# Transport Patterns of Tropical Reef Fish Larvae by Spin-Off Eddies in the Straits of Florida

By Hans C. Graber and Claire B. Limouzy-Paris

Better description of transport patterns . . . is essential for understanding the relationship between replenishment of larvae and their subsequent settlement at sites . . .

TROPICAL REEF FISHES belong to a broad phylogenetic group and, as a result, exhibit considerable diversity. Their only shared characteristic as an ecological entity is their fate as reef-associated adults. Their complex life cycles, in which pelagic larval phases alternate with demersal juvenile and adult phases, varies considerably within the early life history (ELH) stages (i.e., egg, larval, and juvenile stages) (Cowen and Sponaugle, 1997). This variability implies coral reef fishes have adapted differentially to the surrounding dynamic environment and may utilize different pathways while in the pelagic zone, to be transported nearshore at the time they metamorphose. Better description of transport patterns (e.g., dispersal and retention mechanisms) is essential for understanding the relationship between replenishment of larvae and their subsequent settlement at sites where transition into juveniles and adults can be achieved.

Recent large-scale ichthyoplankton and hydrographic surveys in the southern Straits of Florida have suggested that mesoscale circulation processes (i.e., cold core gyres) induce significant recruitment variability of reef fish and lobster larvae along the Florida Keys (Yeung, 1991; Lee *et al.*, 1992, 1994). These gyres of relatively long duration (1–3 mo) often cause shoreward transport and tend to concentrate and retain locally spawned larvae (Porch, 1993; Lee *et al.*, 1994; Criales and Lee, 1995). However, in a nongyre situation, less is known about the dynamics of coastal interactions between the strong frontal boundary of the meandering Florida Current (FC) and the inshore reef system. Numerous researchers have speculated that hydrographic features serve to retain larvae near their spawning sites on the reefs (Leis, 1993; Milicich, 1994; Richards *et al.*, 1995). Cowen *et al.*, (1993) further suggested that dynamic oceanic processes in conjunction with specific behavior patterns may be involved in translocation of diverse reef fish assemblages and specific-level biota. Thus small-scale flow measurements are needed to characterize these mechanisms acting upon the ELH stages.

Here we report on observations of reef fish larval transport mediated by remotely sensed spin-off eddies. Such eddies were first observed by Lee (1975) in current meter data. However, remote sensing of currents using HF radar provides a unique tool to probe repeatedly and noninvasively the ocean surface at high spatial and temporal resolution over a large domain.

**Biological Sampling and Current Observations**

An ichthyoplankton survey was carried out with the R/V *Oregon II* during the 13-h period from 1300 UTC 25 May to 0330 UTC 26 May 1994. The survey consisted of nine stations (7 day and 2 night) along three transects (Figure 1) with 23 hauls sampled via oblique tows using Bongo nets with a 333-$\mu$m mesh. Expendable bathythermographs were deployed before each haul to determine the depth of the thermocline. The results discussed here are limited to surface samples (0–40 m) that were always within the mixed layer. Details of the biological analysis can be found in Limouzy-Paris *et al.* (1997).

The OSCR system measured the surface vector current fields associated with coastal eddies over the coral reefs and the adjacent FC. From two sites located at Boca Chica and Bahia Honda in the South Florida Keys, currents were recorded in near real time (20-min sampling) and at 1-km resolution over a 30 × 40-km domain.

Average surface current maps were computed for each biological transect to represent mean reef and oceanic flow conditions. Horizontal trajectories were computed at 20-min intervals for 12 h before (backward) and after (forward) each station was sampled. In these calculations we assume no mixing or external forces (winds and waves) influenced the trajectories. These trajectories were used to estimate the origination and destination of reef fish larvae.

Hans C. Graber, Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL 33149–1098, USA; Claire B. Limouzy-Paris, Marine Sciences Research Center, State University of New York at Stony Brook, NY 11794–5000, USA.

