



# Larval fish assemblages and mesoscale oceanographic structure along the Mesoamerican Barrier Reef System

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## ABSTRACT

The Mesoamerican Barrier Reef System (MBRS) is of high ecological and economic importance to the western Caribbean region, and contains spawning sites for a number of reef fish species. Despite this, little is known of the distribution and transport of pelagic fish larvae in the area, and basic *in situ* information on larval fish assemblages is lacking. Here we describe the results of two biological oceanography research cruises conducted in winter-spring of 2006 and 2007, focusing on larval fish assemblages. We use multivariate assemblage analyses to examine vertical and horizontal distribution characteristics of larval fish assemblages, to highlight key distinguishing taxa, and to relate these to the observed oceanographic structure. Our results showed a general separation between the Gulf of Honduras region, which was characterized by weaker currents and high abundances of inshore and estuarine taxa (Eleotridae, Priacanthidae), and the northern MBRS, which was subject to strong northward flow and contained a mixture of mesopelagic and reef-associated taxa (Myctophidae, Sparidae). Although distinct patterns of vertical distribution were observed among taxa, both shallow and deep living larvae were broadly distributed throughout the study area. Analysis

of historical drifter tracks highlighted the strong northward flow and low retention conditions typically present along the northern MBRS, as well as potential connectivity between the western Caribbean Sea, the Gulf of Mexico and the Atlantic Ocean.

**Key words:** biological oceanography, ichthyoplankton assemblages, Mesoamerican Reef

## INTRODUCTION

The Mesoamerican Barrier Reef System (MBRS) is the second longest barrier reef system in the world, extending more than 1000 km along the eastern coast of the Yucatan Peninsula. It encompasses barrier, fringe and patch reefs, with mangrove and seagrass habitats found further inshore (McField and Kramer, 2005). In recent decades, several threats have emerged to coral reef health in the Caribbean Sea, including the MBRS. As water temperatures have warmed, bleaching events have increased, with a particularly severe episode in 1998, associated with a strong, positive El Niño (Gardner *et al.*, 2003). Several intense hurricanes and further bleaching events since 2000 have combined to delay recovery, and reduce reef resilience (Carilli *et al.*, 2009). As a result, coral cover on some reefs has declined by more than 50% compared with historical levels (García-Salgado *et al.*, 2008). This has reduced available habitat for species which rely on coral reefs for all or part of their life cycle, including resident reef fish species.

The MBRS provides essential habitat for reef-associated fish species such as groupers (Serranidae) and snappers (Lutjanidae). These fishes are heavily exploited throughout much of the region (Heyman and Kjerfve, 2008; Sale and Kritzer, 2008), providing substantial economic benefits to local communities (Cesar, 2000). Some reef fish species, particularly those in the snapper/grouper complex, gather yearly at well-defined sites for mass spawning events known as spawning aggregations. They are easily located during these times, and are therefore intensively fished, despite depleted populations, due to this predictable reproductive behavior (Aguilar-Perera and Aguilar-Dávila, 1996; Aguilar-Perera, 2006; Heyman and

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Kjerfve, 2008). There are many important reef fish spawning aggregation sites located along the MBRS, including at least 59 off the eastern coast of the Yucatan Peninsula (Sosa-Cordero *et al.*, 2009). At locations north of Tulum (~20.2°N) spawning sites are typically located within strong northward currents, which flow past the northeastern tip of the Yucatan Peninsula into the Gulf of Mexico (GOM), and eventually past the Florida Keys and Dry Tortugas coral reef systems (Soto *et al.*, 2009). There are extensive nursery areas for juvenile fishes along the extreme northwards extent of the MBRS, associated with mangroves, seagrasses and sand shallows (Sosa-Cordero *et al.*, 1998). Along the southern MBRS, currents are typically weaker, and more variable (Centurioni and Niiler, 2003).

On a regional scale, oceanographic circulation in the western Caribbean Sea is influenced by Atlantic inflow, which flows westward through the island passages of the Antilles Arc and continues towards the Yucatan Peninsula as the Caribbean Current. This inflow is a combination of Sverdrup flow associated with the North Atlantic subtropical gyre, and the Atlantic Meridional Overturning Circulation (Badan *et al.*, 2005). As the Caribbean Current impinges upon the Yucatan Peninsula, it turns northward, becoming the Yucatan Current, and flows into the GOM, via the Yucatan Channel. Once in the GOM, the flow is referred to as the Loop Current. The latitude of impingement, where the Caribbean Current approaches the Yucatan coast, fluctuates from the Mexico-Belize border to as far north as Cozumel. This fluctuation drives the variability of mesoscale features along the MBRS (Badan *et al.*, 2005; Ezer *et al.*, 2005; Cetina *et al.*, 2006). The resulting influence of the Caribbean Current and Yucatan Current provides strong northward transport mechanisms, which are often present along much of the reef tract. However, under certain conditions, a cyclonic gyre may form below the latitude of impingement in the Gulf of Honduras (GOH), resulting in southward flow along the coast (Ezer *et al.*, 2005).

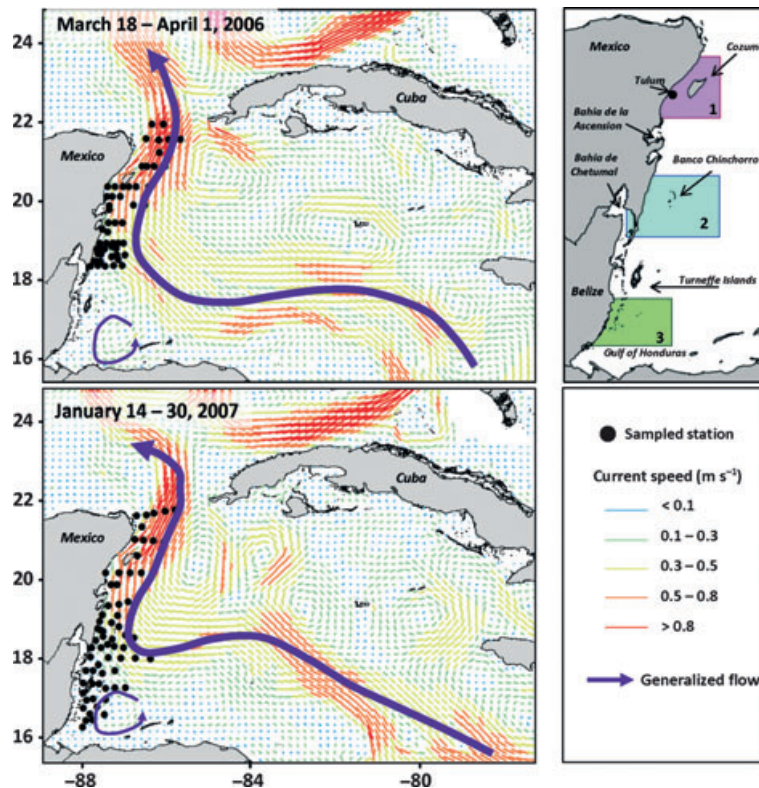
Most marine fishes, including coral reef species, have a pelagic larval phase which enables dispersal of early life stages over large distances. During the early part of this planktonic phase, larvae have limited capacity to determine their dispersal trajectories, and are regarded essentially as passive drifters. However, as they grow, the behavioral capabilities of larvae increase, and they develop abilities to migrate vertically within the water column, swim directionally, and navigate in the direction of suitable settlement habitats (Paris *et al.*, 2007; Butler *et al.*, 2011). A combination

of spawning location, oceanographic conditions and larval behaviors therefore determines the dispersal and distribution of pelagic larvae. Given the variability in oceanographic conditions along the MBRS, larvae spawned in the area may be subject primarily to local retention or to wide dispersal, depending on spawning location along the reef. Although regional oceanographic processes provide a potentially rapid conduit for pelagic larvae to disperse along the MBRS and potentially onto reefs bounding the GOM and Atlantic Ocean, the true extent of larval connectivity is unclear. Although models of transport potential highlight oceanographic connections between Honduran, Mexican and Belizean reefs, studies have shown genetic differentiation among fishes and corals along the reef system (Villegas-Sanchez *et al.*, 2010; Foster *et al.*, 2012). Reasons for this may include spawning behavior, where adults aggregate to spawn in regions of high oceanographic retention, preventing wide-scale dispersal of pelagic eggs and larvae (Karnauskas *et al.*, 2011), and behavior of the larvae themselves (Paris *et al.*, 2007).

Despite the ecological importance of the MBRS, very few *in situ* larval fish collections exist. Richards (1984) recorded larval fish assemblages of primarily mesopelagic origin from the offshore western Caribbean Sea, with some reef-associated families present (e.g., Serranidae, Labridae). Sanchez Velasco and Flores Coto (1994) described larval fish assemblages from the extreme northern portion of the Yucatan Peninsula from one spring cruise completed in 1985. This study reported assemblages of mesopelagic fish species to the east of the Yucatan Peninsula, and more neritic species to the north. However, studies covering the MBRS area itself are rare, despite the potential use of such data for validating model predictions, and for examining effects of mesoscale oceanographic variability on larval transport mechanisms.

Here we describe larval fish assemblages collected by two research cruises along the MBRS in 2006 and 2007. We aimed to (i) describe the composition and spatial structure of assemblages, (ii) examine vertical and horizontal distribution characteristics of different species, and (iii) relate these results to oceanographic patterns observed at the time of sampling. Previous studies suggested that oceanographic conditions along the MBRS could vary greatly depending on the position of the Caribbean Current impingement. We therefore hypothesized that the Caribbean Current would introduce an easily characterized mesopelagic larval fish assemblage to the MBRS region, and that this would be distinct from a more reef-associated assemblage found outside the influence of the Current.

**Figure 1.** Mean surface current velocity during the 2006 cruise (top) and 2007 cruise (bottom), from the HYCOM 1/12° global analysis (HYbrid Coordinate Ocean Model), with sampled stations also shown. Three areas of interest around Cozumel (1), Banco Chinchorro (2) and the Gulf of Honduras (3) used in later analysis are shown at right.



In addition, we expected that the vertical distribution of reef-associated species would influence their dispersal. This would be apparent through shallower-living larvae showing wider spatial distributions, and increased northward entrainment into the Caribbean Current.

