Environmental Development xxx (2017) xxx-xxx

Contents lists available at ScienceDirect

Environmental Development

journal homepage: www.elsevier.com

Linking oceanographic processes and marine resources in the western caribbean sea large marine ecosystem subarea

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ARTICLE INFO

Keywords:
Marine resources
Oceanographic processes
Mesoscale
Large marine ecosystem
Mesoamerican reef
Caribbean

ABSTRACT

The western Caribbean, a subarea of the Caribbean Sea Large Marine Ecosystem, includes the Mesoamerican Barrier Reef System, the Yucatan Basin, the Cayman Basin and the Yucatan Channel. Here we discuss the main oceanographic features of the western Caribbean Sea and present some examples of marine resources distributed throughout the western Caribbean Sea LME subarea along different spatial scales. Particular attention is given to their planktonic stages when physical oceanographic features (such as eddies and gyres, or current systems) can operate either as forces that promote larval dispersal or as barriers enhancing larval retention, as this determines their connectivity. Bluefin tuna, the early life stages (eggs and larvae) of reef fish, the Caribbean Spiny lobster, and the Queen conch are presented as examples. Dispersal distances depend on the oceanographic phenomena, with larger dispersals expected where intense currents occur, such as in the Yucatan Current. Conversely, retention can be expected in the presence of gyres such as the Honduras Gyre and Yucatan Basin eddies. There is a growing body of evidence supporting the need for a multi-scale approach in order to understand the complexity of LMEs. Moreover, the connectivity between regions in the western Caribbean Sea LME subarea, as shown by the exchange of marine resources and physical oceanographic processes, requires an international policy that supports collaborative efforts to monitor the dynamics of coastal and oceanic habitats together with marine resources.

1. Introduction

Within the Caribbean Sea Large Marine Ecosystem (LME) (Richards and Bohnsack, 1990; Fanning et al., 2011), there is the western Caribbean, a dynamic subarea that includes the Mesoamerican Barrier Reef System, the Yucatan Basin, the Cayman Basin and the Yucatan Channel (Fig. 1). This is the region where the Caribbean circulation system connects to the Gulf of Mexico through the Yucatan Channel. The western Caribbean holds a large variety of habitats, a high marine biodiversity, and several fishery resources. These biotic components and inherent biological processes are strongly influenced by oceanographic processes.

In some circumstances, oceanographic processes and marine resources are clearly related, for instance with physical processes driving the dispersion of marine planktonic larval stages. Research on marine resources tends to be focused on the adult and juvenile stages of species, leaving aside the planktonic stages that are present in the majority of marine resources (Sale, 2002; Richards, 2006; Hixon, 2011). Since the early years of fisheries research, it has been hypothesized that planktonic stages (eggs and larvae) represent a "critical period" due to the fragility of these life

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http://dx.doi.org/10.1016/j.envdev.2017.01.004
Received 8 November 2016; Received in revised form 8 January 2017; Accepted 23 January 2017
Available online xxx
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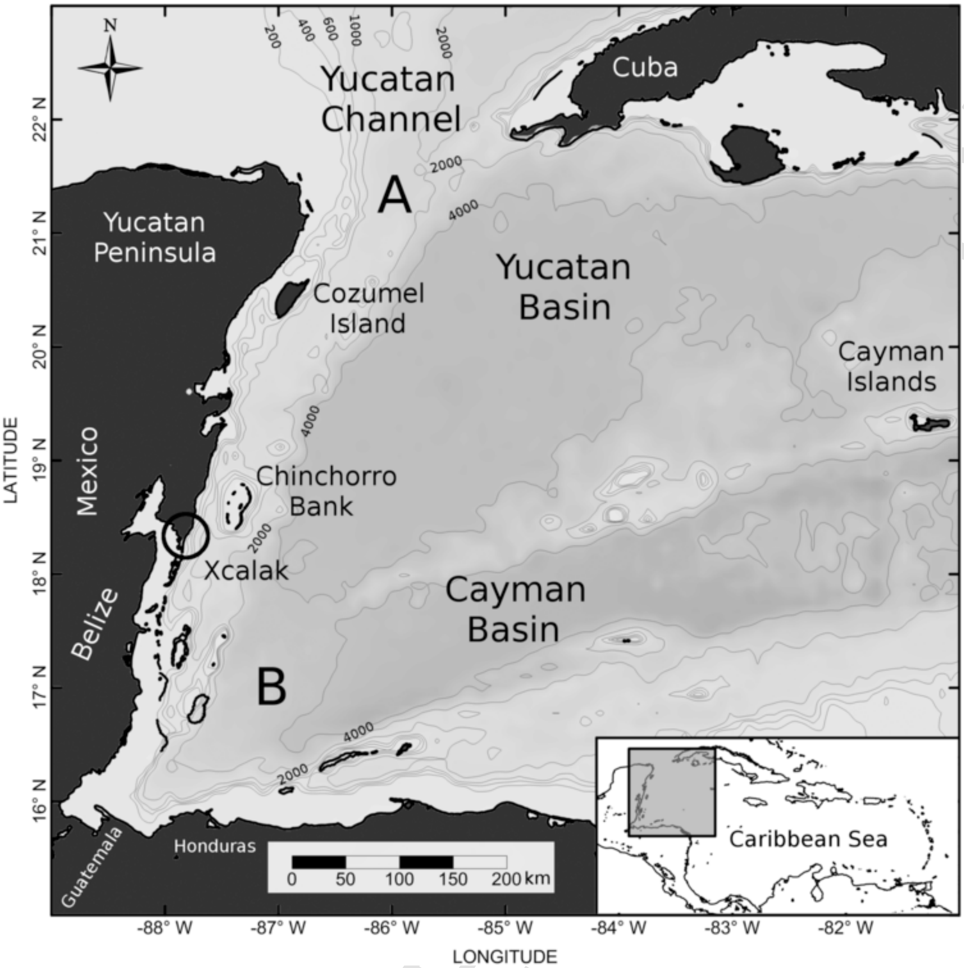

Fig. 1. Western Caribbean Large Marine Ecosystem subarea of the Caribbean Sea LME. Circle shows the position of a current meter located at Xcalak, Mexico. A and B show the position used to calculate dispersal distances referred in Section 3.3.

stages that determine the strength of the year class (Hjort, 1914). During the 1970s, a new perspective on marine research was proposed, dealing with the recruitment processes of marine resources as they relate to early life stages (Lasker, 1975; Houde, 2008). More recently, with a new millennium approach, the interest has shifted to marine metapopulations (Kritzer and Sale, 2004) and connectivity (Hixon, 2011; Cowen et al., 2006; Kough et al., 2013, 2016). At present, the role of planktonic life stages has been widely accepted as one of the most important stages, allowing the flow of genes and enhancing population connectivity through dispersal by oceanic and coastal currents (Botsford et al., 2009; Planes et al., 2009; Cowen et al., 2006; Cowen and Sponaugle, 2009; Salas et al., 2010). Thus, physical oceanographic features (such as eddies and gyres, or predominant current systems) can operate either as forces that promote larval dispersal or as barriers enhancing larval retention. Hence, the challenging problem is to ascertain the physical mechanisms and interaction between the oceanographic processes and the reproductive strategies of the marine resources which allow enhanced survival of larval stages by reducing predation and allowing them to reach nursery habitats for shelter and sufficient food supply (Levin, 2006; D'Alessandro et al., 2007; Houde, 2008). Oceanographic processes on multiple scales lead to large variability in the main oceanic current systems influencing the larval distribution of marine resources. Therefore, the understanding of physical oceanographic processes and their relationship with early life history is key to the effective and sustainable management of marine resources in the western Caribbean LME (Fogarty and Botsford, 2007; Kough et al., 2013).

