

Transport of Larvae Originating in Southwest Cuba and the Dry Tortugas: Evidence for Partial Retention in Grunts and Snappers

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ABSTRACT

New and existing information was assembled to parameterize forthcoming models examining transport scenarios of larvae spawned within and outside of protected areas of the lower Florida Keys and southwest Cuba. This information suggests that in some valuable fish families, partial retention of larvae frequently occurs in areas often assumed to primarily export spawning products. Four categories of biotic variables were emphasized: locations and timing of spawning, larval durations, growth rates, and larval behaviors. Over 30 spawning aggregation sites for eight snapper species have been tentatively identified. Based on otolith increment counts, mean larval durations ranged from 31–42 d post-fertilization in six snapper species (*Lutjanus* and *Ocyurus*) and from 13–20 d in four grunt species (*Haemulon* and *Anisotremus*). Behaviors that foster retention may influence recruitment more than larval durations, and vertical and horizontal distributional patterns differ markedly between grunts and snappers. Snapper larvae occur offshore while grunt larvae are rare in offshore or inshore surface waters despite often gregarious settlement events. Based on these information sets, grunt populations may be less subject to advection than snappers. Off southwest Cuba and within the Yucatan channel, many cyclonic and anticyclonic eddies have been recently identified by satellite-tracked drifters and over the horizon radar. Gyres associated with the Dry Tortugas and the Pourtales platform can also be present during spawning seasons. All of these recirculation systems can have residence times exceeding known larval durations. At least four sets of evidence can favor larval retention:

- i) the larval biology of grunts practically precludes long-distance transport
- ii) the numerous long-term eddy systems off of southwest Cuba
- iii) the semi-continuous eddy system in the eastern margin of the Yucatan

Lindeman, K.C. et al. GCFI:52 (2001)

Channel and associated backflow and countercurrents; and
iv) the gyres, eddies, and countercurrents along the Florida Reef Tract.

KEY WORDS: Haemulidae, larval transport, lutjanidae

INTRODUCTION

Biotic and abiotic variables influencing larval transport can underlie variability in local recruitment, genetic structure, recent zoogeographic distribution patterns, and optimal management of fishery stocks. At least four categories of biotic variables have a primary influence on larval transport: locations and timing of spawning; larval durations; rates of growth and mortality, and larval behaviors. Temporally-variable interactions between complex current systems and these developmental patterns determine the potential for larval dispersal.

Mean current speeds associated with the Florida Current and surface drifter tracks imply that larvae are transported in rapid, unidirectional manners off the Florida Keys and areas upstream. However, data on pink shrimp larvae have long suggested a moderate degree of larval retention within the Florida Bay/Florida Reef Tract system (Munro et al. 1967, Rehner et al. 1967). Recently, a variety of large cyclonic and anticyclonic eddies and nearshore counter-currents that may favor retention have been detailed in this area (Lee et al. 1994, Lee and Williams 1999). In other regions, studies using mark and recapture, otolith microchemistry, and physical models have recently documented varying levels of self recruitment in reef fishes (Jones et al. in press, Swearer et al. in press, Cowen et al. in press).

Larval behaviors that foster retention may influence transport more than larval durations or surface current patterns. The rapid evolution of physical features that may promote retention, complex interactions among adjacent water masses, and constraints on the study of larval behavior present serious challenges to standard observational methods. Models which couple primary physical and biological parameters are needed to predict larval transport pathways into, within, and from the Florida Keys, and subsequent patterns of habitat use (Ault et al. 1999).

We assembled new and existing information necessary to parameterize and interpret coupled bio-physical models to predict potential larval transport paths off southwest Cuba and the Florida Keys. This work reflects preliminary efforts to model the release of particle clouds within eddies passing through marine reserve boundaries of these areas during known periods of spawning of snappers and grunts. Parameterization of these models requires empirical physical and biological data or, in their absence, logical proxies. We summarize new and existing information on:

- i) spawning aggregation sites
- ii) larval durations and growth rates
- iii) larval behaviors, and
- iv) physical patterns at primary scales

While assembling this information, several biotic and abiotic information sets suggested highly plausible mechanisms for at least partial retention of larvae. Primary examples are summarized here as alternatives to traditional hypotheses of larval transport.