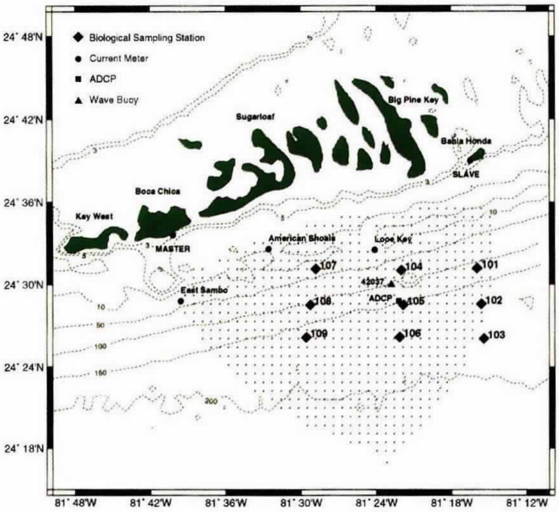


*Fig. 1: Experimental setting in the lower South Florida Keys. The small dots show the OSCR cell positions.*

## Eddy Dynamics

During the 13-h synoptic sampling period a cyclonic spin-off eddy, 10 km in diameter, with a swirl speed of ≈50 cm $s^{-1}$, migrated along the inshore edge of the meandering FC. It had an eastward translation speed of about 25 km/d (see Fig. 1 in Haus *et al.,* 1997). This feature produced a strong cyclonic current reversal and westward flow of 20–30 cm $s^{-1}$ in the upper 50 m (above the thermocline) at a mooring equipped with an acoustic Doppler current profiler (ADCP) offshore of Looe Reef. Shay *et al.,* (1997) compared OSCR surface current vectors with the upper most bin (15 m below surface) of the ADCP and found very high correlation (>0.8) during this sampling period. The vertical distribution of the horizontal flow was uniform during this period, suggesting little shear in the upper ocean layer above the thermocline. The presence of the eddies was also observed in the subsurface temperature field that showed distinct doming of the 27°C isotherm surface (Graber *et al.,* 1995) that extended to a depth of 50–75 m.

The following flow patterns were observed during the survey of the eastern transect (101–103); these stations sat on the eastern edge of a well-defined eddy causing strong onshore flow (Fig. 2). At the western end of this feature (between the middle and western transects) a strong alongshore flow convergence and offshore jet was observed. In the wake of this eddy, a weak, less-defined eddy formed in the western part of the OSCR array. The dominant FC initially intruded far reefward.

The temporal coverage of the OSCR data showed how these features evolved during the survey. During the middle transect (104–106) the main eddy advected eastward and moved partially out of the domain, producing a weak convergence near the reefward stations. The offshore station was then located on the boundary of the stronger (>1 m $s^{-1}$), eastward flowing FC. A weak trailing disturbance was observed near the western transect. By the time stations 107–109 were sampled, the main eddy feature had totally vanished from the OSCR domain and the FC had moved further offshore. For the biological analysis these flow scenarios were related to the micro-distribution and abundance of larval fishes.

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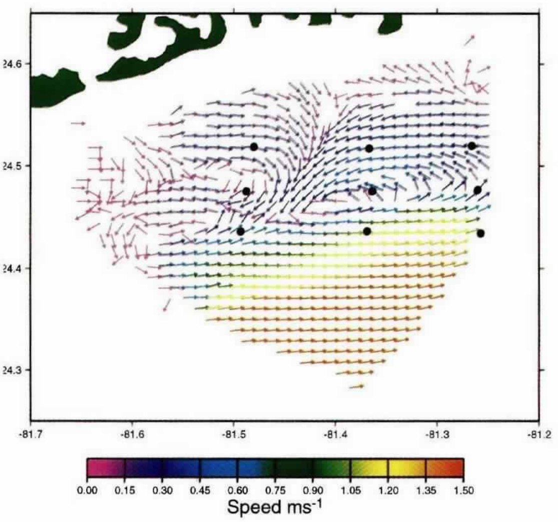


*Fig. 2: Average surface vector currents observed by OSCR during the sampling period of the easternmost transect (Stations 101–103). The dots (•) indicate biological sampling stations as defined in Figure 1.*

## Ichthyoplankton

Results from the 13-h sampling period were representative of the very high biodiversity previously observed in the Florida Straits (Limouzy-Paris, 1994). More than 5,000 fish larvae, representing 246 taxa, were collected. The dominant taxa (61%) were reef fishes. Abundance and distributions were determined for reef, coastal, and oceanic groups. Limouzy-Paris *et al.,* (1997) compared larval fish assemblages over the entire water column to the upper strata; their results indicated the importance of eddies as a mechanism for alongshore dispersal of posthatch larvae and for translocation of late stage reef fish larvae to inshore settlement sites.