The underlying premise of this article is that the major oceanographic processes that occur in the western Caribbean Sea LME subarea define the connectivity between habitats, by either promoting dispersal or acting as barriers that restrict the propagules of the marine resources. Here we will present some examples of the most representative marine resources distributed throughout the Caribbean and their link with oceanographic processes. Particular attention will be given to the early life stages (eggs and larvae) of reef fish and two economically important benthonic marine resources, namely the Caribbean Spiny lobster and the Queen conch.

2. Main oceanographic features of the western caribbean sea LME

The region's oceanographic circulation is dominated by the western branch of the subtropical gyre, referred to as the Caribbean Current as it travels through the Caribbean Sea as a zonal stream from the Lesser Antilles with speeds of 0.5–1.0 m/s (Kinder, 1983; Schmitz and McCartney, 1993; Moers and Maul, 1998; Andrade and Barton, 2000; Johns et al., 2002). When the Caribbean Current passes though the Cayman Basin it is referred to as the Cayman Current (CC), and when the CC approaches the coast of the Yucatan Peninsula it becomes the Yucatan Current (YC) as it turns to the north (Badan et al., 2005; Carrillo et al., 2015) (Fig. 2). The YC intensifies in its northward flow and enters the Gulf of Mexico through the Yucatan Channel with speeds of up to 2 m/s (Carrillo et al., 2015). Once in the Gulf of Mexico, the YC becomes the spatially variable Loop Current which ultimately exits the Gulf though the Straits of Florida as the Florida Current. Once free of the confines of the Straits, the current flows into the North Atlantic Ocean as the Gulf Stream (Mooers and Maul, 1998; Gallegos and Czitrom, 1997; and others).

These currents are highly variable in space and time due to the frequent passage of mesoscale eddies (Carton and Chao, 1999; Murphy et al., 1999; Andrade and Barton, 2000; Oey et al., 2003; Centurioni and Niiler, 2003; Ezer et al., 2005). Studies of surface drifter tracks by Richardson (2005) have noted the prevalence of mesoscale eddies in the fluctuation and circulation of currents in this region, and their important implications for the dispersal of fish larvae. Observations (Centurioni and Niiler, 2003; Richardson, 2005; Cetina et al., 2006; Carrillo et al., 2015) and modeling results (Ezer et al., 2005; Briones-Fourzán et al., 2008) indicate that eddies have a significant impact on determining the direction and strength of flow of the CC and YC. Analysis of historical drifter and satellite data has shown periods when the CC impinges against the Yucatan Peninsula and bifurcates into northeast and southwest branches at a latitude approximately perpendicular to the coastline of the central Yucatan Peninsula, result-

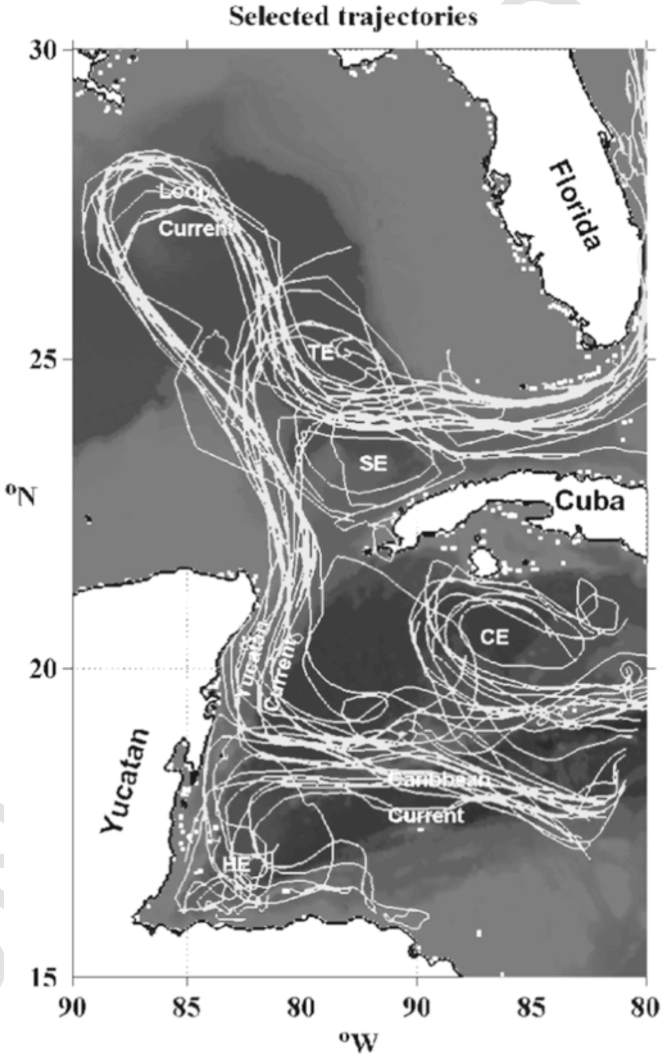

Fig. 2. Caribbean, Yucatan, and Loop Current circulation from the western Caribbean to the Florida Straits, as depicted by drifter trajectories. The figure shows recurrent eddies, two in the Caribbean Sea, the cyclonic Honduras Eddy (HE), an anticyclonic Cayman Eddy (CE), and two in the Gulf of Mexico associated with the Loop Current, the cyclonic Tortugas Eddy (TE) and an anticyclonic eddy just north of the northwest end of Cuba (SE).

ing in southward flow through Chinchorro Channel (Fig. 2). The impingement of the CC upon the coast may be caused by the passage of mesoscale eddies that cause it to meander (Ezer et al., 2005; Carrillo et al., 2015). This causes mesoscale variability along the 1000 km-long reef tract (Badan et al., 2005; Ezer et al., 2005; Cetina et al., 2006; Carrillo et al., 2015). The latitude at which the CC meets the continental coast fluctuates up to 3° latitude north and south from the Mexico-Belize border, and this fluctuation determines the circulation along the Mesoamerican Barrier Reef System (MBRS) (Badan et al., 2005; Ezer et al., 2005; Cherubin et al., 2008; Carrillo et al., 2015). The latitude of impingement of the CC separates three main dynamical environments: a northern region with a well-defined YC, a southern region with weak southward and/or variable flow, and a transitional region where the CC impinges upon the coast (Carrillo et al., 2015). The northern portion of the MBRS shows a generally strong northwesterly current sweeping along the southern coast of Quintana Roo, Mexico, turning northward to form a strong flow along the Yucatan coast. Shipboard acoustic Doppler current profiler (ADCP)-derived flow fields and CTD analyses indicated a strong, generally northward flow, especially from Cozumel north (see Carrillo et al., 2015 and Carrillo et al., 2016 for a detailed description of the observational data and methods, including satellite-tracked surface drifter deployments). Though some variations in the current were noted south of Cozumel, the northward flow extended from Banco Chinchorro to southeast of Cozumel, with indications of a westward flow at depths >75 m (Fig. 3). This westward flow is part of an observed submesoscale eddy-like feature that will be described in more detail later in this section (Figs. 3–5).