METHODS

Taxa Examined and Spawning Site Identification

We focused on two families to account for taxa-specific differences in spawning, larval durations, growth rates, and larval behaviors. These families, snappers (Lutjanidae: genera *Lutjanus* and *Ocyurus*) and grunts (Haemulidae: genera *Haemulon* and *Anisotremus*), are among the most widespread and economically valuable of western Atlantic reef fishes (Robins and Ray 1986). At least nine of these species are overfished in the Florida Keys (Ault et al. 1998).

Information on spawning aggregations sites and seasonality in five snapper species from Cuba was obtained from Claro (1981, 1982), García-Cagide et al. (1994) and Claro et al. (in press). Similar information was obtained for aggregations of eight species from the Florida Keys (Domeier and Colin 1997, Lindeman et al. in press a). Spawning events in grunts are undocumented. Information on temporal patterns was assembled from studies of recruitment and gonad histology (e.g., McFarland et al. 1985, García-Cagide et al. 1994).

Larval Durations, Growth, and Vertical Positioning

Estimates of larval durations and early growth rates for 10 species of snappers and grunts were based on:

- i) validation of daily deposition of otolith increments in several species
- ii) identification of transitions in otolith increment spacing that may reflect age of settlement, and
- iii) counts of otolith increments up to and beyond the settlement marks (Lindeman et al. in press a).

Direct information on larval behaviors is unavailable for almost all western Atlantic reef fishes. However, relevant information is available from horizontal and vertical distributional patterns in ichthyoplankton surveys (e.g., Richards 1984), and comparative patterns of morphological development and metamorphosis for grunts (Lindeman 1986) and snappers (Lindeman et al. in press b).

Physical Data and Potential Transport Paths

Southwest Cuba — Coarse-scale current systems and the primary physical literature for this area are summarized in Claro et al. (in press). Much new information is becoming available from satellite-tracked drifters deployed as part of the National Ocean Partnership Program - Year of the Ocean (NOPP-YOTO). These drifters were drogued at depths of 10 - 20 m and transmitted positions at sub-daily intervals. We plotted the paths of the drifters entering waters off southwest or south-central Cuba during periods of snapper and grunt spawning activity.

Yucatan Channel — New synoptic measurements of surface currents are being made for the Florida Straits and Yucatan Channel by over-the-horizon radar facilities. This technology can remotely monitor data-sparse areas that would otherwise require hundreds of widely dispersed *in-situ* instruments (Georges et al. 1998). We surveyed surface current maps of the Yucatan Channel based on several Relocatable Over the Horizon Radar (ROTHR) experiments conducted in 1998 and 1999 by the NOAA Environmental Technology Laboratory.

Florida Keys — As part of ongoing studies of current systems of the Florida Keys and interactions with Florida Bay and the Gulf of Mexico, several long-term current moorings are deployed along the Florida Keys outer shelf and the southwest FL shelf. Acoustic Doppler Current Profilers (ADCPs) are also moored in the middle and northern Keys. Via these tools, satellite-tracked surface drifters, and additional studies, considerable information on horizontal and vertical flow-field variation was available for nearshore and offshore components of the area (Lee et al. 1994, Smith 1994, Pitts 1994, Georges et al. 1998, Lee and Williams 1999).

RESULTS

Egg Release Sites

For many snapper species, spawning aggregation sites are not uniformly distributed across the shelves of southwest Cuba and southeast Florida. For example, Claro (1982) and García-Cagide et al. (1994) documented that lane snapper of the Golfo de Batabanó migrate to the east in April, against mean currents, to the margin of a deep and wide trough extending into nearshore waters, the Golfo de Cazones. At night, on days after the full moon, they spawn on this shelf edge at a depth of 30 - 40 m. Each individual spawns 4- 5 times during one week. At the same time of the year, evidence suggests that a gyre is present in the center of the Golfo de Cazones for at least four week intervals. This gyre abuts the eastern margin of the Golfo de Batabanó, an area of abundant shallow habitats that may be favorable to settlement-stage larvae. A similar pattern is described for mutton snapper of the northeast Cuban shelf (Claro 1981). In total, seven and ten potential aggregation sites have been

identified in Cuba for lane and mutton snapper, respectively (Claro et al. in press). In south Florida, probable spawning aggregations of eight snapper species at 25 sites have been identified (Domeier and Colin 1997, Lindeman et al. in press a). Peak spawning in most species occurs between May and September (García-Cagide et al. 1994).