## METHODS

From 18 March to 1 April 2006 and from 14 January to 30 January 2007, scientists from the National Oceanic and Atmospheric Administration (NOAA), the University of Miami (UM) and El Colegio de la Frontera Sur (ECOSUR) Unidad Chetumal conducted large-scale physical and biological oceanographic surveys in coastal and offshore areas from the Yucatan channel south along the MBRs, aboard the NOAA Ship *Gordon Gunter* (Fig. 1).

### *Environmental and oceanographic data*

Regional oceanographic patterns were inferred from current vector outputs from the HYCOM 1/12° global analysis (HYbrid Coordinate Ocean Model: [hycom.org](http://hycom.org)), averaged across the cruise period for each

year. Concurrent *in situ* environmental data utilized for this study included continuous water velocity profiles of the upper ocean water column recorded with an RD Instruments 75 kHz Ocean Surveyor hull-mounted (shipboard) acoustic Doppler current profiler (SAD-CP), and surface drifter trajectories resulting from satellite-tracked drifting buoy deployments conducted during each cruise.

SADCP data were collected with a vertical resolution (bin size) of 16 m, and were processed using the University of Hawaii's Common Ocean Data Access System (CODAS, West O'ahu, HI, USA) software suite to remove ship motion and to correct for instrument heading misalignment. Processed 5-min velocity data were interpolated onto a  $0.1^\circ \times 0.1^\circ$  spatial grid. Data from two primary depths were examined in our analysis: 35 m data (bin 27–43 m), the shallowest depth available, were utilized for a representation of the surface/near-surface currents relevant to larval fish in the upper two MOCNESS depth strata, and 105 m (bin 97–113 m) data were utilized for a representation of the conditions relevant to the deepest-living larvae sampled by the MOCNESS.

**Table 1.** Identification level of all families contributing at least 0.1% to total larval concentrations, along with the taxonomic level for further analysis. The number of genera and species within the study region (western central Atlantic Ocean) is also shown, from fishbase.org.

	No. of larvae (both years)	Percent identified genetically (both years) (%)	Identified to species: 2006 (%)	Identified to species: 2007 (%)	Identified to genus or species: 2006 (%)	Identified to genus or species: 2007 (%)	Total contribution (%)	Taxonomic level for analysis	Genera in study region	Species in study region
Myctophidae	18 044	0.2	30.9	0.0	48.5	0.1	28.3	Family	19	70
Scaridae	8600	0.3	2.6	6.3	97.5	98.9	13.4	Genus	4	16
Labridae	4259	1.0	45.1	27.6	90.8	89.0	6.7	Genus	10	24
Gonostomatidae	3699	0.2	4.2	0.3	50.2	0.3	5.3	Family	8	16
Gobiidae	3175	2.5	20.1	24.7	93.2	91.7	5.1	Genus	32	127
Eleotridae	2933	0.1	35.0	25.5	36.0	25.5	4.8	Family	6	8
Phosichthyidae	2769	0.5	45.9	0.3	45.9	0.4	4.2	Family	5	9
Bothidae	2174	0.4	0.1	1.4	0.1	2.9	3.4	Family	5	15
Bregmacerotidae	1713	0.1	0.4	8.5	100.0	100.0	2.3	Genus	1	6
Paralepididae	1444	0.3	1.0	0.3	2.3	13.3	2.2	Family	8	16
Chlorophthalmidae	1317	0.6	0.3	0.9	0.3	5.7	2.1	Family	2	2
Carangidae	1228	2.8	49.2	20.6	68.2	55.5	2.0	Family	16	36
Gempylidae	1031	1.3	1.0	4.0	1.0	4.5	1.6	Family	9	10
Acanthuridae	1330	1.3	6.4	0.0	100.0	100.0	1.5	Genus	2	6
Serranidae	986	14.4	52.7	41.7	93.9	90.0	1.5	Genus	27	95
Scombridae	789	5.8	42.1	43.3	88.0	77.1	1.2	Genus	8	17
Callionymidae	556	1.1	0.0	3.5	0.0	3.5	0.8	Family	4	5
Pomacentridae	470	3.8	2.3	3.6	6.6	21.0	0.8	Family	5	19
Paralichthyidae	451	3.5	0.0	4.7	4.7	14.4	0.7	Family	8	35
Howellidae	471	1.7	100.0	100.0	100.0	100.0	0.7	Species	2	2
Balistidae	439	2.7	0.0	14.7	0.0	14.7	0.7	Family	4	6
Holocentridae	439	2.3	3.7	1.8	3.7	1.8	0.7	Family	7	12
Apogonidae	274	10.6	2.1	10.8	2.1	19.7	0.5	Family	3	24
Tetraodontidae	292	0.3	0.0	0.7	0.0	1.2	0.5	Family	4	17
Scorpaenidae	265	4.2	0.0	7.1	0.0	9.2	0.4	Family	7	26
Evermannellidae	243	1.2	0.0	0.6	1.5	7.2	0.4	Family	2	2
Nomeidae	116	6.0	7.6	4.5	44.4	15.8	0.4	Family	3	8
Scombrabrachidae	187	5.3	100.0	100.0	100.0	100.0	0.3	Species	1	1
Ophichthidae	261	18.0	77.3	57.3	79.4	100.0	0.3	Genus	21	47
Symphysanodontidae	198	1.5	0.0	23.4	0.0	100.0	0.3	Genus	1	3
Sphyracnidae	188	0.0	0.0	32.5	100.0	100.0	0.3	Genus	1	4
Priacanthidae	178	4.5	10.0	85.1	10.0	85.1	0.3	Family	4	4
Pomacanthidae	168	3.6	5.1	10.3	6.6	10.3	0.3	Family	3	9

Table 1. (Continued)

	No. of larvae (both years)	Percent identified genetically (both years) (%)	Identified to species: 2006 (%)	Identified to species: 2007 (%)	Identified to genus or species: 2006 (%)	Identified to genus or species: 2007 (%)	Total contribution (%)	Taxonomic level for analysis	Genera in study region	Species in study region
Stomiidae	135	6.7	2.9	0.0	2.9	4.9	0.3	Family	21	118
Coryphaenidae	156	1.3	1.9	30.8	100.0	30.8	0.2	Genus	1	2
Syngnathidae	159	3.8	0.0	7.0	0.0	7.5	0.2	Family	11	29
Synodontidae	149	4.7	3.9	1.4	3.9	17.3	0.2	Family	3	10
Bramidae	145	9.0	5.0	4.2	5.0	5.8	0.2	Family	6	8
Lutjanidae	174	17.8	40.5	47.2	80.1	95.0	0.2	Genus	6	20
Muraenidae	144	7.6	74.6	77.3	86.1	89.2	0.2	Genus	8	22
Echeneidae	151	0.0	0.0	0.0	0.0	0.0	0.2	Family	3	8
Mullidae	95	14.7	81.5	4.2	81.5	4.2	0.2	Family	4	4
Moringuidae	128	8.6	100.0	100.0	100.0	100.0	0.2	Species	2	2
Scopelarchidae	110	1.8	8.5	3.7	11.0	5.2	0.2	Family	3	6
Antennariidae	112	2.7	0.0	15.6	0.0	15.6	0.2	Family	4	7
Monacanthidae	104	4.8	0.0	16.7	0.0	18.3	0.2	Family	4	10
Acropomatidae	98	23.5	0.0	4.9	0.0	4.9	0.2	Family	3	6
Chaetodontidae	99	5.1	0.0	1.5	14.9	100.0	0.2	Family	2	7
Engraulidae	92	0.0	0.0	20.6	0.0	20.6	0.2	Family	6	25
Diodontidae	95	1.1	3.2	0.0	3.2	1.8	0.1	Family	2	7
Mugilidae	77	10.4	0.0	10.5	0.0	13.4	0.1	Family	3	12
Cynoglossidae	84	3.6	0.0	0.0	100.0	100.0	0.1	Genus	1	20
Malacanthidae	74	2.7	0.0	15.2	0.0	34.6	0.1	Family	3	10
Caproidae	78	5.1	11.8	5.7	100.0	100.0	0.1	Genus	1	2
Microdesmidae	69	2.9	4.2	1.5	4.2	10.9	0.1	Family	2	6
Notosudidae	60	1.7	14.7	0.0	14.7	0.9	0.1	Family	2	5
Prereleotridae	58	0.0	0.0	12.1	100.0	100.0	0.1	Genus	1	2
Gerreidae	70	18.6	0.0	0.0	0.0	0.0	0.1	Family	5	13
Ophidiidae	64	6.3	0.0	16.2	0.0	22.9	0.1	Family	28	71
Dirremidae	60	1.7	5.7	0.0	5.7	0.0	0.1	Family	3	3
Congridae	84	22.6	64.6	65.4	100.0	100.0	0.1	Genus	14	32
Exocoetidae	52	7.7	0.0	6.7	0.0	14.5	0.1	Family	6	17
Xiphiidae	52	32.7	100.0	100.0	100.0	100.0	0.1	Species	1	1
Chlopsidae	42	23.8	86.7	98.2	86.7	98.2	0.1	Species	5	8
Lobotidae	35	0.0	100.0	100.0	100.0	100.0	0.1	Species	1	1
Haemulidae	34	41.2	9.7	5.4	28.3	91.3	0.1	Family	6	25
Oneirodidae	30	0.0	0.0	0.0	0.0	0.0	0.1	Family	6	10
Albulidae	33	69.7	100.0	0.0	100.0	100.0	0.1	Genus	1	2



NOAA's Global Drifter Program provided nine surface drifting buoys for deployment during the 2006 survey, and seven buoys for the 2007 survey. These drifters were constructed with a surface float diameter of 35–40 cm and a drogue centered at 15 m. Trajectories were tracked for several months, usually until the drifters either grounded in shallow water or left the Intra-Americas Sea (IAS) region. These trajectories were compared with an archived NOAA/AOML drifter data set containing all available trajectories for drifters which passed through the broader study area between 15 February 1979 and 30 September 2011 ([http://www.aoml.noaa.gov/envids/gld/dirkrig/parttrk\\_spatial\\_temporal.php](http://www.aoml.noaa.gov/envids/gld/dirkrig/parttrk_spatial_temporal.php)). Velocities from these trajectories were interpolated onto a  $1^\circ \times 1^\circ$  grid for the study domain ( $79^\circ$ – $91^\circ$ W,  $15^\circ$ – $31^\circ$ N), for all grid points containing data from at least five different drifters.