The transitional region is characterized by the impingement of the CC on the coast. In this region, most of the CC turns west with strong onshore flow at the Belize-Mexico border, and the bifurcation of this current with a divergence zone results in a southerly flow along the coast of Belize and a northward flow along the coast of Mexico (Carrillo et al., 2015). Measured current flow fields indicate a strong northward flow throughout the Xcalak Channel, and west and south of Banco Chinchorro. Strong northward flow continues further north along the coast. On a finer scale, the flow regime around Banco Chinchorro and the area between the atoll and mainland is much more complex. This can be observed from satellite-tracked surface drifters dropped in the Xcalak – Banco Chinchorro Channel and in an east-west line beginning at 87° W (Fig. 4). Initially, the trajectories of the drifters moved westward, before tracking northwards past the Yucatan Peninsula and into the Gulf of Mexico. The influence of the bathymetry is evident, and westward and southwestward flow is observed to the south of the atoll, indicating either the presence of the northern edge of a cyclonic gyre located north of Turneff, Belize and/or a strong westward bend in the CC (Fig. 4).

The southern MBRS region is characterized by a flow regime dominated by a large cyclonic gyre located north of Honduras (the Honduras Gyre). The trajectory from a surface drifter deployed in the gyre in 2007 clearly illustrated the cyclonic nature of this feature (Fig. 4). Concurrent with the development of this gyre was a shift in the direction of the CC. A southward current was measured south of this feature along the coast of Belize. This shift in current direction may have been caused by increased vorticity associated with the development of the eddy north of Honduras at 17°N. As this cyclonic gyre developed, it appeared to pull water from the CC westward and southward. Both the initial strong northward flow and the gyre are visible in the satellite-tracked drifter deployments (Fig. 4). This major shift in the flow of the CC occurred in less than seven days. During this time period, current flow just south of Banco Chinchorro shifted from a northward direction to due west, as measured by shipboard ADCP.

Submesoscale eddies can also be observed in the circulation of the MBRS, with an unusual southward current located southeast of Cozumel, where satellite imagery, drifter tracks, and shipboard ADCP observations indicated a probable cyclonic flow pattern. Southward flow was also

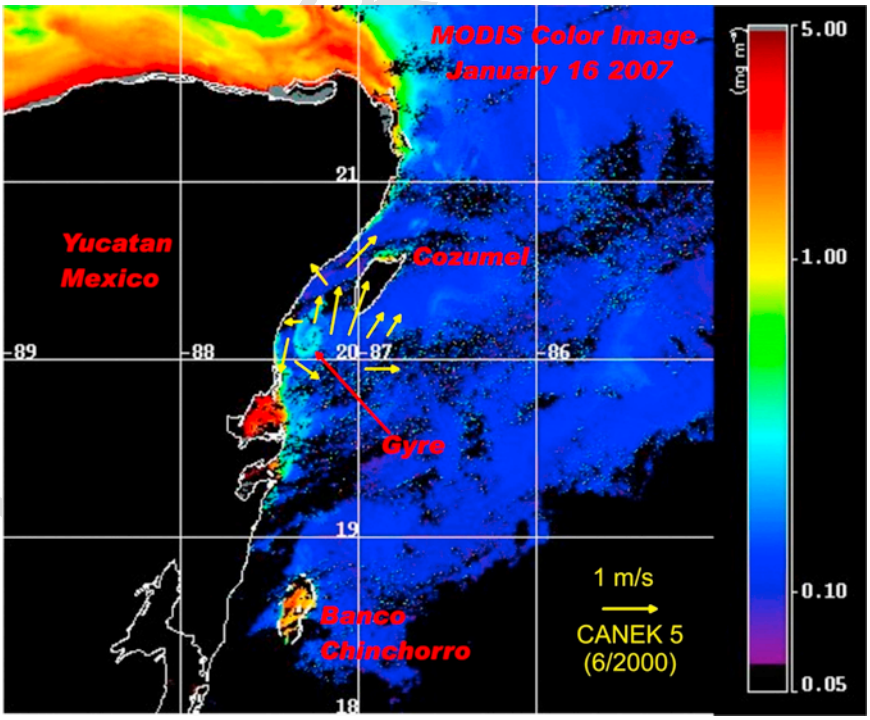

Fig. 3. MODIS color image of cyclonic gyre south of Cozumel, and near surface currents from shipboard ADCP (yellow arrows) from CANEK 5 campaign. Image from Jan 17, 2007.

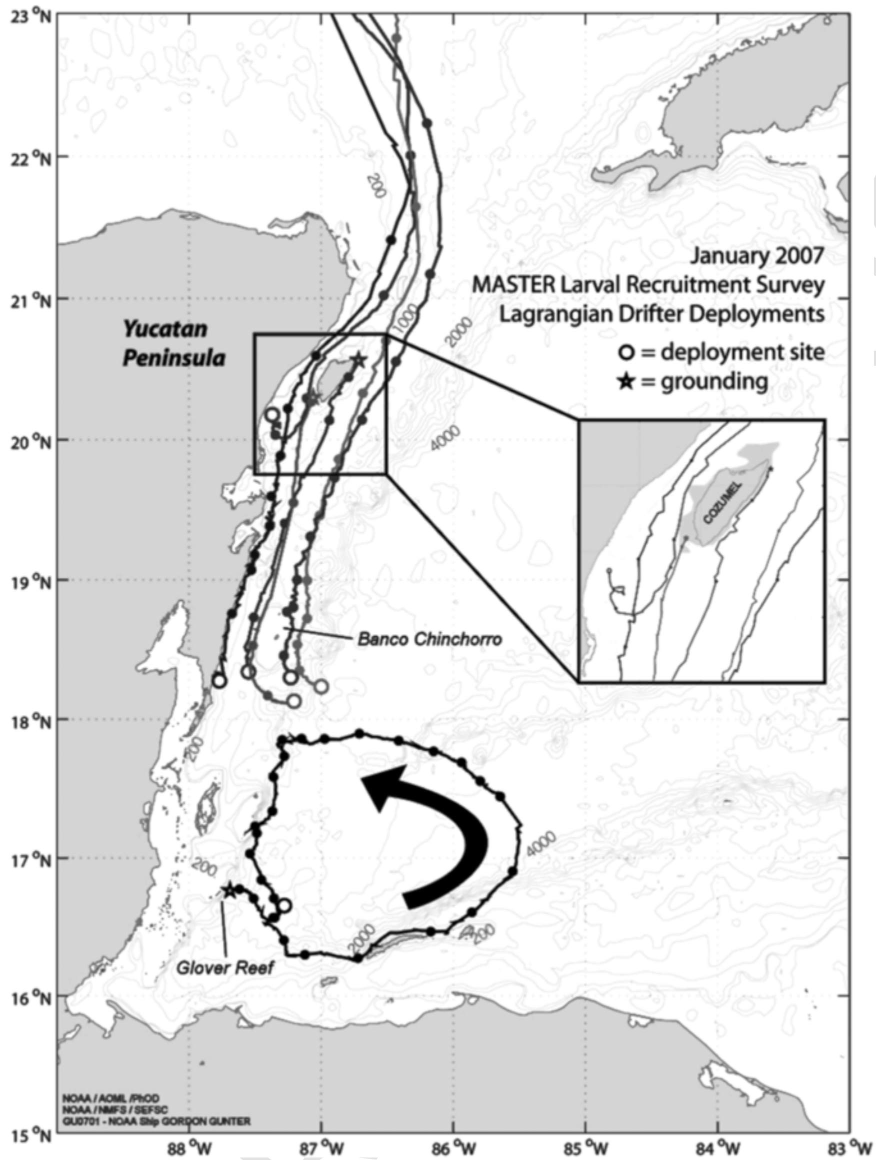

Fig. 4. Five ARGOS drifter deployments south of Banco Chinchorro and one in the Honduras Eddy during the 2007 MASTER Larval Recruitment Survey. A close-up shows the drifter tracks close to Cozumel Island.