Spawning in most grunts occurs year-round, with spring and summer peaks in many species (McFarland et al. 1985, García-Cagide et al. 1994). Social behavior and habitat use during spawning are completely unknown despite many observation attempts. This suggests spawning occurs well after dusk. High abundances of recruits semi-continuously occur throughout the region and older life stages typically occur in deeper reef habitats. Therefore, we assumed that most egg release sites for grunts are near depths of 20 - 30 m in mid-shelf and shelf-edge areas.

Larval Durations and Growth Rates

Based on otolith increment transitions associated with settlement, estimates of mean planktonic larval durations (PLDs) ranged from 31 to 42 d post-fertilization in six snapper species. No significant differences were found among species and the mean for all was 32 day (Lindeman et al. MSa). Sample sizes were low and these estimates are preliminary. Settlement marks are not documented in grunts and PLDs were based on total daily ring counts from newly-settled individuals. Estimated PLDs ranged from 13 - 20 days in four grunt species. Larval duration estimates are plotted for both families in Figure 1, with groupers, evolutionarily similar percoids, included for comparison. The mean growth rate of all snapper species pooled (0.81 mm/day, $n = 63$) was significantly higher than grunts (0.47 mm/day, $n = 76$) (Lindeman et al. MSa). These rates are for sizes ranging from 10 - 70 mm SL. Evidence suggests that larval growth rates may show a similar pattern between families, at least after the flexion stage.

Vertical and Horizontal Distributions of Larvae

PLDs are not the only or best measure of retention/advection potential. Larval behaviors that foster retention can take many forms and may influence recruitment more than larval durations. Direct information on larval behaviors and their size-specific variation is limited. However, considerable amounts of relevant information were available on horizontal and vertical distribution patterns from ichthyoplankton sampling (e.g., Leis 1987, Richards et al. 1993, Paris-Limouzy et al. 1997). Coupled with information on ecological and morphological patterns of metamorphosis (Lindeman 1986, Lindeman and Snyder 1999, Lindeman et al. MSb), it is possible to outline known developmental patterns and to posit logical hypotheses of the behavioral

alternatives that explain these patterns.

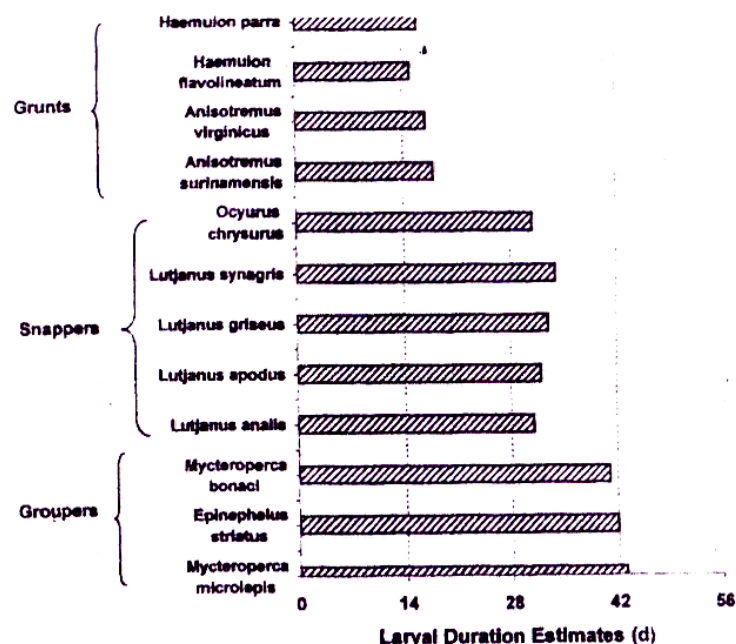


Figure 1. Larval duration estimates for grunt, snapper, and grouper species based on otolith increment counts. Data sources detailed in Lindeman et al. (in press a). Only specimens from southeast Florida and Cuba used for grunts and snappers.