To examine typical retention times for planktonic particles in the upper mixed layer along the MBRS, historical drifters were tagged as they passed through three predefined boxes (Fig. 1), and their locations determined at 1 week and 2 weeks after first entering each box. The three boxes were chosen to cover three important reef habitats along the MBRS: Cozumel, Banco Chinchorro Biosphere Reserve and the western GOH. After 2 weeks, each drifter was classified as being in the MBRS region (retained below  $21^\circ$ N), in the GOM or as exiting the GOM through the Florida Straits (passing north of Cuba, and east of  $81^\circ$ W). Drifters which grounded in shallow waters on the MBRS within 2 weeks were considered to be retained. Although drifters cannot simulate complex behaviors shown by many reef fish larvae, they provided some basic information on trajectories of floating objects in the upper mixed layer along the MBRS.

#### Larval fish collections

Depth-stratified plankton sampling was completed using a 1-m multiple opening and closing net environmental sensing system (MOCNESS). In 2006, samples were collected at 56 stations along the northern portion of the MBRS within Mexican waters. In 2007, sampling was extended south into the GOH to include Mexican and Belizean waters, with 90 stations sampled.

The MOCNESS net was fitted with  $333\text{-}\mu\text{m}$ -mesh nets, which sampled four depth strata: 0–25 m, 25–50 m, 50–75 m and 75–100 m. These depths were chosen to encompass the typical vertical range of larvae from neritic, benthic and reef-associated families (e.g., Conway *et al.*, 1997; Sabates, 2004). All

plankton samples collected were preserved in 95% ethanol, which was replaced after 24 h to ensure proper preservation. Larval fish were sorted from plankton samples and identified visually to the lowest taxonomic level possible (Richards, 2006). Larvae from selected families were then identified to species level using genetic techniques (Table 1) (see Valdez-Moreno *et al.*, 2010 for methodology details).

The proportion of larvae identified to species level through genetic techniques was not equal among families. In addition, larvae of some families are much easier to identify visually to genus or species level than others. This also partially depends on the number of genera and species recorded for a family within the broader study area. We therefore used specific criteria to determine at which taxonomic level larvae from each family should be included in multivariate assemblage analyses. Where  $>75\%$  of larvae from a particular family were identified to species level in both 2006 and 2007, larvae were analyzed at species level for that family, and larvae identified to only genus or family level were excluded. An example of this is the family Moringuidae, where 100% of larvae from both 2006 and 2007 were identified to species level, through both visual and genetic techniques (Table 1). The presence of only two moringuid species from two genera in the western central Atlantic (fishbase.org) also clearly makes species-level identification easier than for Myctophidae larvae, for example (70 species from 19 genera in the study region). Where  $>75\%$  of larvae from a family were identified to at least genus level in both years, but not to species level, larvae were analyzed at genus level, and larvae identified to family only were excluded. An example of this is the family Scaridae, where  $>90\%$  of larvae were identified to genus level in both 2006 and 2007, but  $<10\%$  were identified to species level. Where  $<75\%$  of larvae from a particular family were identified to at least genus level in both years, larvae were analyzed at family level only (Table 1). This was the case with the family Myctophidae, where  $<50\%$  of larvae were identified below family level in either year. This family was therefore analyzed at family level in multivariate assemblage analyses, although a species-level analysis of depth distributions using the 30.9% of larvae identified to species level from 2006 was completed separately (see below). If a family contributed less than 0.1% to the total assemblage, it was excluded from further analyses. This resulted in 135 taxa for further assemblage analyses (Table 1). Larval fish concentrations per  $\text{m}^3$  were determined using the volume of seawater filtered, as recorded by a General Oceanics flowmeter fitted to the mouth of the net.

### Data analyses

Assemblage analyses were completed in the PRIMER-6 statistical package (with Permanova + add-on: Clarke, 1993; Clarke and Gorley, 2006). Larval fish concentrations were fourth-root transformed before further analysis, to down-weight the contribution of highly abundant taxa. To investigate the spatial distribution of assemblage groups, regardless of vertical distribution, larval fish concentrations were first combined for all four depth strata from each sampled station. Total larval fish abundances for each taxa were summed for each station sampled, and divided by summed total volumes of seawater filtered for the four sampled strata. This resulted in one depth-aggregated assemblage per station. Station assemblages were then compared using a group-average cluster analysis, with a Simprof (Similarity Profile) test added to define statistically significant assemblage groups at  $P < 0.002$  (Clakre *et al.*, 2008). Relationships among assemblage groups were further visualized using canonical analysis of principal coordinates (CAP: Anderson, 2001), and classification success was quantified through cross-validation. This procedure assigns a percentage success rate to separation of *a priori* groups, where 100% represents perfect separation, and thus no overlap among groups, and 0% represents no distinction among groups (Anderson and Willis, 2003). Taxa which tended to distinguish between assemblage groups were determined by Spearman Rank correlations between larval concentrations and the first two CAP axes. In addition, the spatial distributions of both larval fish assemblage groups, and important distinguishing taxa, were examined by plotting in SURFER 9 (Golden Software, Golden, CO, USA).

Depth-stratified larval fish concentrations were then examined in more detail. A CAP analysis was first employed to show the influence of sampling depth on assemblage structure. Samples were classified as having been completed during the day if the time the last net exited the water was between sunrise and sunset, or during the night if the last net left the water between sunset and sunrise, as determined from timeanddate.com using Belize local time (UTC-6). Vertical distributions of the most common taxa (those contributing at least 1% to total larval concentrations) were then summarized by calculating the abundance-weighted mean depth for both day and night samples (cf. Nye *et al.*, 2009). Specifically, larval concentrations of each taxa at each station were multiplied by the depth of capture (the midpoint of the depth strata), and then summed across all daytime and all nighttime stations separately. These values were then divided by the sum of larval concentrations for the

relevant taxa for all daytime or all nighttime stations, respectively.

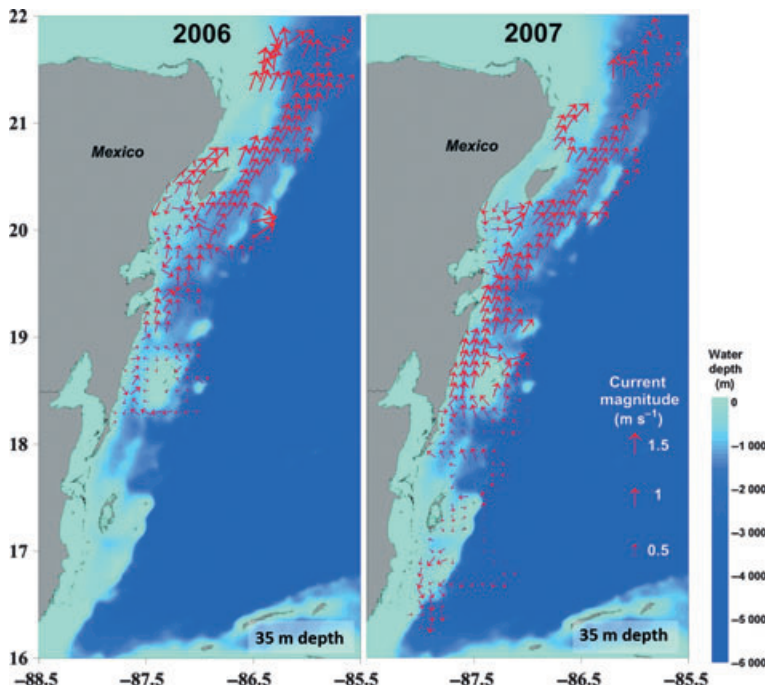
Abundance-weighted mean depths were calculated for each taxa, for both day and night samples. Depths of capture were estimated as the median value for the strata (i.e., capture depth of larvae in the 0–25 m strata was assumed to be 12.5 m depth). Due to our sampling regime, the abundance-weighted mean depths for deeper-living species, such as mesopelagics, may have been underestimated, as we only sampled to 100 m depth. However, results did show which taxa tended to be found at greater depths versus those which were collected higher in the water column, and which taxa tended to show diel vertical migration, as evidenced by a change in the abundance-weighted mean depth between day and night samples.

## RESULTS

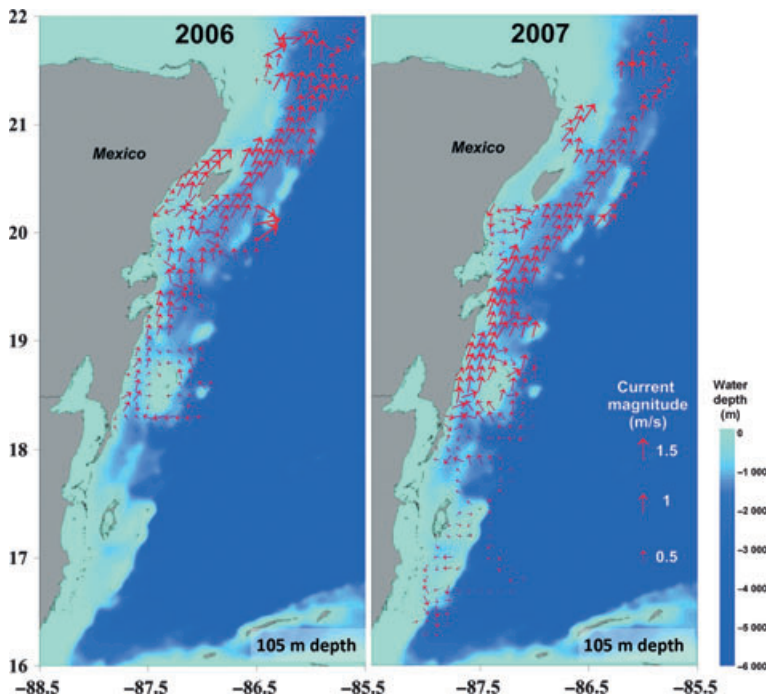
### *Regional environment and oceanographic circulation*

The Caribbean Current/Yucatan Current system was the dominant oceanographic feature observed in the study region during the 2006 and 2007 cruises (Fig. 1). On both surveys, the westward trajectory of the Caribbean Current impinged upon the Yucatan Peninsula at a latitude of approximately 18°N, east of Banco Chinchorro, before flowing northward along the coast, and passing through the Yucatan Channel into the GOM. This resulted in strong northward flow close to the northern Yucatan coast, including along both the eastern and western coastlines of Cozumel Island. In general, currents were much weaker south of the latitude of impingement, including within the GOH (Fig. 1). The Honduran gyre was present within the GOH during both surveys, but was only sampled during the 2007 cruise.