noted southwest of Cozumel (Figs. 3–5). The MODIS color image and ADCP current measurements (Figs. 3 and 5) showed the presence of a cyclonic eddy of as yet undetermined vorticity and variability. Shipboard ADCP measurements from several cruises in the area also showed evidence of this eddy (see Carrillo et al., 2015). Analyses of this feature showing the depth of the 12 °C isotherm indicates significant cyclonic flow just north of Punta Allen, and southwest of Cozumel (Fig. 5). The drifter followed the cyclonic flow before becoming entrained in the strong northward flow in the Cozumel Channel. Due to subsequent cloudy conditions, it was not possible to continue tracking this feature using remote sensing. It has been suggested that this submesoscale feature (which we will henceforth refer to as the Cozumel eddy) is the result of interactions between the YC and the local bathymetry (Carrillo et al., 2015).

The circulation in the Yucatan Basin (with depths of 4600 m) is dominated by mesoscale and submesoscale eddies (Fig. 2). These eddies are both cyclonic and anticyclonic with periods up to 30 days, and are the product of the interaction between the Cuban Countercurrent and the CC (Claro and Reshetnikov, 1994; Pérez-Santos et al., 2015). The Cuban Countercurrent is a southward flow originating in the eastern part of the Yucatan Channel with mean speeds of 0.25–0.30 m/s and a maximum of up to 1 m/s (García et al., 1991). During winter it extends southeastward from Cabo San Antonio (Cuba) to the Cayman Islands (García et al., 1991). The rest of the year, it flows eastward along the shallow waters of the Gulf of Batabano, on the southwestern Cuba shelf.

The interaction between the topography and the currents generates an important effect on the circulation. For instance, for the most part the eastern coast of the Yucatan Peninsula has a narrow continental shelf (< 10 km); however, it widens near the northern tip of the Yucatan Peninsula.

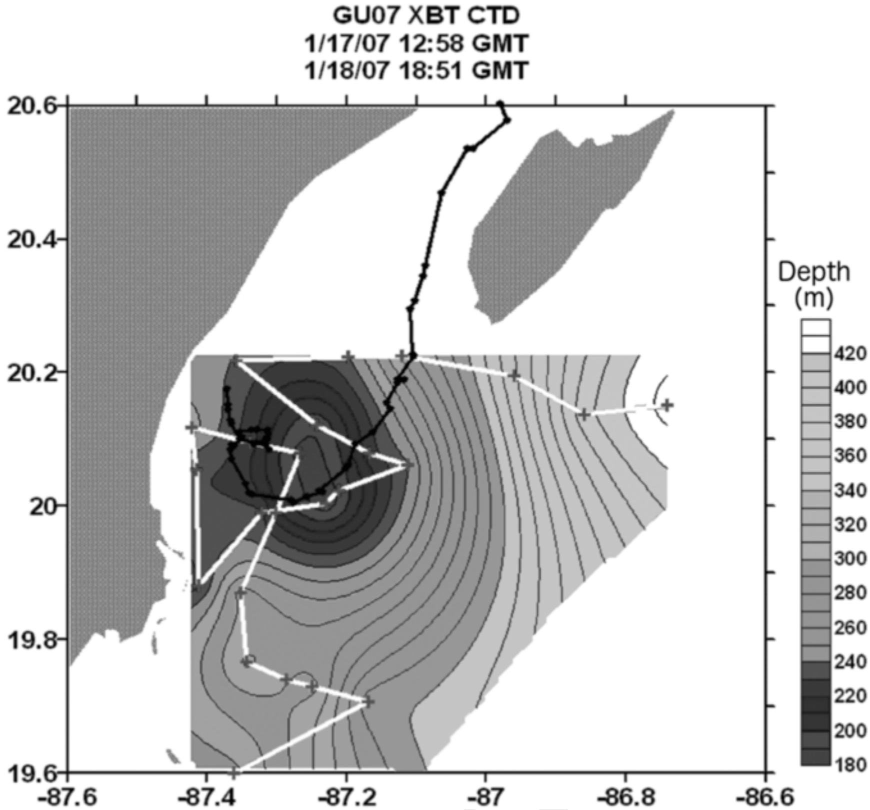

Fig. 5. Depth of the 12 °C isotherm in the cyclonic gyre January 17–18, 2007 from XBT data. Drifter track is indicated in black lines. White line indicates ship track.

This region is characterized by a seasonal upwelling (Merino, 1997) that may be associated with the strengthening and separation of the YC (Carrillo et al., 2015). Another effect of the interaction between the YC and bathymetric features is the Cozumel Eddy, which is presumed to be generated by the separation of the YC from the coast (Carrillo et al., 2015). Another direct effect of topography is the intensification of the YC through narrow passages such as the Cozumel Channel and the Yucatan Channel. Here, stronger currents that exceeded 1–2 m/s were observed. The presence of Cozumel Island causes the YC to bifurcate, with one third of the YC passing through the Cozumel Channel while the other two-thirds flow north along the Caribbean side of Cozumel Island (Chávez et al., 2003).

3. Marine resources and scales

3.1. *Pelagic fish*

An adult fish's mobility and migration are influenced by the ocean environment, often with temperature functioning as the signal triggering migration (Binder et al., 2011; Aldvén et al., 2015); however, it is egg and larval dispersal that determine most of the flow of genes (Levin, 2006; Hellberg, 2009). The early life stages (eggs and larvae) of fish represent the period during which marine currents play a determinant role, because due to their limited swimming capacity they are at the mercy of the currents. Also, it is the most vulnerable stage, showing up to 99.5% mortality (Houde, 2002). However, different species of fish use different strategies for succeeding in their life commitment of replenishing and maintaining their populations (Levin, 2006). How the seasonality of reproduction, developmental traits, and the behavior of larvae allows them to take advantage of, and/or face the challenges imposed by the oceanographic processes, is a key aspect of their life history strategy. Thus, post-larval coral reef fish need to return to the reef to complete their life cycle, whereas post-larval pelagic fish need to remain in open, deep waters.

