchange. *J. Mar. Res.* **49**: 801–823.
- KINGSFORD, M. J., AND J. H. CHOAT. 1986. The influence of surface slicks on the distribution and onshore movement of small fish. *Mar. Biol.* **91**: 161–171.
- LEE, T. N. 1975. Florida Current spin-off eddies. *Deep-Sea Res.* **22**: 753–765.
- , M. E. CLARKE, E. WILLIAMS, A. F. SZMANT, AND T. BERGER. 1994. Evolution of the Tortugas Gyre and its influence on recruitment in the Florida Keys. *Bull. Mar. Sci.* **54**: 621–646.
- , AND D. A. MAYER. 1977. Low-frequency current variability and spin-off eddies on the shelf off Southeast Florida. *J. Mar. Res.* **35**: 193–220.
- , C. ROTH, E. WILLIAMS, M. MCGOWAN, A. F. SZMANT, AND M. E. CLARKE. 1992. Influence of Florida Current, gyres and wind-driven circulation on transport of larvae and recruitment in the Florida Keys coral reefs. *Cont. Shelf. Res.* **12**: 971–1002.
- , AND E. WILLIAMS. 1999. Mean distribution and seasonal variability of coastal currents and temperature in the Florida Keys with implications for larval recruitment. *Bull. Mar. Sci.* **64**: 35–56.
- , J. A. YODER, AND L. P. ATKINSON. 1991. Gulf Stream frontal eddy influence on productivity of the southeast U. S. continental shelf. *J. Geophys. Res.* **96**: 22191–22205.
- LEICHTER, J. J., G. SHELLNBARGER, S. J. GENOVESE, AND S. R. WING. 1998. Breaking internal waves on a Florida (USA) coral reef: A plankton pump at work? *Mar. Ecol. Prog. Ser.* **166**: 83–97.
- , H. L. STEWART, AND S. L. MILLER. 2003. Episodic nutrient transport to Florida current reefs. *Limnol. Oceanogr.* **48**: 1394–1407.
- , S. R. WING, S. L. MILLER, AND M. W. DENNY. 1996. Pulsed delivery of subthermocline water to Conch Reef (Florida Keys) by internal tidal bores. *Limnol. Oceanogr.* **41**: 1490–1501.
- LEIS, J. M. 1991. The pelagic stage of reef fishes: The larval biology of coral reef fishes, p. 183–230. *In* P. F. Sale [ed.], *The ecology of fishes on coral reefs*. Academic.
- , AND M. I. MCCORMICK. 2002. The biology, behavior, and ecology of the pelagic, larval stage of coral-reef fishes, p. 171–199. *In* P. F. Sale [ed.], *Coral reef fishes: Dynamics and diversity in a complex ecosystem*. Academic.