SADCP-derived flow fields indicated a general northward flow at both the 35 m and 105 m depth layers during both years (Figs 2 and 3). During 2006, currents were weaker and more variable south of Bahía de la Ascensión, whereas in 2007, flow was consistently northwards along the continental shelf from Banco Chinchorro to the north of the study area. Currents south of Banco Chinchorro into the GOH were much weaker than farther north, and were onshore on the edge of the continental shelf, shifting to southwards, south of the Turneffe Islands. Currents at 35 m depth were generally very similar in velocity and direction to those at 105 m depth. In 2006, the currents across the study area were observed to have a mean velocity of  $0.61 \text{ ms}^{-1}$  at 35 m depth, and  $0.54 \text{ ms}^{-1}$  at 105 m depth. In 2007, the mean currents were  $0.54 \text{ ms}^{-1}$  at 35 m depth and  $0.47 \text{ ms}^{-1}$  at 105 m depth.



**Figure 2.** Shipboard ADCP current velocity measurements at 35 m depth (27–43 m bin) for March 2006 and January 2007, averaged for  $0.1^\circ$  latitude-longitude squares. Water depth is also shown (from NOAA GEODAS: GEOphysical DATA System).



**Figure 3.** Shipboard ADCP current velocity measurements at 105 m depth (98–113 m bin) for March 2006 and January 2007, averaged for  $0.1^\circ$  latitude-longitude squares. Water depth is also shown (from NOAA GEODAS: GEOphysical DATA System).

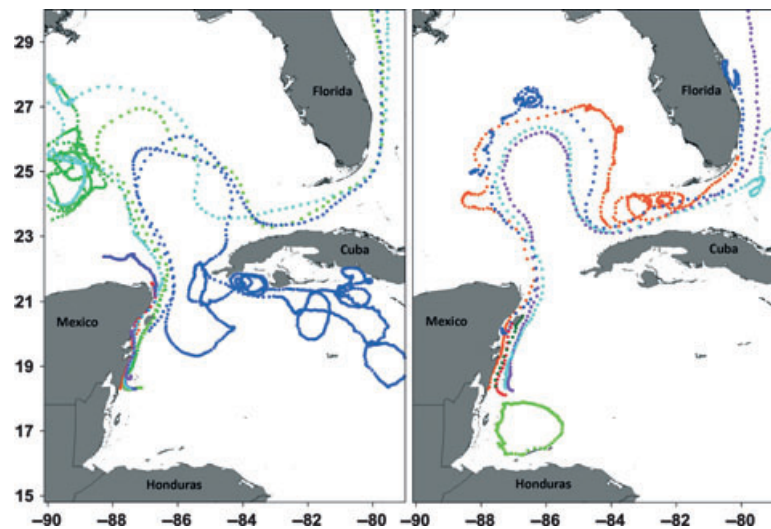
Some evidence of finer-scale circulation features was also apparent in the SADC data. A small cyclonic flow was present south of Cozumel in both years, resulting in southward flow against the coast. In 2007, onshore flow east of the Turneffe Islands appeared to bifurcate into weak northward flow towards Banco Chinchorro, and weak southward flow into the GOH

(Figs 2 and 3). Modeled Hycom outputs (Fig. 1) showed this southward flow turning eastward along the coast of Honduras, forming the cyclonic Honduras Gyre.

Drifters released during both 2006 and 2007 generally tracked northwards along the Yucatan coastal shelf (Fig. 4). In 2006, nine drifters were released, three of which grounded along the Yucatan coast prior



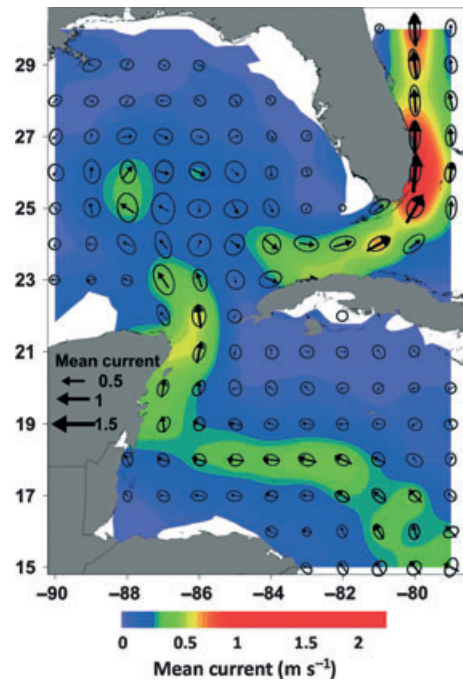
**Figure 4.** Trajectories of nine Lagrangian drifters released in March 2006 (left panel), and seven drifters released in January 2007 (right panel).



to reaching the Yucatan Channel and entering the GOM. Of the remaining six drifters, all were advected rapidly into the GOM. Two of these died north of the peninsula on the Campeche Bank. Two were entrained in the Loop Current, one of which was ejected into the North Atlantic via the Florida Straits in less than 1 month, and one of which returned to the Caribbean Sea, crossing the eastern Yucatan Strait near Cuba. The remaining two drifters were entrained in cyclonic and anticyclonic mesoscale circulation features west of the Loop Current. One of these drifters was finally ejected from the GOM via the Loop Current more than 8 months after its initial deployment. Drifters released during 2007 followed northward trajectories along the MBRS, similar to those released in 2006. One exception was a deployment made in the GOH. This drifter remained in the Honduran Gyre, south of the latitude of impingement, and executed one cyclonic rotation around the gyre before it died 27 days after its deployment (Fig. 4). Drifters released at adjacent locations often ended up showing very different trajectories. Some released very close to the coast tracked northwards and quickly left the study region for the GOM, whereas others released further offshore eventually grounded along the MBRS.

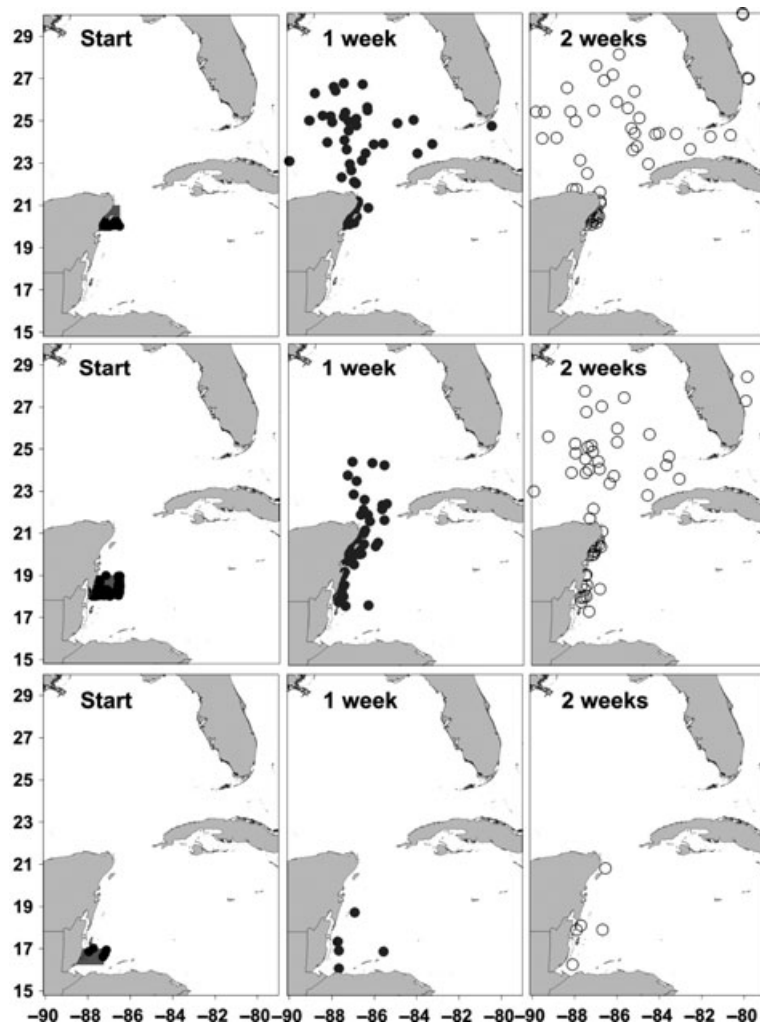
To place the 2 yr of drifter data obtained during 2006 and 2007 into historical context for the region, mean current velocities and directions from 32 yr of drifter data were examined (Fig. 5). Results highlighted the strong northwards flow along the northern MBRS, even at locations close to the coast. Velocities in the GOH and wider Caribbean were considerably less, and contrasted with the intensified flow associated with the Caribbean Current impingement and northward flowing Yucatan Current. Note that the apparent

**Figure 5.** Mean velocity and direction of all drifters to have passed through the study area between 15 February 1979 and 30 September 2011 ( $n = 162$ ), averaged for  $1^\circ$  latitude-longitude squares. Standard deviation ellipses of current velocity are also shown. Areas with no historical drifter tracks are masked in white.



discontinuity of the mean Loop Current as it flows from the Yucatan Channel to the Straits of Florida, is an artifact of averaging velocities within a current that has a highly variable frontal location.