## Trajectories

The hypothesis of translocation and longshore dispersal was evaluated by simulating horizontal transport with particle trajectories through each station, using the ocean surface current vectors recorded during the experiment. Figure 3 shows three examples of trajectories passing through positions near selected stations. The trajectories reveal that station 102, at the inshore edge of the FC, was strongly influenced by the passage of the eddy. Water, originating in the FC, was entrained by the eddy and transported onshore and westward (Fig.

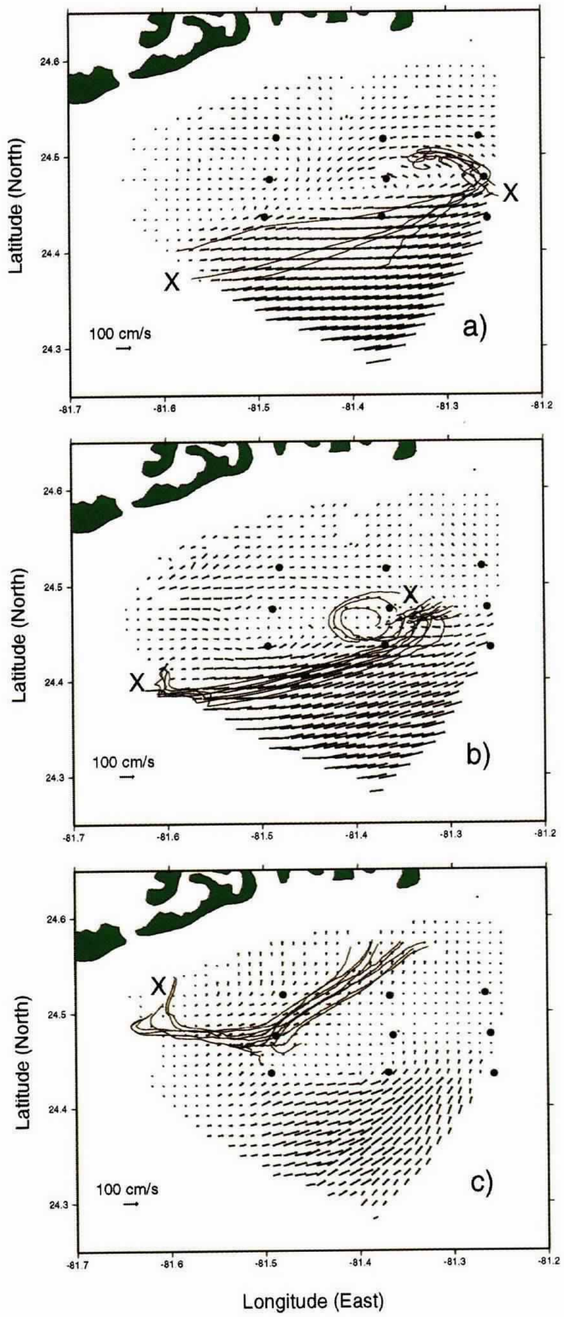


*Fig. 3: The trajectories represent the simulated transport patterns of fish larvae when treated as passive particles. The surface current maps in each panel corresponds to the flow field at the sampling time, $T_0$, of the selected station. A cluster of trajectories from the nine OSCR cells surrounding a station were computed for a period of 12 h before and after the sampling time. ×, start of each trajectory bundle (i.e., $T_0$–12).*

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3a). Similar conditions existed at the offshore station (106) of the central transect. Here FC water was mixed with entrained coastal water as a result of a current reversal induced by the eddy (Fig. 3b). This clearly shows that the central stations (105 and 106) were both exposed to water of oceanic origin, which crossed the boundary current into the coastal domain by means of eddy entrainment. During the western transect at station 108 (Fig. 3c), the trajectories showed purely coastal origin, with possible tidal influence, moving slower but in the same direction (alongshore) as the main eastward flowing FC.