Snapper larvae are commonly known from offshore and surface plankton sampling, whereas grunt early larval stages rarely enter offshore or surface waters. Haemulids are also rare in surface nets or nightlights at inshore stations despite often being the most abundant "settlers" on nearby benthic habitats (Table 1). These consistent patterns and an extremely gradual metamorphosis imply that grunts may associate with the mid or lower water column over continental or insular shelves from the flexion stage or earlier (Lindeman et al. in press a).

Table 1. Comparative patterns of early development among four genera of haemulids and lutjanids. Based on specimens from southeast Florida and Cuba. Modified from Lindeman et al. in press a.

Attribute	Haemulon & Anisotremus	Lutjanus & Ocyurus
Pre-settlement Stages:		
Offshore larvae	Rare/Absent	Occasional
Surface occurrence	Rare/Absent	Occasional
Diel vertical	Absent?	Present
Metamorphosis:		
Age range at	13 - 20 d	24 - 42 d
Typical settlement	6.5 - 9 mm	10 - 18 mm
Otolith settlement	No?	Yes
Morphological	Slow (months), subtle	Rapid (days), distinct
Newly-settled Stages:		
Demersal growth	Slow; 0.27 - 0.65 mm-d-1	Fast; 0.68 - 0.94 mm-d-1
Schooling behavior	Gregarious; often school	Solitary; or in small, non-schooling groups
Adult pigment acquisition	Delayed (months)	Rapid (days/weeks)

Based on the differences identified in Table 1 and the source literature, we hypothesize that positioning and larval durations of post-flexion stages of snappers and grunts can be characterized as follows:

	Larval Duration	Vertical Position		Horizontal Distribution
		Day	Night	
Snappers	30 d	20 - 40 m	0 - 20 m	Offshore/inshore
Grunts	14 d	Near bottom	Near bottom	Inshore only

Variations in these parameters exist within the families and probably within species (e.g., among geographic regions). However, based on currently available information, these variations are not large enough to contradict these primary hypotheses. The ultimate proportion of larval retention or advection within each family involves the interplay of these parameters with the physical environment of the two study regions during peak spawning periods.

Physical Processes

Characterizations of the primary current systems and their forcing mechanisms in these regions include Sukhovoy et al. 1980, Lee et al. 1991, 1994, Smith 1994, Victoria del Río and Pené 1998, and Lee and Williams 1999). We focus here on new information of relevance to larval transport processes.

Southwest Cuba - New information on upper mixed layer current patterns and their variability have recently become available for waters off southwest Cuba based on satellite-tracked drifter paths from 10 m depths. Plots of four drifter paths that entered southwest Cuban waters in 1998 and 1999 are given in Figure 2. Drifter 23472 was released Julian day 291/98 at 10.7 N 76.7 W. It made one cyclonic loop within the Panama-Colombia gyre in approximately 60 days and entered southwest Cuban waters in February 1999. Circulation was then dominated by cyclonic eddies with swirl diameters of 10-100 km (Figure 2). This drifter remained south of Isla de la Juventud for 3 months. Drifter 30659 was released 151/98 at 10.9 N 76.7 W. It moved north and entered the region from the west, south of Cabo San Antonio, in July 1998. It spent eight months in various eddies in the region before exiting the region in March 1999. It subsequently drifted west and north through the Florida Straits in April 1999. Drifter 30660 was released 150/98 at 11.2 N 77.4 W. It made two cyclonic loops of the Panama-Colombia gyre before entering the region in October 1998. It made one large anticyclonic loop with many smaller cyclonic eddies before exiting the region to the west in March (Figure 2) and grounding in Belize in April 1999. Drifter 15592 was released in February 1999 off southwest Cuba. It resided for over 30 d in cyclonic eddies with swirl diameters of 20-50 km (Figure 2).