Historically, drifters passing through the Cozumel area of interest (54 in total) tended to continue



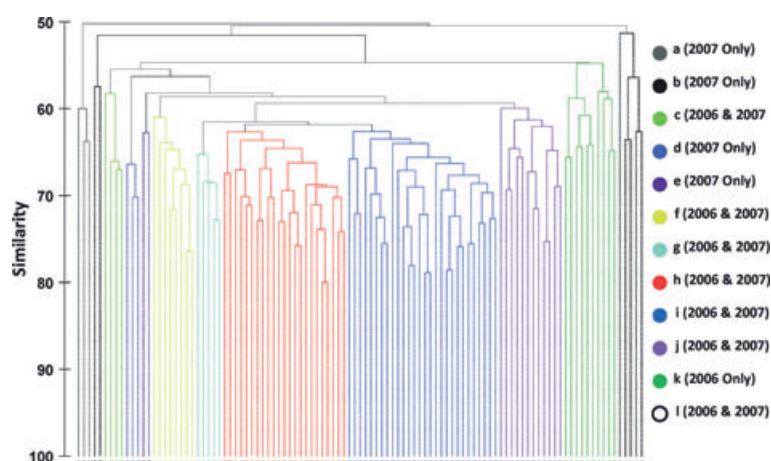
**Figure 6.** Drifters passing through three areas of interest between 15 February 1979 and 30 September 2011: Cozumel, Banco Chinchorro Biosphere Reserve and the western GOH. Positions are shown when the drifter first entered the area of interest (left), 1 week after entering the area of interest (center), and 2 weeks after entering the area of interest (right).

northwards (Fig. 6). After 2 weeks, 15 were retained south of 21°N (27.8%), 34 were in the GOM (63.0%), and five had exited through the Straits of Florida (9.3%). Drifters passing through the Banco Chinchorro area of interest also generally continued northwards along the MBRS. One week after passing through this area of interest, drifters were widely distributed along the northern Yucatan coast, with some entering the GOM. After 2 weeks, 24 of the 56 drifters (42.9%) were retained south of 21°N, usually by grounding north of Bahia de Ascension. Thirty drifters (53.6%) were located within the GOM, and two (3.6%) had continued into the Gulf Stream (passing 81°W). Only five drifters had historically passed through the GOH area of interest, including the southernmost drifter deployed during the 2007 cruise. All five drifters were retained south of 21°N, although four of the five had moved northwards along the MBRS. None of these drifters had reached the GOM after a period of 2 weeks (Fig. 6).

#### Larval fish assemblages

**Composition.** Across all MOCNESS samples, 28 523 larvae were collected during the 2006 cruise, and 51 361 during the 2007 cruise. These larvae came from 113 families during 2006, and 120 families during 2007. Larvae from the family Myctophidae were most abundant overall, comprising 30.8% of all larvae collected during 2006, and 28.2% of larvae from 2007. *Sparisoma* spp. (Scaridae) was the next most abundant taxa in both years, contributing 10.3 and 12.0% to 2006 and 2007 assemblages, respectively. The mesopelagic families Phosichthyidae (5.8% in 2006, 3.7% in 2007) and Gonostomatidae (5.1% in 2006, 5.6% in 2007) were also abundant across both cruises. Eleotriidae larvae were more dominant during 2007 (6.6%) than 2006 (0.8%), as were *Xyrichtys* spp. (Labridae: 3.9% during 2007, 2.7% during 2006). At family level, Myctophidae larvae contributed 28.3% of all larvae collected across both years, followed by Scaridae

**Figure 7.** Cluster analysis with Simprof test on depth-aggregated larval fish assemblages from MOCNESS tows at each sampled station, March 2006 and January 2007. Significant assemblage groups at  $P = 0.01$  are shown by colors, and designated by letters 'a' through 'l'.

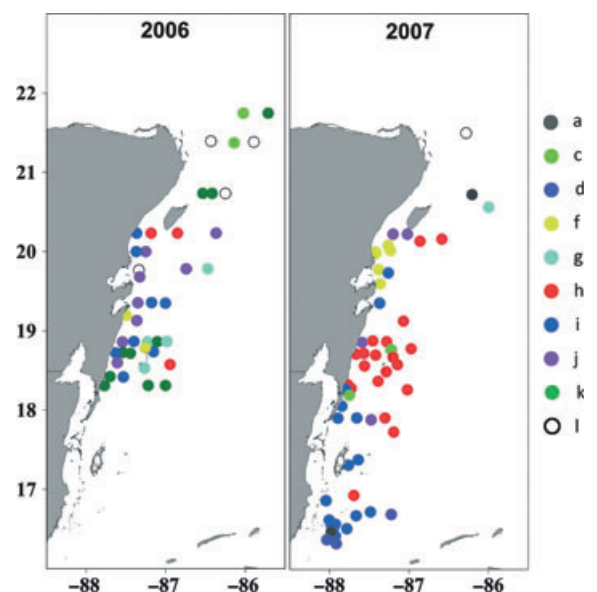


(13.4%), Labridae (6.7%), Gonostomatidae (5.3%) and Gobiidae (5.1%) (Table 1). Most larvae were aggregated to either family or genus level for assemblage analyses. This was due to the impossibility of identifying all larvae to species using genetic and/or visual techniques, and the occurrence of many different species within most fish families in the western central Atlantic Ocean (Table 1).

*Spatial distribution of assemblages.* Depth-aggregated larval fish assemblages were first compared using cluster analysis with a Simprof test. Twelve distinct cluster groups were identified (Fig. 7). Assemblages 'b' and 'e' contained only two samples each and were therefore excluded from further analysis. The remaining 10 assemblage groups were plotted for both 2006 and 2007, to show the distribution of assemblages across the study area (Fig. 8). During 2006, clear spatial separation of assemblage groups was not evident, with assemblages 'g', 'i', 'j' and 'k' distributed across the study area. In 2007, however, a stronger north–south separation was evident, partially due to the southwards extension of sampling. Assemblages 'd' and 'i' were more characteristic of the southern study area, in and around the GOH. Assemblage 'h' was most common midway along the coast, in the vicinity of Banco Chinchorro. Assemblage 'f' was concentrated between Bahia de la Ascension and Cozumel, and assemblage 'j' was found at scattered locations along the reef, at a lower frequency than in 2006 (Fig. 8).

Myctophidae larvae were the most abundant in all of the 10 assemblage groups, contributing between 27.50 and 56.10% (Table 2). *Sparisoma* spp. (Labridae) larvae were the second most abundant in assemblages 'c', 'g', 'h', 'i', 'j' and 'k', contributing between 5.49 and 14.38%. Phosichthyidae, Gonostomatidae, Bothidae and *Xyrichtys* spp. (Labridae) larvae were also

**Figure 8.** Spatial distribution of assemblage groups determined from the Simprof test for March 2006 (left), and January 2007 (right).



important, with Eleotridae larvae abundant in assemblage groups 'a', 'd' and 'f' only.

A CAP ordination among cluster groups showed fairly clear separation among assemblage groups, with a classification success of 77.14% (Fig. 9). This analysis also highlighted taxa which most strongly distinguished between assemblage groups, and thus which were most responsible for the spatial variability observed. CAP axis 1 separated assemblages 'k' and 'l', which were found predominantly during 2006, from the other assemblages. CAP axis 2 clearly separated the GOH assemblages to the top from the northern MBRS assemblages to the bottom (Fig. 9). Of all the taxa identified, *Serranus* spp. (Serranidae), *Xyrichtys* spp. (Labridae) and

**Table 2.** Mean abundance and % contribution of five most abundant taxa in the 10 larval fish assemblage groups, as determined by Simprof test. The number of taxa in each assemblage group is also shown.

Taxa	Mean abundance (per 100 m <sup>3</sup> )	Contribution (%)	Cumulative contribution (%)
Assemblage 'a': 26 taxa			
Myctophidae	4.56	56.10	56.10
Eleotridae	2.86	7.76	63.85
Phosichthyidae	0.68	6.69	70.55
<i>Bregmaceros</i> spp.	1.32	5.09	75.64
Bothidae	0.64	4.80	80.43
Assemblage 'c': 41 taxa			
Myctophidae	1.63	28.02	28.02
<i>Sparisoma</i> spp.	1.01	11.98	40.00
Gonostomatidae	0.50	6.54	46.54
Bothidae	0.46	6.28	52.82
Chlorophthalmidae	0.28	5.10	57.92
Assemblage 'd': 43 taxa			
Eleotridae	4.81	27.50	27.50
Myctophidae	2.75	18.42	45.93
<i>Ctenogobius</i> spp.	2.82	11.07	57.00
<i>Sparisoma</i> spp.	1.21	10.09	67.08
Gonostomatidae	0.93	4.44	71.52
Assemblage 'f': 63 taxa			
Myctophidae	6.09	53.00	53.00
Phosichthyidae	0.69	5.35	58.35
Eleotridae	1.04	5.24	63.59
Gonostomatidae	0.67	4.37	67.96
<i>Ctenogobius</i> spp.	0.75	4.17	72.13
Assemblage 'g': 52 taxa			
Myctophidae	4.77	32.53	32.53
<i>Sparisoma</i> spp.	2.66	14.11	46.64
<i>Ctenogobius</i> spp.	1.09	6.89	53.52
<i>Xyrichtys</i> spp.	0.86	6.05	59.58
Bothidae	1.54	5.40	64.98
Assemblage 'h': 82 taxa			
Myctophidae	3.87	35.79	35.79
<i>Sparisoma</i> spp.	2.12	14.38	50.16
<i>Xyrichtys</i> spp.	1.05	7.14	57.30
Bothidae	0.59	5.02	62.33
Gonostomatidae	0.62	4.91	67.23
Assemblage 'i': 104 taxa			
Myctophidae	5.70	38.76	38.76
<i>Sparisoma</i> spp.	2.38	12.99	51.75
Gonostomatidae	1.13	6.34	58.09
Phosichthyidae	0.98	5.03	63.12
Bothidae	0.53	3.32	66.45
Assemblage 'j': 60 taxa			
Myctophidae	4.20	55.80	55.80
<i>Sparisoma</i> spp.	0.63	5.49	61.29
Phosichthyidae	0.52	5.29	66.57
Gonostomatidae	0.48	5.00	71.57
Gempylidae	0.42	4.21	75.79
Assemblage 'k': 61 taxa			
Myctophidae	2.34	45.78	45.78
<i>Sparisoma</i> spp.	0.63	10.38	56.15
Phosichthyidae	0.39	6.77	62.92
Gonostomatidae	0.47	6.68	69.59

**Table 2.** (Continued)

Taxa	Mean abundance (per 100 m <sup>3</sup> )	Contribution (%)	Cumulative contribution (%)
Bothidae	0.40	5.95	75.54
Assemblage 'l': 28 taxa			
Myctophidae	1.50	40.06	40.06
Gonostomatidae	0.62	15.38	55.44
Phosichthyidae	0.50	9.66	65.10
<i>Sparisoma</i> spp.	0.44	9.12	74.22
Bothidae	0.17	4.04	78.26

*Sparisoma* spp. (Scaridae) were most strongly correlated with CAP axis 1, with all showing positive correlations. Eleotridae larvae, *Gobionellus* spp. (Gobiidae) and Priacanthidae larvae were strongly and positively correlated with CAP axis 2 (Fig. 9).