One of the icons of a marine fish resource from a large-scale perspective is the Atlantic Bluefin tuna (*Thunnus thynnus*), which is classified as an endangered species on the IUCN Red List (Collette et al., 2011; http://www.iucnredlist.org/details/21860/0), and is the target of one of the most economically important fisheries in the world. This large migratory pelagic fish (up to 4.6 m in length and 684 kg of weight) lives as long as 30 years, and its habitat occupies a large portion of the Atlantic basin including the Gulf of Mexico and the Caribbean Sea. The Atlantic Bluefin tuna (ABFT) is a good example of large-scale connectivity between the Mediterranean Sea and the Gulf of Mexico as well as the Caribbean Sea. The northern Gulf of Mexico and the Mediterranean Sea are considered to be the main spawning habitats of ABFT. However, recently, spawning activity in the Western Caribbean has been also reported (Muhling et al., 2011). Even though warm waters represent a stressful environment for adult ABFT, they spawn in tropical waters apparently to increase the growth rate of their larvae (Miyashita et al., 2000). From Fig. 6, which shows the abundance of tuna larvae in the Yucatan Channel, it is clear that ABFT fish larvae follow the margins of the YC and the Loop Current. The pres-

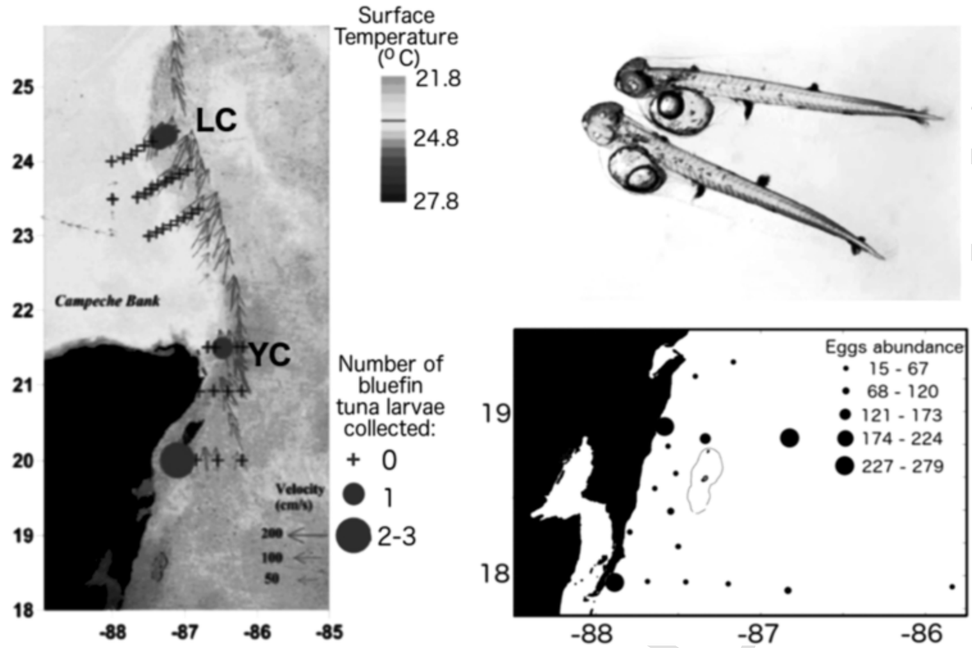

Fig. 6. Abundance of bluefin tuna fish larvae collected along the track of the YC and LP (left panel; from Muhling et al., 2011), and pelagic eggs abundance distribution around Chinchorro Bank (right-bottom panel; from Leyva-Cruz et al., 2016). Newly hatched Bluefin tuna fish larvae (*Thunnus thynnus);* right-upper panel courtesy from R. Laiz Instituto Español de Oceanografia-Malaga Laboratory.

ence of eggs and larvae confirm that adult ABFT are also present in the Western Caribbean LME. Here, some questions arise - is the highly variable environment of the Western Caribbean LME suitable for spawning in an earlier period than the Gulf of Mexico? Is there an exportation of ABFT larvae from the Western Caribbean LME to the Gulf of Mexico? Are ABFT larvae using the YC as a rapid escape route to get into the Gulf of Mexico?

Analysis of fish eggs collected from oceanographic cruises conducted during 2006 and 2007 (Leyva-Cruz et al., 2016) revealed that there are other large pelagic fish of economic importance that also use the Western Caribbean LME as a spawning area. Among some of the other fish eggs identified by genetic techniques (DNA Barcodes) were frigate tuna (*Auxis thazard*), skipjack tuna (*Katsuwonus pelamis*), blackfin tuna (*Thunnus atlanticus*), crevalle jack (*Caranx hippos*), common dolphinfish (*Coryphaena hippurus*), sailfish (*Istiophorus platypterus*), white marlin (*Kajikia albida*), and swordfish (*Xiphias gladius*) (Leyva-Cruz et al., 2016).

3.2. Reef fish

Reef fish species are particularly susceptible to overfishing because of their life history characteristics: slow growth, large size, late sexual maturity, multiple spawning, and long lifespan (Coleman et al., 2000). Groupers (Serranidae) and snappers (Lutjanidae), often known as the grouper-snapper complex, are reef fish subject to high fishing pressure, and represent the major fishery resources of the region (Sosa Cordero and Ramírez González, 2011; Graham et al., 2008, 2009). Several reef fish species, including those in the snapper/grouper complex, gather yearly at well-defined sites for mass spawning events known as spawning aggregations (Heyman and Kjerfve, 2008; Sosa-Cordero et al., 2002; Sadovy de Mitcheson and Colin, 2012). They are easily located during these times, and are therefore intensively fished, despite depleted populations due to this predictable reproductive behavior (Bohnsack and Ault, 1996; Sadovy and Domeier, 2005).

Coral reef fish rely on a pelagic larval phase to ensure reproductive success and survival of offspring, and pelagic life stages or larvae, by their very nature, tend to be dispersive (Fig. 7). For many years the accepted paradigm suggested that Caribbean coral reef fish are not derived from eggs spawned on their natal reef but from eggs spawned upstream (open populations) (Roberts, 1997). However, recent studies of larval fish and small-scale movements of water suggest that this may be a simplistic or incorrect assumption, and that self recruitment (closed populations) may be the rule rather than the exception (Cowen et al., 2006, 2007; Mora and Sale, 2002; Sale and Kritzer, 2008). Further investigations of these dynamics will provide information central to the effective design and establishment of coral reef marine protected areas (MPAs), because establishing an estimate of larval transport from upstream sources can provide an improved understanding of the connectivity between coral reef fish stocks (Green et al., 2014). For example, if there is strong current-mediated connectivity across subarea boundaries, then reef fish populations may depend significantly on upstream sources for larval recruitment. If so, the countries in the Western Caribbean LME have a major stake in cooperating with and encouraging region-wide international marine conservation planning. On the other hand, if local recruitment is the dominating factor in sustaining populations, then local MPAs and other conservation measures may become the management priority. Developing testable hypotheses regarding mechanisms of larval transport are, therefore, essential to developing effective management strategies.