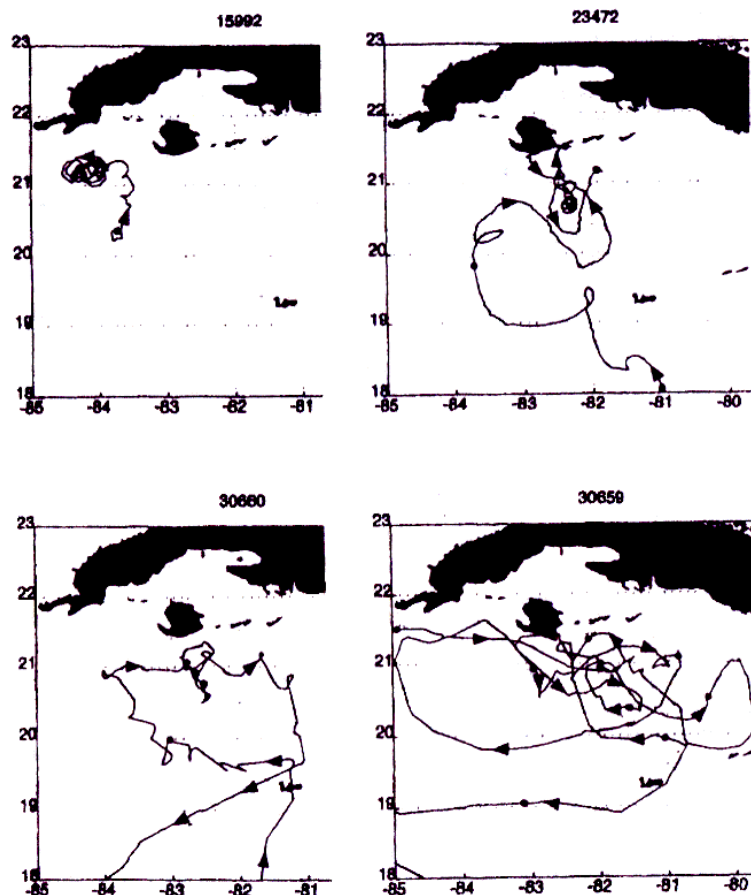


Figure 2. Eddy systems off southwest Cuba. Based on satellite-tracked drifters tracking currents at 10-20 m depths. Dates and durations of drifter paths in text.

Yucatan Channel - ROTHF data for surface currents in the Yucatan Channel were available for 16 days from June 1998 to October 1999. The western margin of the channel consistently showed strong northerly currents at speeds of 0.75-2.0 m/s. However, the central axis and eastern margin of the channel were typically dominated by a large anticyclonic eddy feature (Figure 3). The eddy system showed complex spatial dynamics and appeared to often meander to the north and south of the channel. However, this system was present in all seasons and almost all of the ROTHF images. The system varied from elliptical to spherical in shape with diameters ranging from approximately 50-120 km. Two examples of eddy positioning are given in Figure 3. Data from 6 May and 21 May 1999 show a large eddy southwest of Cabo San Antonio that was generating strong southerly backflow. Other imagery suggests that portions of this backflow may bifurcate and form a substantial component of the easterly Cuban Countercurrent.

Florida Keys - Potential recruitment pathways for larvae spawned in the Florida Keys or from external sources are driven by at least four physical processes: the Florida Current; cyclonic circulation of the Tortugas and Pourtales Gyres; onshore surface Ekman transport; and coastal countercurrents. Physical characteristics of these features relevant to larval retention and advection have been reviewed thoroughly by Lee et al. (1994), Yeung (1996) and Lee and Williams (1999). The shoreward front of the Florida Current is an area of near-surface current convergence. Therefore, larvae and their planktonic foods tend to be concentrated in the frontal zone. Onshore meanders and shoreward displacement of this front transport larvae closer to the coastal zone in the middle and upper Keys. Lobster and conch larvae occur near the outer reefs when the Florida Current is nearshore (Stoner et al. 1997). Small frontal eddies (20 - 50 km diameter) and the larger Tortugas gyre (100 - 200 km) aid the inshore exchange of larvae (Crales and Lee 1995, Limouzy-Paris et al. 1997). The Tortugas Gyre and smaller eddies can entrain larvae for weeks or months and enhance food availability through upwelling and the concentration of zooplankton (Lee et al. 1994).