Priacanthidae and Eleotridae larvae were most abundant in the GOH, with lower numbers collected as far north as Cozumel (Fig. 10). Eleotridae larvae were also abundant near the mouths of Bahía de la Ascension, and Bahía de Chetumal. *Serranus* spp. larvae were concentrated around Banco Chinchorro and the GOH, with low numbers north of Cozumel. Myctophidae larvae were abundant across most of the study area, including stations very close to the coast (Fig. 10). Although concentrations were lower at northernmost stations, they were still the most abundant taxa in this area, reflecting low overall catches north of Cozumel.

*Vertical structure of assemblages.* A CAP ordination of samples from each of the four depth strata showed a general gradation from shallow to deep samples along CAP axis 1, with a classification success of 55.7% (Fig. 11). Correlation of more abundant taxa (>1% contribution to total concentrations) with CAP axis 1 highlighted a progression from deeper-living taxa (*Bregmaceros* spp., *Xyrichtys* spp., Phosichthyidae) to more shallow-living taxa (Bothidae, Carangidae) (Fig. 12). The depth of the abundance-weighted mean depth for *Bregmaceros* spp. was approximately 80 m, whereas for Carangidae it was between 15 and 30 m depth, with other common taxa found between these ranges (Fig. 12). Some taxa showed evidence of diel vertical migration, with *Xyrichtys* spp. Paralepididae and Eleotridae larvae found 10–20 m deeper during the day than at night. In contrast, Carangidae and *Thalassoma bifasciatum*, in particular, were found at deeper depths during the night than during the day.

A comparison of two taxa from the same family (*T. bifasciatum* and *Xyrichtys* spp.: Labridae) showed considerable differences in vertical distributions (Fig. 13). *Thalassoma bifasciatum* was more abundant



Figure 9. Canonical analysis of principal coordinates (CAP) on depth-aggregated larval fish assemblages (left). Assemblage groups from Simprof test are shown by colors, and taxa most strongly correlated with CAP axis 1 (top right), and CAP axis 2 (bottom right) are also shown.

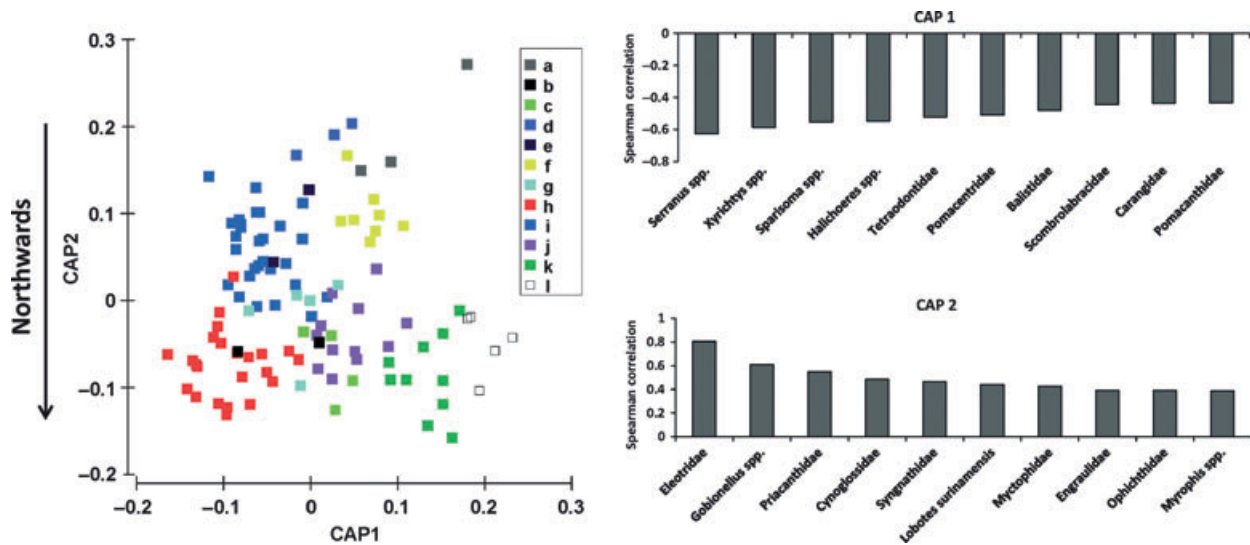
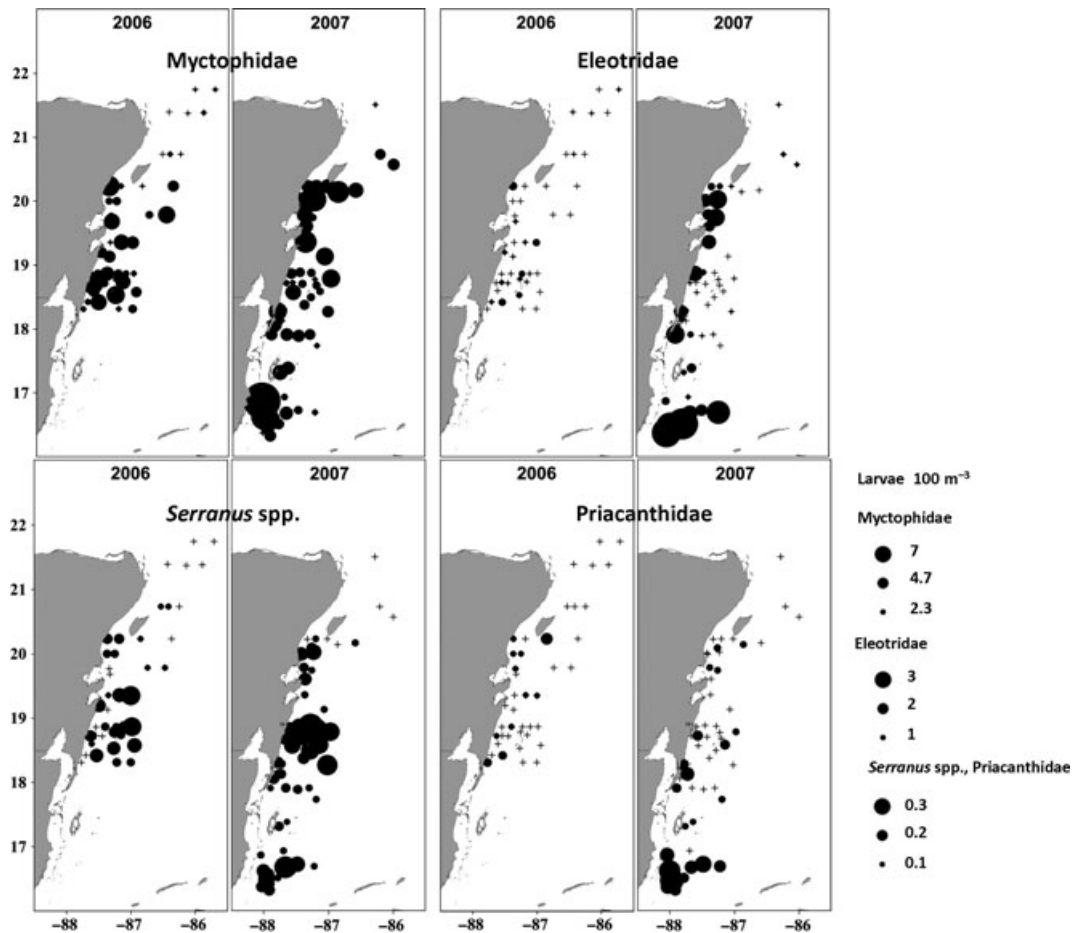


Figure 10. Spatial distribution of depth-aggregated concentrations of selected larval fish taxa in March 2006 and January 2007.