Larval transport, dispersal and oceanographic connectivity are, generally, poorly understood in the wide region of Caribbean LMEs. Even less is known about dispersal kernels, behavioral components, and temporal and spatial variability of marine larvae. Reef fish larvae are also found in

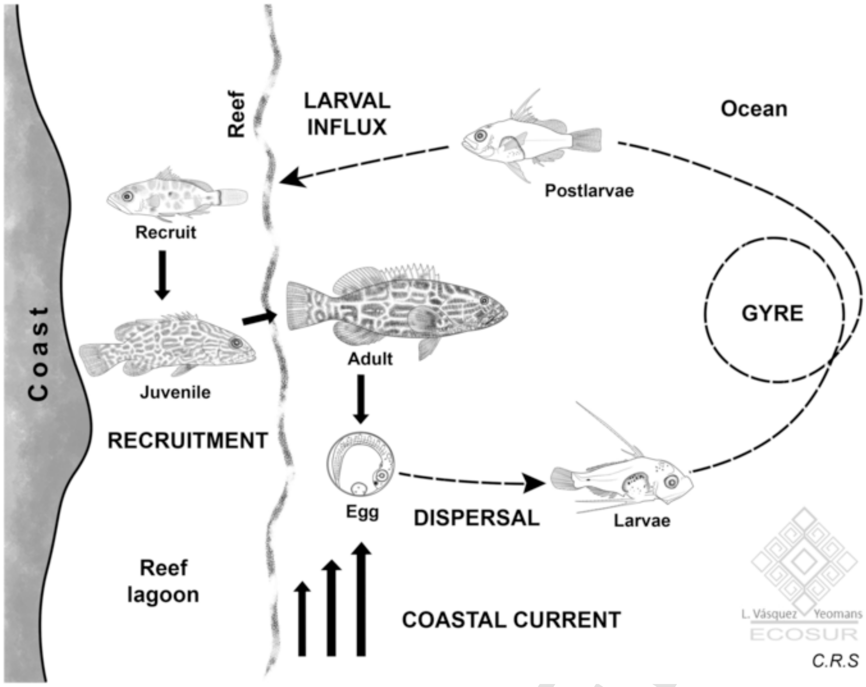

Fig. 7. Schematic representation of life cycle and dominant physical processes of Mycteroperca sp. (grouper).

ichthyoplankton samples collected along the Loop Current waters in the northern Gulf of Mexico. However, the degree to which tropical larvae are dispersed polewards by ocean currents is unclear. The strong northward flow of the CC along the MBRS would suggest that significant biological connectivity with the Gulf of Mexico may exist. Transport pathways between the MBRS and the Florida Keys could be as short as 7–10 days based on drifter tracks. However, the cyclonic gyre formation noted south of Cozumel would be expected to strongly impact larval dispersal and distribution along the coast. Sub-mesoscale cyclonic gyres will tend to retain and concentrate larvae. For example, more grouper larvae were noted during sampling concentrated around the gyre south of Cozumel. The shift in the CC where it approaches the MBRS from northward to due west, concurrent with the development of the Honduras Gyre, further acts to retain larvae, change larval transport trajectories, and potentially isolate spawning populations.

Ichthyoplankton abundance data from 2006, collected during a strong northerly current regime, showed a gradation from high abundance in the south to a lower abundance further north at the Yucatan Channel (Fig. 8), and the distribution and abundance of Scaridae mirrored this pattern. However, other reef fish such as wrasses' (Labridae) peak abundances occurred both in the north and south (Muhling et al., 2013). Tovar et al. (2009) suggested that changes in the YC flow along the coast may play an important role at the local level (100 km); they found changes in the composition of reef chaetognath communities associated with the strength of the YC flow. Inshore larval reef fish collections suggest that local recruitment in some areas was strongly influenced by small-scale circulation patterns (Vásquez-Yeomans et al., 2011); however, the known distribution of spawning aggregations along the Yucatan coast (Sosa-Cordero et al., 2002) suggests a potentially larger role for the CC. It is likely that transport of reef fish larvae may have episodic events related to the reversal of coastal currents depending upon the presence of gyres and eddies, and the strength of the CC and YC. An example of the reversal of currents has been observed at coastal current meters moored on the Xcalak (Fig. 9).

Results from these cruises (Muhling et al., 2013; Carrillo et al., 2015, 2016) and supplementary data show that the coastal northern and central MBRS is hydrographically connected, with relatively rapid transport time-scales. Furthermore, eddies and gyres may play an important role in establishing the relevant time and distance scales of connectivity. Such direct physical connectivity through ocean currents between the coral reef biota of these geographically separated spawning grounds may have an important influence on the degree of biological connectivity between regional populations of ecologically and economically important tropical marine species.

3.3. Caribbean spiny lobster (Panulirus argus)

There are regional scales of connectivity determined by the duration of the planktonic phase, where it is relatively long enough to allow a much broader dispersion, such as the Caribbean Spiny lobster. Caribbean Spiny lobster is an important income source for the developing countries and a cultural representative of small and regional scale cooperative fisheries in Mexico, Belize, Honduras and Cuba. The spiny lobster is a crustacean with a relatively long planktonic period (mean of 6.5 months, range: 4.5–8 months) before it returns to its coastal benthic habitats. Butler et al. (2011) found evidence for both self-recruitment and more widespread dispersal for lobster larvae (phyllosoma). According to numerical models, lobster larvae have two dispersion distances, one smaller than 400 km and other larger than 1000 km (Butler et al., 2011; Kough et al., 2013). The complex, eddy-dominated circulation in the Yucatan Basin favors retention of phyllosoma that are spawned and later either recruited into the Gulf

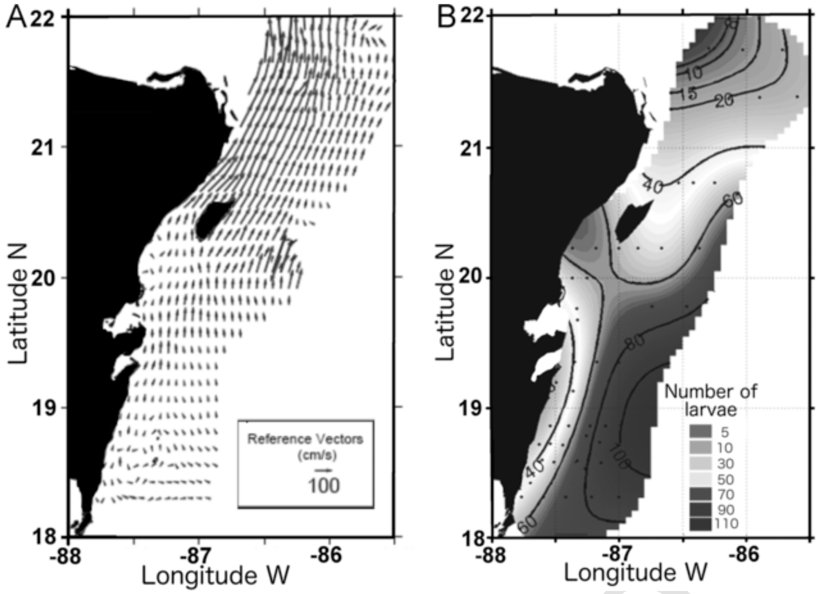

Fig. 8. (a) Surface currents from ADCP data during March 2006 in the Mexican Caribbean and (b) distribution and total abundance of larval fish of Scaridae collected during March 2006.