A westward countercurrent inside the outer reefs results from the influences of downwelling winds and coastal gyres, and can extend from the middle Keys to the Tortugas. Its northern extent is limited by the curving coastline that causes prevailing westward winds to orient alongshore in the lower Keys and onshore in the upper Keys. There is also evidence that the coastal countercurrent extends shoreward to Hawk Channel and other nearshore waters (Lee 1986, Pitts 1994). Thus, larvae that are detrained from the Florida Current can be transported westward and shoreward by the coastal countercurrent, providing opportunities for recruitment to nearshore areas.

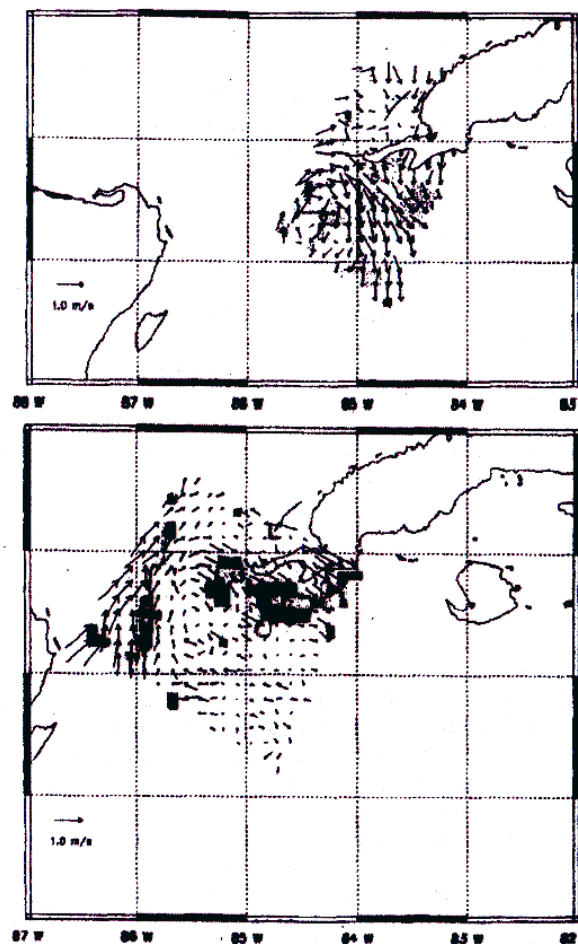


Figure 3. Two representations of anticyclonic eddy systems within the Yucatan Channel. Surface current images from relocatable over the horizon radar (Images from T.M. Georges and colleagues). Top: Eddy positioned in the southeast portion of the channel with backflow exceeding 1 m/s, 6 May 1999. Bottom: Centrally-positioned eddy, 13 November 1998.

DISCUSSION

Alternative Larval Transport Scenarios

New subsurface drifter tracks off southwest Cuba and radar data from the Yucatan Channel suggest that larvae spawned from the massive reef system bordering the southern margin of the Golfo de Batabanó are not necessarily entrained into a unidirectional current field flowing towards and through the Yucatan Channel. Larvae may have to traverse a variety of physical retention mechanism before even reaching the axis of the Yucatan Channel. The residence times of the various eddies south of the Golfo de Batabanó easily exceed the PLDs of both snappers and grunts (Figures 1 and 2). Larvae that are not entrained in these eddies and travel west may still encounter the eastward Cuban Countercurrent which is produced in part from backflow from the eddy often at the eastern margin or center of the Yucatan Channel (Figure 3), or be entrained in this eddy itself.