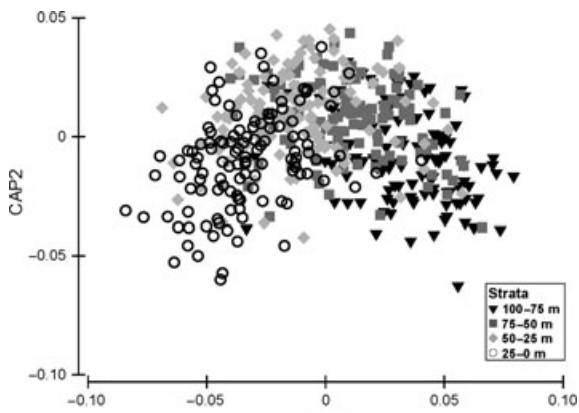
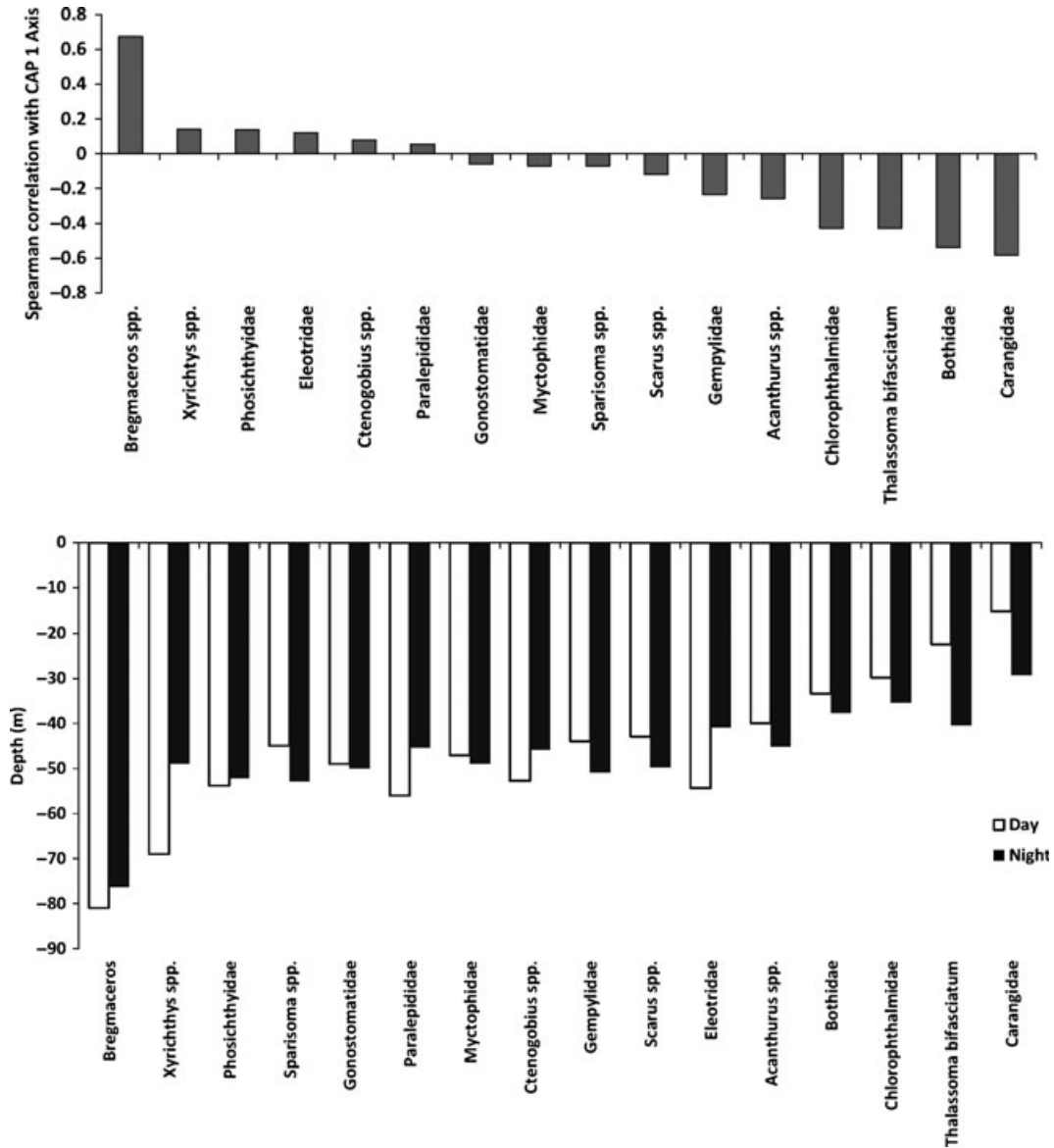
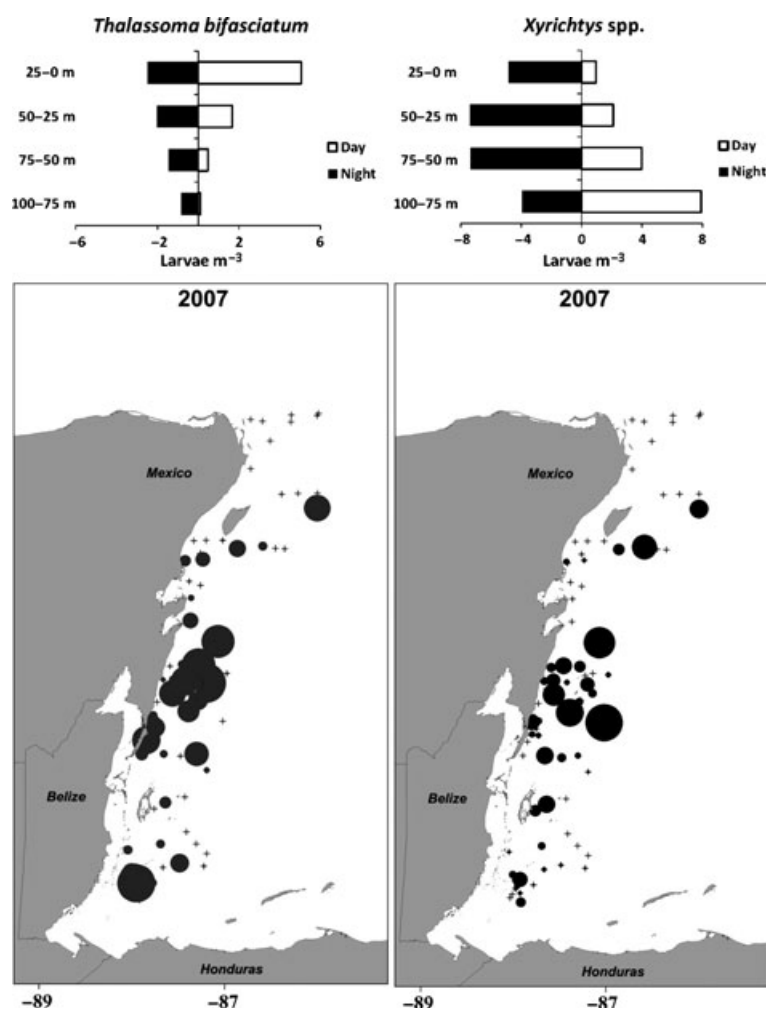


Figure 11. Canonical analysis of principal coordinates (CAP) on larval fish assemblages from each strata of the MOCNESS net at each sampled station in March 2006 and January 2007. The four depth strata sampled by the MOCNESS net are shown by different symbols.

Figure 12. Correlations of common larval fish taxa with CAP axis 1 from the ordination shown in Figure 11 (top). Abundance-weighted mean depths of common taxa, for both day and night samples, are shown at bottom.





**Figure 13.** Mean vertical distribution (top), and spatial distribution during January 2007 (bottom) of two taxa from the family Labridae.

in the upper water column, especially during the day. In contrast, *Xyrichtys* spp. were distributed at deeper depths during the day, with both taxa found throughout the water column at night. However, larvae of both taxa were found throughout the study area, particularly during 2007 (Fig. 13). The deeper-living *Xyrichtys* spp. thus did not show a spatially restricted distribution compared with the shallower-living *T. bifasciatum*.

Myctophidae was the most speciose family, with 29 species identified from 13 genera (*Bentosema*, *Ceratoscopelus*, *Diaphus*, *Hygophum*, *Lampadena*, *Lampanyctus*, *Lepidophanes*, *Lobianchia*, *Myctophum*, *Nannobranchium*, *Notolychnus*, *Notoscopelus* and *Symbolophorus*). Although Myctophidae larvae were included in assemblage analyses at family level, due to <1% being identified past genera in 2007, 30.9% of myctophids were identified to species in 2006. The vertical distributions of the 10 most abundant myctophid species from 2006 (constituting 88% of total species-level Myctophidae abundances) were examined further. A strong separation was evident

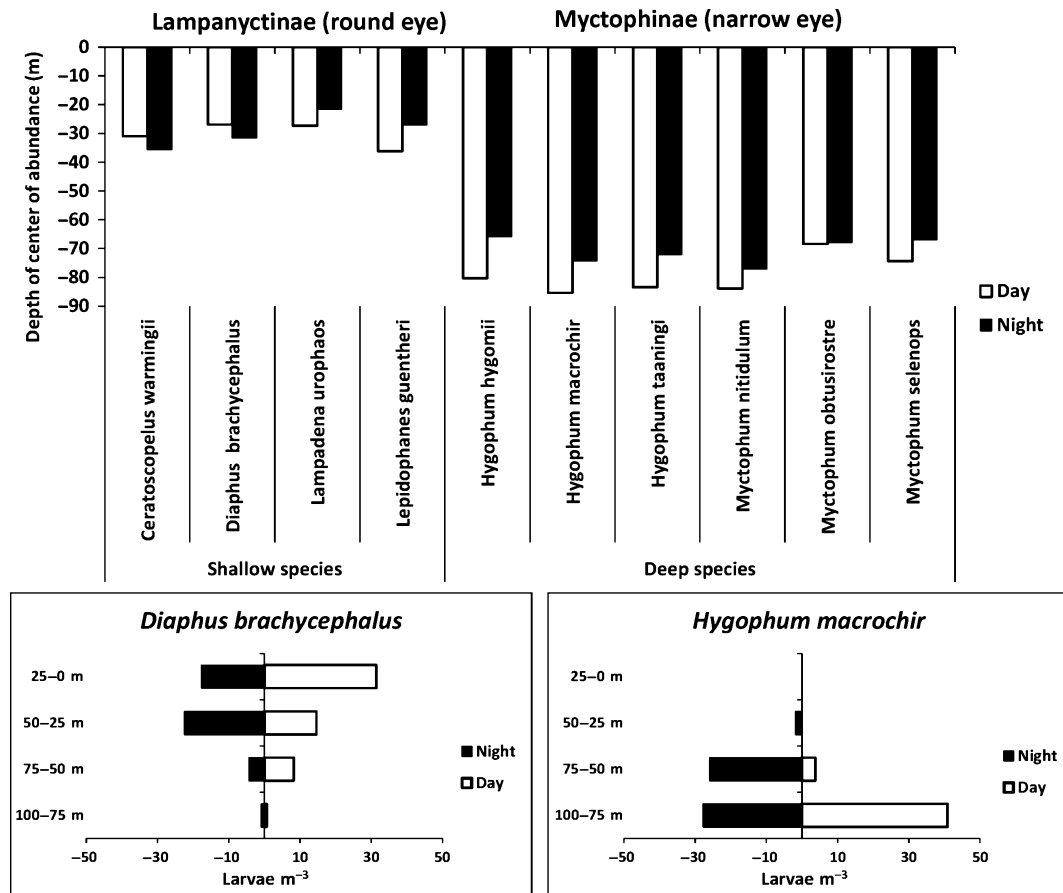
between four species from the genera *Ceratoscopelus*, *Diaphus*, *Lampadena* and *Lepidophanes*, and six species from *Hygophum* and *Myctophum* (Fig. 14). The former group all belonged to the sub-family Lampanyctinae, or round-eyed myctophids, and showed generally shallow abundance-weighted mean depths at around 30 m depth. In contrast, the latter group all belonged to the sub-family Myctophinae, or narrow-eyed myctophids, and these larvae had abundance-weighted mean depths of between 65 and 85 m depth. Depth distributions of two representative species, *D. brachycephalus* and *H. macrochir*, showed that overlap between shallow and deep-living Myctophidae larvae would be minimal during both day and night (Fig. 14).