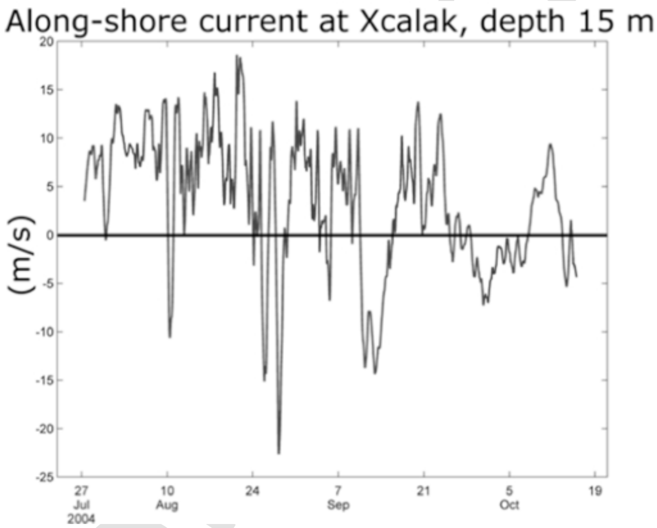

Fig. 9. Moored ADCP measurements in Xcalak, showing the intense current reversal that lasted several days. See location in Fig. 1.

of Batabano shelf or exported to the MBRS (Pérez-Santos et al., 2015). Butler et al. (2011) suggests that phyllosoma spawned at Glovers Atoll, Belize, may be retained by the Honduran Gyre, whereas those spawning at Ambergris Cay, just to the north of Glovers Atoll, are transported out of the system and into the Gulf of Mexico. However, the Honduras Gyre is not always present nor having the same strength or size, and at these times, larvae may also be advected and dispersed. As it was presented in Carrillo et al. (2015), by using altimetry data, we calculated potential weekly dispersal distances along the year from releasing particles in the YC regime (Yucatan Channel) and Honduras Gyre regime (Honduras Gulf) showed clearly the potential transport by the currents highlighting its differences (Fig. 10). Even though both sites showed variability, however, the YC in the Yucatan Channel showed a constant advection up to 580 km in the northward direction. Meanwhile, the southern part of the MBRS showed smaller dispersal distances and more variability including reversals. Previous work by Briones et al. (2008) suggest that spiny lobster populations are mostly 'open' with only a small fraction of self recruitment. Lobster population distributions throughout the Caribbean may, therefore, be influenced by both open and closed recruitment dynamics. Another important aspect is the advection of phyllosoma by the YC in the northern part of the MBRS (Muñoz de Cote, 2016), and the enhanced probability of retention of early stages in two locales (i) off the central bays pertaining to Sian Ka´an barrier reef, probably due to the gyre south of Cozumel I., and (ii) northeast of Chinchorro Bank (Canto-García et al., 2016), where the wake island effect may produce small-scale features such small eddies. However, further studies remain to be done before this process is fully understood.

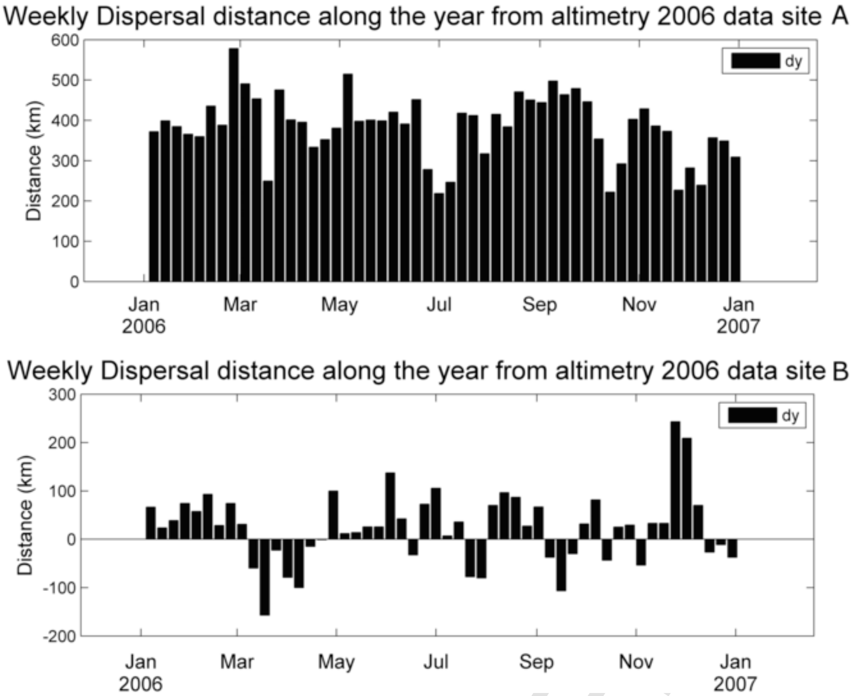

Fig. 10. Potential weekly dispersal distances along the year for two regions of the Mesoamerican Barrier Reef System. Upper panel shows the Yucatan Channel area, while the lower panel indicates the Gulf of Honduras. See Fig. 1 for locations of sites A and B.

3.4. *Caribbean queen conch (Strombus gigas)*

One example of large gastropods of economic and cultural importance in the Western Caribbean LME is the Queen conch (*Strombus gigas*). Queen conch adults can be found in shallow water and have a limited movement that makes them easy to capture, leading to severe overfishing. *S. gigas* have been included in the Convention on International Trade of Endangered Species of Wild Fauna and Flora since 1992 (CITES, 2003), and in 1994 they were added to the International Union for the Conservation of [the] Nature´s Red List (IUCN) (Baqueiro Cárdenas and Aldana Aranda, 2000). The *S. gigas* planktonic larval period ranges from 12 to 35 days with a mean of 21 days, under laboratory conditions (Ballantine and Appeldoorn, 1983; Davis and Hesse, 1983), however, in their natural environment larvae can last 60–75 days before metamorphosis (Ballantine and Appeldoorn, 1983). This implies that if there are not conditions conducive to settlement or metamorphosis, the larval stage lasts longer. This difference has important implications for the dispersal distance of these mollusk larvae, as there may be a link between variability of the larval period and variability of the oceanic conditions. This would be expected in regions with strong currents such as the YC. However, mesoscale eddies can provide retention mechanisms limiting the net transport (Kinder et al., 1985; Lessios et al., 1984). But dispersion cannot be simplified as constant flow of genes due to the oceanic currents. Genetic studies of *S. gigas* in the Western Caribbean LME presented similar allelic frequencies, however, with some discontinuities. Thus, there are different stocks. It has been observed that the *S. gigas* populations on the Alacranes reef, over the Yucatan shelf, seem to be isolated from the populations of the rest of the western Caribbean LME, even when the YC flows close to the shelf.