- LIMOUZY-PARIS, C. B., H. C. GRABER, D. L. JONES, A. W. RÖPKE, AND W. J. RICHARDS. 1997. Translocation of larval coral reef fishes via sub-mesoscale spin-off eddies from the Florida Current. *Bull. Mar. Sci.* **60**: 966–983.
- LINDEMAN, K. C., T. N. LEE, W. D. WILSON, R. CLARO, AND J. S. AULT. 2001. Transport of larvae originating in southwest Cuba and the Dry Tortugas: Evidence for partial retention in grunts and snappers. *Proc. Gulf Carib. Fish. Inst.* **52**: 732–747.
- , R. PUGLIESE, G. T. WAUGH, AND J. S. AULT. 2000. Developmental patterns within a multispecies reef fishery: Management applications for essential fish habitats and protected areas. *Bull. Mar. Sci.* **66**: 929–956.
- MEEKAN, M. G., M. J. MILICICH, AND P. J. DOHERTY. 1993. Larval production drives temporal patterns of larval supply and recruitment of a coral reef damselfish. *Mar. Ecol. Prog. Ser.* **93**: 217–225.
- MILICICH, M. J. 1994. Dynamic coupling of reef fish replenishment and oceanographic processes. *Mar. Ecol. Prog. Ser.* **110**: 135–144.
- MILLER, J. L., AND T. N. LEE. 1995. Gulf Stream meanders in the South Atlantic Bight 2. Momentum balances. *J. Geophys. Res.* **100**: 6705–6723.
- OKAZAKI, Y., H. NAKATA, AND S. KIMURA. 2002. Effects of frontal eddies on the distribution and food availability of anchovy larvae in the Kuroshio Extension. *Mar. Freshw. Res.* **53**: 403–410.
- PALUMBI, S. R. 2003. Population genetics, demographic connectivity, and the design of marine reserves. *Ecol. Appl.* **13**: S146–S158.
- PARIS-LIMOUZY, C. B. 2001. Transport dynamics and survival of the pelagic larval stages of a coral reef fish, the bicolor damselfish, *Stegastes partitus* (Poey). Ph.D. thesis, Marine Sciences Research Center, State Univ. of New York at Stony Brook.
- PINEDA, J. 1991. Predictable upwelling and the shoreward transport of planktonic larvae by internal tidal bores. *Science* **253**: 548–551.
- REYNS, N., AND S. SPONAUAGLE. 1999. Patterns and processes of brachyuran crab settlement to Caribbean coral reefs. *Mar. Ecol. Prog. Ser.* **185**: 155–170.
- ROBERTS, C. M. 1997. Connectivity and management of Caribbean coral reefs. *Science* **278**: 1454–1456.
- ROBERTSON, D. R. 1992. Patterns of lunar settlement and early recruitment in Caribbean reef fishes at Panama. *Mar. Biol.* **114**: 527–537.
- ROGERS, J. S., J. A. HARE, AND D. G. LINDQUIST. 2001. Otolith record of age, growth, and ontogeny in larval and pelagic juvenile *Stephanolepis hispidus* (Pisces: Monacanthidae). *Mar. Biol.* **138**: 945–953.
- SALE, P. J. 1970. Distribution of larval Acanthuridae off Hawaii. *Copeia* **1970**: 765–766.
- SHANKS, A. L. 1983. Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. *Mar. Ecol. Prog. Ser.* **13**: 311–315.
- SHAY, N., T. N. LEE, E. J. WILLIAMS, H. C. GRABER, AND C. ROTH. 1998. Effects of low-frequency current variability on near-inertial sub-mesoscale vortices. *J. Geophys. Res.* **103**: 18691–18714.
- SHENKER, J. M., E. D. MADDOX, R. WISHINSKI, A. PEARL, S. R. THORROLD, AND N. SMITH. 1993. Onshore transport of settlement-stage Nassau grouper *Epinephelus striatus* and other fishes in Exuma Sound, Bahamas. *Mar. Ecol. Prog. Ser.* **98**: 31–43.
- SPONAUAGLE, S., AND R. K. COWEN. 1996a. Nearshore patterns of larval supply to Barbados, West Indies. *Mar. Ecol. Prog. Ser.* **133**: 13–28.
- , AND ———. 1996b. Larval supply and patterns of recruitment for two Caribbean reef fishes, *Stegastes partitus* and *Acanthurus bahianus*. *Mar. Freshw. Res.* **47**: 433–447.
- , AND OTHERS. 2002. Predicting self-recruitment in marine populations: Biophysical correlates and mechanisms. *Bull. Mar. Sci.* **70S**: 341–375.
- , J. FORTUNA, K. GRORUD, AND T. LEE. 2003. Dynamics of larval fish assemblages over a shallow coral reef in the Florida Keys. *Mar. Biol.* **143**: 175–189.
- , AND D. R. PINKARD. 2004. Impact of variable pelagic environments on natural larval growth and recruitment of the reef fish *Thalassoma bifasciatum*. *J. Fish Biol.* **64**: 34–54.
- STOBUTSKI, I. C., AND D. R. BELLWOOD. 1997. Sustained swimming abilities of the late pelagic stages of coral reef fishes. *Mar. Ecol. Prog. Ser.* **149**: 35–41.
- STONER, A. W., N. MEHTA, AND T. N. LEE. 1997. Recruitment of *Strombus* veligers to the Florida Keys reef tract: Relation to hydrographic events. *J. Shellfish Res.* **16**: 1–6.
- THORROLD, S. R., J. M. SHENKER, R. MOJICA, E. D. MADDOX, AND E. WISHINSKI. 1994. Temporal patterns in the larval supply of summer-recruitment reef fishes to Lee Stocking Island, Bahamas. *Mar. Ecol. Prog. Ser.* **112**: 75–86.
- VICTOR, B. C. 1986. Duration of the larval stage of one hundred species of Pacific and Atlantic wrasses (family Labridae). *Mar. Biol.* **90**: 317–326.
- WARNER, R. R., AND R. K. COWEN. 2002. Local retention of production in marine populations: Evidence, mechanisms, and consequences. *Bull. Mar. Sci.* **70S**: 245–249.
- , S. E. SWEARER, AND J. E. CASSELLE. 2000. Larval accumulation and retention: Implications for the design of marine reserves and essential fish habitat. *Bull. Mar. Sci.* **66**: 821–830.
- YEUNG, C., D. L. JONES, M. M. CRIALES, T. L. JACKSON, AND W. J. RICHARDS. 2001. Influence of coastal eddies and counter-currents on the influx of spiny lobster, *Panulirus argus*, post-larvae into Florida Bay. *Mar. Freshw. Res.* **52**: 1217–1232.
- , AND T. N. LEE. 2002. Larval transport and retention of the spiny lobster, *Panulirus argus*, in the coastal zone of the Florida Keys, USA. *Fish. Oceanogr.* **11**: 286–309.
- ZETLER, B. D., AND D. V. HANSEN. 1970. Tides in the Gulf of Mexico—a review and proposed program. *Bull. Mar. Sci.* **20**: 57–69.

Received: 9 June 2004

Accepted: 2 January 2005

Amended: 5 February 2005