## DISCUSSION

### *Spatial assemblage structure and oceanography*

This study examined the horizontal and vertical structure of larval assemblages, in relation to oceanographic

**Figure 14.** Abundance-weighted mean depths of 10 Myctophidae species during 2006 from day and night samples (top), and mean vertical distributions of a shallow-living species (*Diaphus brachycephalus*) and a deep-living species (*Hygophum macrochir*).



structure between 2 yr of sampling. The dominant taxa recorded were generally consistent with other studies of larval fishes in the region. Richards (1984) described results from one of the first broad-scale ichthyoplankton surveys of the Caribbean Sea, although sampling did not extend as close to the MBRS as in this study. He showed that mesopelagic species were the most abundant taxa, even at locations close to the coast, and that larvae of reef-associated families (Labridae, Scaridae, Serranidae) were distributed across the study area. Similarly, Sanchez Velasco and Flores Coto (1994) found a mesopelagic dominated assemblage to the east of the northern Yucatan Peninsula, with more neritic species to the north, in regions of lower current velocities. Several previous studies of very nearshore waters and coastal lagoons found that small benthic species from families such as Gobiidae, Tripterygiidae and Clupeidae were most abundant in the assemblages sampled (Vásquez-Yeomans *et al.*, 1998, 2011; Vásquez-Yeomans and Richards, 1999; Ordóñez-López, 2004; Alvarez-Cadena *et al.*, 2007).

Results from the current study also showed a general dominance of mesopelagic families, such as Myctophidae, Gonostomatidae and Phosichthyidae. Some reef-associated taxa, such as those from the families Scaridae, Labridae, Gobiidae and Serranidae, were abundant across the study area in both years sampled. In contrast, Tripterygiidae and Clupeidae were rare, likely reflecting more inshore adult distributions and alternate spawning behaviors such as benthic eggs (Ishihara and Tachihara, 2011).

Sampling during 2006 concentrated on the northern MBRS area, whereas sampling in 2007 extended southwards into the GOH. During 2006, there was little spatial structure observed within larval fish assemblages, whereas in 2007, assemblages from the GOH, Banco Chinchorro, and Bahía de la Ascensión area were distinct. These differences were largely due to spatial patterns of abundance in the larvae of several inshore fish taxa, such as Eleotridae, *Gobionellus* spp. and Priacanthidae. The majority of Eleotridae larvae identified further were *Dormitator maculatus* (87%),



whereas most Priacanthidae larvae were *Pristigenys alta* (96%). *Dormitator maculatus* and *Gobionellus* adults are mostly found in estuaries (Teixeira, 1994; Nordlie, 2012). *Pristigenys alta* is also a benthic, reef-associated species (Starnes, 1988). High abundances of these larvae within the GOH region suggest the presence of a more coastal water mass, sourced from an inshore area. Although spatially restricted, SADCP and drifter data suggested a cyclonic circulation, similar to that observed by Cherubin *et al.* (2008) and Soto *et al.* (2009). These authors note that considerable freshwater runoff may be discharged into the GOH from October to February, and entrained into the cyclonic gyre.

In contrast to the southern MBRS, the northern portion of the study area was subject to strong northward flow in both 2006 and 2007, consistent with previous studies from the region (e.g., Centurioni and Niiler, 2003). Historical drifter tracks suggested that rapid northward transport mechanisms along the Yucatan Peninsula are common north of Banco Chinchorro, with drifters located further north along the MBRS having higher probabilities of being lost into the GOM and Gulf Stream. Larval assemblages in the northern MBRS contained both mesopelagic families (Myctophidae, Phosichthyidae) and more benthic and reef-associated taxa (*Sparisoma* spp., Bothidae). Larval fish assemblage results thus partially supported our initial hypothesis that the Caribbean Current would introduce an easily characterized mesopelagic larval fish assemblage to the MBRS region, and that this would be distinct from a more reef-associated assemblage found outside the influence of the current. While reef- and estuarine-associated taxa were more abundant in the GOH area, outside the region of influence of the Caribbean Current, mesopelagic families were dominant across the majority of the study area in both years sampled. Due to the narrow continental shelf, and strong northwards flow along the coast, even stations less than 10 miles from the coast contained mesopelagic larval assemblages.

Northern MBRS larval assemblages were thus likely a product of shoreward intrusions of the Caribbean Current/Yucatan Current, and subsequent mixing and northward entrainment of more coastal water masses. Previous studies of transport processes and connectivity along the MBRS suggest some separation between the GOH region and the more northern reef areas (Cowen *et al.*, 2006; Heyman *et al.*, 2006; Paris *et al.*, 2007; Andras *et al.*, 2011). However, the degree of potential connectivity between the southern and northern MBRS appears to vary considerably by organism and species (Kool *et al.*, 2010; Villegas-Sanchez

*et al.*, 2010; Foster *et al.*, 2012), with large interannual variability in recruitment mechanisms likely (Hogan *et al.*, 2010).

#### Vertical structure of assemblages

Fish larvae frequently show behaviors which strongly affect their dispersal trajectories (Kingsford *et al.*, 2002). Vertical migration through the water column exposes larvae to different currents at different depths, with some reef fish larvae utilizing onshore flows to facilitate transport to settlement habitats (Kingsford and Choat, 1989; Cowen and Castro, 1994). However, current velocities measured during this study were similar throughout the upper 100 m of the water column, suggesting that both shallower and deeper living larvae would have been subject to low retention conditions. Two Labridae taxa with distinct vertical distributions were widely distributed across the study area, although concentrations of both were highest around Banco Chinchorro. Richards (1984) also found that Labridae larvae, including *Xyrichtys* spp., were abundant in deeper waters far from shore, despite being associated with reef habitats as adults. Our second study hypothesis, that the vertical distribution of reef-associated species would influence their dispersal, with shallower-living larvae showing wider spatial distributions, and increased northwards entrainment into the Caribbean Current, was therefore not supported. However, our sampling only extended to 100 m depth. Had taxa with deeper depth distributions been examined, a larger difference between shallow and deep-living larvae might have been observed.

Ten Myctophidae species collected in 2006 also had strongly distinct vertical distributions between sub-families; however, larvae of mesopelagic species are much more likely to use vertical migration behavior to target prey items than to facilitate retention (Sabates and Saiz, 2000). This suggests that the vertical structure observed in larval assemblages was likely a product of both feeding and settlement behaviors, which differ strongly among taxa with different life history strategies.

#### Implications for connectivity

Results from this study suggest that the planktonic environment along much of the MBRS is characterized by low retention conditions. Although we present only 2 yr of samples, analyses of historical data both here and elsewhere (Centurioni and Niiler, 2003) tend to support this conclusion. Given this low-retention environment, adult spawning strategies and larval behaviors may be highly influential in determining the dispersal of pelagic stages, and the eventual

contribution of self-recruitment to population replenishment. Although strong northward transport was present along much of the northern MBRS, smaller-scale eddy features were observed in some areas, such as to the south of Cozumel. This region contained a distinct larval fish assemblage (assemblage 'f') during 2007. Adults of some reef fish species may choose sites of strong eddy generation along the MBRS for spawning (Karnauskas *et al.*, 2011), potentially enhancing larval retention. A combination of spatially and temporally targeted spawning effort, and larval behaviors, may thus combine to promote some degree of larval retention along the MBRS, even though a strong boundary current flows close to the coast. However, the potential for self-recruitment in the northern MBRS is generally predicted to be quite low (Cowen *et al.*, 2006). Recruitment from upstream sources is therefore likely to be important to the maintenance of MBRS fish populations (Cowen *et al.*, 2006; Hogan *et al.*, 2012).

Drifter tracks suggested that transport times between the northern MBRS and the Florida Keys could be as short as 7–10 days. Once larvae reach the Florida Straits, Loop Current frontal eddies may provide effective delivery mechanisms to inshore reefs (Sponaugle *et al.*, 2005). Larvae of reef fish taxa such as *Sparisoma* and *Xyrichtys* are often collected within the Loop Current in the northern Gulf of Mexico (NOAA-NMFS, unpublished data). These larvae were found far from any coastal waters, and most likely came from an upstream source such as the MBRS. However, despite the probable dispersal of reef fish larvae from the MBRS to the Florida Keys region and beyond, there is little evidence of strong genetic connectivity between the two regions (Richards *et al.*, 2007; Kool *et al.*, 2010; Andras *et al.*, 2011). Although high abundances of reef fish larvae were observed within the Caribbean Current/Yucatan Current, it is unclear how many of these larvae may survive to recruit to distant reefs.

Overall, results described here showed the strong influence of the Caribbean Current and Yucatan Current in structuring regional larval fish assemblages. There was some evidence of a separation between the GOH region, which is characterized by much weaker current velocities, and the northern MBRS. The GOH region may therefore act as an important retention area for pelagic larvae, whereas conditions further north favor dispersion. The small cyclonic eddy south of Cozumel may also act as an area of local larval retention. Although highly distinct patterns of vertical distribution were noted among closely related taxa, current strengths in the northern MBRS were similar

throughout the depth range sampled for larvae, and both shallow- and deep-living larvae were often broadly distributed along the reef tract. The collection of reef fish larvae within regions of strong northward flow reconfirms the high connectivity potential between the MBRS and the Florida Keys; however, much remains to be discovered about the contribution of larvae from distant sources to both regions.

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