## Translocation

Results from the upper 40-m samples strongly suggest species specific distributions were largely influenced by the dynamics of eddies. As a response to the eddy effect, representative species of each ecological grouping (i.e., reef, coastal, and oceanic) showed anomalies in regard to their distribution across the strong FC frontal boundary. The displacement of oceanic tuna larvae (*Thunnus* sp.) toward shore in the middle transect in the convergence zone suggests that eddy dynamics allowed cross-frontal exchanges, translocating larvae shoreward (Fig. 4a). Most coral reef species spawn pelagic eggs; these eggs and newly hatched larvae move passively through the water column. They could be entrained from upstream locations in the FC front, having distributions more like larvae of oceanic fishes than reef fishes (Leis, 1993). Larvae from squirrelfishes (*Holocentrus* sp.) behaved in the same way as tuna larvae and were translocated shoreward by the spin-off eddy (not shown).

The spawning behavior of nonreef shorefishes (i.e., coastal group) in tropical areas is less understood. They apparently migrate to the shelf edge to spawn (Leis and Reader, 1991). Tonguefish (*Symphurus* sp.) larvae representative of the coastal group were distributed further from shore than the tuna larvae, with highest abundance in the convergence zone of the main eddy (Fig. 4b).

The spin-off eddies could also contribute to alongshore dispersal of shore fishes which spawn on the reef zone. Lower swirl speeds on the inshore edge of the eddy compared to its offshore edge could possibly trap early larvae. The simulated trajectories agree well with these biological interpretations; Figure 4 depicts the influence of eddies on the spatial distribution of members of oceanic, shore, and reef fish groups depending on their origin.

## Conclusions

This study has demonstrated the importance of eddy dynamics in assessing the distribution and abundance of reef fish larvae. The employment of radar remote sensing has provided not only a new perspective on larval ecology but also a viable approach to direct biological sampling and made it possible to interpret the biological response to observations of the dynamics of small-scale flow features. Our results revealed that the evolution of spin-off eddies along the edge of the FC front serve as recruitment mechanism for reef fishes by enhancing the following: 1) longshore dispersal of larvae from coastal origin and 2) cross-frontal exchange of larvae from the adjacent oceanic FC (i.e., from oceanic origin) into settlement sites. Because of the highly dynamic nature of coastal processes and the complexity of larval behavior, re-

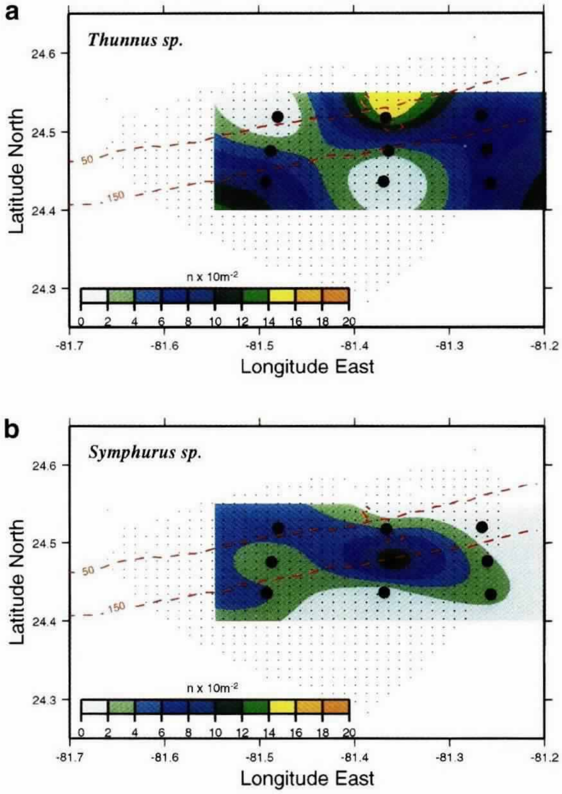


*Fig. 4: Spatial distribution of tropical larval fish abundances for representative species of the oceanic group (**a**) tuna (*Thunnus sp.*) and of the coastal group (**b**) tonguefish (*Symphyrus sp.*).

mote sensing of surface processes provide crucial observations to advance our understanding in variations of larval supply and recruitment rates. By linking remote sensing with other *in situ* and biological measurements, we will not only identify the influence of nearshore physical forcing (tides, winds, and waves) on reef fish larvae transport, but we will also be able to determine the predictability of small-scale eddies in the Florida Straits and their impact in the coral reef ecosystems.


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