From biophysical numerical models of veliger larval drift and survival, Paris et al. (2009) did not show connectivity of *S. gigas* larvae between the MBRS and Yucatan shelf. Occasionally, the YC separates from the shelf allowing an intrusion of cold water over the shelf of subsurface Caribbean water (Enriquez et al., 2013). This is an example of how oceanographic processes can disconnect habitats, as the YC flow northward through the Yucatan Channel without reaching the populations of the Alacranes Reef. Isolated populations rely on local circulation and retention mechanisms, such as eddies formed in the lee of islands, to allow recruitment. However, there was a clear connectivity between populations along the Mexican Caribbean. Recently, more genetic studies of Caribbean Queen conch reinforce the hypothesis that oceanographic processes either isolate or connect populations in the Western Caribbean. There is a genetic separation between Queen conch populations along the southern MBRS, central MBRS and northern MBRS (S. Machkour pers. comm) which correlates with the three regimes: strong advection via the YC, CC impingement areas, and the Honduras Gyre (Carrillo et al., 2015). Successful management strategies of the Caribbean Queen conch for fisheries recovery will require a good understanding of the ambient oceanographic processes as well as careful genetic studies. Overfishing will decimate the *S. gigas* stocks rapidly in isolated populations that are restricted by the oceanographic processes, for instance along the Yucatan shelf and over the MBRS. Moreover, it might be expected that *S. gigas* populations along the MBRS can be influenced accordingly by the currents, i.e. the CC, YC, and the Honduras Gyre.

4. International efforts and cooperation

In 2004 the NOAA Coral Reef Conservation Program funded a research proposal to study the distribution and potential transport pathways of the larvae of commercially important fisheries species such as groupers (Serranidae) from western Caribbean spawning sites into the northern Gulf of Mexico and the Florida Straits. This funding brought together scientists from NOAA's Southeast Fisheries Science Center (SEFSC) and Atlantic Oceanographic and Meteorological Laboratory (AOML), El Colegio de La Frontera Sur (ECOSUR) in Chetumal, Centro de Investigación y de Estudios Avanzados (CINVESTAV) in Mérida, and Centro de Investigacion Científica y de Educación Superior de Ensenada (CICESE) in Baja California, México, the University of Belize, Boston University, and the University of Miami. A cooperative research program was developed to provide a baseline study of the fisheries oceanography of the western Caribbean during the winter grouper spawning season and to provide valuable information for potential future fisheries management decisions at an ecosystem scale. The priority was to study larval reef fish transport mechanisms (physical and biological) on local and regional scales between the Florida Keys and the northern extension of the MBRS. Mexico's Yucatan coast contains 39 identified and mapped spawning aggregations (Sosa-Cordero et al., 2002) located along a strong western boundary current flowing northward into the Gulf of Mexico. The Florida Keys and Dry Tortugas coral reef systems lie downstream of these spawning areas (Fig. 2). The Yucatan coast plays a potentially important but as yet unknown role in the biological production and transport of larval fish throughout the region.

As part of this initiative, several oceanographic cruises were conducted during 2006, 2007, and 2010–2016 in the Western Caribbean LME collecting larval fish and oceanographic data. These studies have yielded a better understanding of the larval fish distributions as they relate to mesoscale oceanographic processes. More recently, this effort has evolved into an international research project between Spain/USA/Mexico called ECOLATUN funded by Spanish Government. ECOLATUN will investigate the early life ecology of ABFT larvae based on trophic levels, growth, and oceanographic features, comparing the northwestern Mediterranean and the Gulf of Mexico and western Caribbean. The results of this research will impact the management of this marine resource by defining stock population units, examining stock-recruit relationships, and taking into account the physical connectivity between the western Caribbean Sea LME subarea and other LMEs on large spatial scales. ECOLATUN represents an effort toward generating data to further support international policy.

Coastal monitoring of post-larval stages of marine life is fundamental to assessing reef fish recruitment. To replicate the herein described effort of monitoring along a reef system such as the MBRS would require a large amount of money to obtain measurements in all of the relevant areas of the Caribbean, and it would be logistically difficult to apply the monitoring simultaneously. In order to overcome these difficulties, an initiative to enhance local expertise and to build capacity in monitoring early life fish and oceanographic parameters in the reef area of the MBRS was developed in 2010 (Malca et al., 2015). Since then, an innovative capacity and research effort was carried out in ten Marine Protected Areas (MPAs) during the new moon in September 2013, February/March 2014 and August 2014, September 2015 and August/September 2016 to assess the arrival of post-larvae and juvenile fishes into Mesoamerican MPAs (Malca et al., 2015). Monitoring was applied simultaneously with standardized methodology and low-cost sensors. This post-larval fish monitoring effort was called ECOME (Exercise COnnectivity MEsoamerican, from Spanish) with the participation of MPAs from Honduras, Guatemala, Belize and Mexico. This exercise proved to be successful, with a widespread participation and an improved capacity among neighboring countries to increase activities related to connectivity research in order to support the conservation and management of reef fishes in the Mesoamerican Region.

5. Conclusions

Herein we have presented examples of some marine resources distributed throughout the Caribbean linked with oceanographic processes on different spatial scales. The range of these scales runs from small scale processes of about 1 km, submesoscale at 10 km, a mesoscale at the 100 km interval and large scale at 1000 km, each of them related to a characteristic oceanographic phenomena. For instance, large scale processes can be represented by the large pelagics such as Bluefin tuna (i.e. uses the habitats and connects to other large ecosystems). On a subarea scale are the resources of reef fish and Queen Conch and Caribbean Lobster. However, the complexity and dynamics of the marine environment depend on the simultaneous occurrence of processes on multiple scales to determine its variability. Dispersal distances depend on the oceanographic phenomena whereby larger dispersals are expected where intense currents occur, such as in the YC. In other cases, retention can be expected in the presence of gyres such as Honduras Gyre and Yucatan Basin eddies. There is a growing body of evidence supporting the need for a multi-scale approach in order to understand the complexity of LMEs. A multiple-scale approach will enhance our understanding of the interaction between the key physical and biological processes driving the connectivity and/or isolation between habitats and populations (Fogarty and Botsford, 2007; Botsford et al., 2009). Moreover, the connectivity between regions in the western Caribbean Sea LME subarea, shown by the exchange of resources and physical oceanographic processes, requires an international policy that supports collaborative efforts to monitoring the dynamics of coastal and oceanic habitats together with marine resources. Additionally, given the dynamic oceanographic processes presented in this paper, there may be consideration of Mexican Caribbean MPAs to be included in this MPA network collaboration together with Florida Keys Sanctuary and Guanahacabibes (Cuba).

Uncited reference

Sale (2004).

Acknowledgements

ADCP and XBT data were provided to the NOAA Coral Reef Conservation Program and are on file at the National Oceanographic Data Center (NODC) and Southeast Fisheries Science Center (SEFSC) Library. ARGOS satellite-tracked surface drifter data can be found at NOAA's Global Drifter Program (http://www.aoml.noaa.gov/phod/dac/index.php). This work has been partially supported by NOAA´s Coral Reef Conservation Program #1244. This work was partially supported by the base funding of NOAA's Atlantic Oceanographic and Meteorological Laboratory, Southeast Fisheries Science Center, and ECOSUR. ECOSUR Zooplankton Laboratory is thanked for the sorting and identification of the fish larvae, in particular S. Morales. Ship time was provided by NOAA under the projects Larval Fish and Physical Oceanography Survey of the Mesoamerican Reef System, and Meso-American System Transport and Ecology Research. We thank the Captain and crew of the NOAA Ship Gordon Gunter and NOAA Ship *Nancy Foster*. We also thank Nelson Melo for providing the MODIS image (Fig. 3) and J. Ochoa for ADCP data for Fig. 3 from CANEK Campaign 2000.

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