Rapid downstream transport may occur in the western margin of the Yucatan Channel and Florida Current at velocities of 2 m/s. However, mean surface currents do not fully capture the dynamics of larval transport. Vertically stratified flows may transport larvae in manners that contradict assumptions from unidirectional surface flows and PLD estimates. Many current systems commonly thought to be dominated by unidirectional flow frequently generate cyclonic or anticyclonic circulation systems along frontal boundaries in response to a variety of shearing forces. These frontal boundaries are often areas of high plankton density (Richards et al. 1993).

NOPP-YOTO drifter releases of 1998 - 1999 increased the database on Lagrangian flows in the Caribbean by an order of magnitude and their trajectories are revealing very complicated patterns (Figure 2) in areas often considered to have relatively unidirectional flow. The 10 - 20 m operational depths of these drifters may be more representative of larval vertical positioning than surface drifters, thus providing more realistic larval transport trajectories. However, additional information on the vertical stratification of both flow-fields and larval distributions is needed. Recent work in Australia has identified exceptional swimming speeds and maneuvering abilities in late pelagic larvae of many taxa (Stobutzki and Bellwood 1997, Leis and Stobutzki 1999). Laboratory and field investigation of these processes in western Atlantic species, particularly vertical maneuvering, will shed considerable light on the capacities of larval fishes to maximize retention or advection, and to traverse frontal boundaries.

Phylogenetic and Geographic Scales

Transport scenarios may vary widely among and within families. Grunts and snappers showed major contrasts in many early demographic parameters, despite close phylogenetic affinities. Along with differing PLDs, these families showed

many developmental contrasts that suggest very different transport potential (Table 1). These include differences in:

- i) inshore/offshore distribution patterns
- ii) vertical distributions
- iii) comparative larval morphologies and growth rates
- iv) microstructure of otolith increment transitions
- v) diel larval behaviors
- vi) settlement size; and g) patterns of schooling at settlement.

Given the evidence that snappers are in the plankton for 10 - 20 days longer than grunts and that grunts do not exit the shelf, do not use surface waters, and may engage in near-bottom associations by the flexion stage, it is hypothesized that grunt populations are more likely to self-recruit than snappers. If correct, this hypothesis may have several consequences for the metapopulation structure of these wide-ranging species. For example, grunt stocks may have less potential for genetic exchange with both up- and down-stream populations than snappers.

Considerable evidence now suggests logical alternatives to the assumption that physical transport in the northern Caribbean is largely unidirectional and that larvae behave as passive particles. However, this evidence does not exclude hypotheses of extended transport in some taxa; particularly in our study area which includes adjacent islands and continental shelf subsystems.

Outside of isolated islands, mean larval transport patterns over decadal time scales probably consist of both retention and intermediate-distance advection episodes that vary in frequency within and between years, and as a function of specific locations. In the Caribbean, the distributions of some species may be influenced by larval transport processes operating on the scale of individual basins or areas within. For example, two species of grunts commonly recorded from coastal areas of the Colombian Basin, *Haemulon steindachneri* and *H. bonariense*, are not present or rare in seemingly downstream areas such as Honduras and Belize (Lindeman et al. in press b). A viable hypothesis to explain these disjunct distributions is the combination of the Panama-Columbia Gyre and the apparent lack of larval dispersal capabilities in grunts. This large, cyclonic system may limit the downstream transport of some larvae from the western Colombian Basin. If correct, this hypothesis may not be universal as other *Haemulon* species do not show such disjunct distributions although subject to the same gyre. Explanations for these patterns may involve differences in spawning times, larval behavior, or juvenile ecology at the species level. This highlights the need for more information on geographic variation in population parameters within key species and genera.

ACKNOWLEDGEMENTS

ROTHR imagery was made available through the work of T. M. Georges and colleagues at the NOAA Environmental Technology Laboratory. Many workers have been involved in the NOPP-YOTO drifter program in the Caribbean, in particular we thank Kevin Leaman, Bob Cowen and Bill Richards provided valuable comments on the manuscript. This research received partial support from NOAA Coastal Ocean Program Grant No. NA37RJ0200, United States Man and the Biosphere Marine and Coastal Ecosystems Directorate Grant No. 471014223B, and S. Fl. Ecosystem Restoration Protection Modeling Grant No. NA67RJ0149.

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