DISPERSAL OF REEF FISH LARVAE FROM KNOWN SPAWNING SITES IN LA PARGUERA

By

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Abstract

The objective of this study was to examine potential dispersal trajectories of mutton snapper (*Lutjanus analis*) eggs and early stage larvae during spawning events at La Parguera. Larval fishes were collected during four cruises between March and May 2003 along three transects running perpendicular to the shelf-edge. The Acoustic Doppler Current Profiler (ADCP) velocity profile Vertical velocity structure and temperature variations during the April 17 lunar perigee-zizygy event suggest that an internal wave collided with the shelf, resulting in an influx of deeper colder water, while displacing near-surface waters out to the Caribbean Sea. The mean westward flow of 7.3 km per day favors eggs and planktonic larvae spawned at the shelf-edge being transported offshore. However, the surface flow follows the bathymetry northward potentially leading to final recruitment destinations along the west coast of the island during spring 2003.

Resumen

El propósito de este estudio fue examinar las posibles trayectorias de los huevos de sama (*Lutjanus analis*) y sus larvas en estadíos tempranos durante la epoca de desove en La Parguera para evaluar su potencial de dispersión. Las larvas fueron capturadas a lo largo de tres transectos perpendiculares al borde de la plataforma insular durante un periodo de muestreo de marzo a mayo del 2003. La estructura vertical del flujo y las variaciones en temperatura medidos por un metro acústico *doppler* de corriente (ADCP) durante el evento de perigeo-zyzygeo del 17 de abril sugieren que una ola interna chocó con la plataforma insular resultando en la entrada de aguas profundas más frías que desplazaron las aguas superficiales hacia el Mar Caribe. El flujo promedio de 7.3 km por día en dirección oeste favoreció a que los huevos y las larvas planctónicas depositados en el borde de la plataforma insular fueran transportados mar afuera. El flujo superficial predominante en el borde sur-oeste de la isla sigue los contornos batimétricos en dirección norte, por lo cual los arrecifes de la costa oeste pudieran haber sido los principales destinos de reclutamiento para larvas de peces desovados durante el periodo de estudio.

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To my committee for their guidance. To the ñ's (Jorge, Milton, Bob and Yuni) for the good times. To the girls (Aury, Janneth, Yira, and Stacey) for all their help. To Mickey and Jennie for a home. To Taty for always watching out for me. To my family for their love.

DEDICATION

To mama.

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INTRODUCTION

The evolution and persistence of many species, including coral reef fishes and other demersal marine organisms with pelagic larvae are highly dependent on dispersal (Sale, 1980). Most coral reef fishes remain sedentary throughout their adult life and dispersal takes place during their pelagic larval phase. Recruitment to coral reef systems may be determined by the high mortality occurring during this planktonic stage (Richards and Lindeman, 1987; Doherty, 1991; Leis, 1991). Dispersal of the newly spawned larvae also dictates the degree of spatial connectivity, thus holding key knowledge regarding population dynamics vital to conservation and management of the species (Sale, 2002).

Early work assumed local populations to be replenished mainly by larvae from outside populations (Sale, 1978). The extended pelagic larval duration of many coral reef fishes suggested the potential of currents passively transporting larvae through long distances (Sale, 1978, 1980, 2002; Doherty, 1991). However, recent research on water current dynamics near reefs (Cowen et. al, 2000), larval behavior (Leis and McCormick, 2002; Fisher and Bellwood, 2002), tagging (Jones et. al, 1999) and genetic studies (Planes, 2002) challenge the initial open population concept. Modern dispersal models suggest retention of larvae from natal reefs (Cowen et. al, 2000). Yet, there is not enough evidence at present to determine the degree of openness or closeness of coral reef populations (Sale, 2002).

The interaction between the species behavioral capabilities and the physical features of the environment at relevant temporal and spatial scales are responsible for structuring dispersal of coral reef populations (Sale, 2002). The lack of knowledge concerning patterns of larval dispersal remains a limiting factor to our understanding of coral reef recruitment dynamics. Spawning aggregation of mutton snapper at the shelf edge reef in La Parguera presents an ideal scenario to examine the prevailing oceanographic conditions influencing dispersal of fish eggs and of the early pre-flexion larvae during the snapper spawning season.

OBJECTIVES

The main objectives of this study were to:

1. Propose initial dispersal trajectories of pelagically spawned fish eggs and early larvae from a known snapper spawning aggregation site at the shelf edge reef off La Parguera during the period between March and May, 2003.
2. Determine the abundance of snapper larvae at the shelf edge and adjacent oceanic and neritic stations during the period of mutton snapper (*Lutjanus analis*) group spawning aggregations (March-May 2003).
3. Provide fisheries documentation of adult mutton snapper during their reproductive season in La Parguera.

PREVIOUS WORK

The mutton snapper (*Lutjanus analis*) is found in the American Atlantic from the Gulf of Maine all the way down to Brazil. It is more abundant in the Antilles, Bahamas and Florida where it is considered of great economic importance. According to the information obtained from the statistical program of DNER's Laboratorio de Investigaciones Pesqueras (Matos Caraballo, 2000), commercial fishermen reported landings of 89,583 pounds for mutton snapper in Puerto Rico during the year 2000. This study places the "Sama", as the mutton snapper is locally named, as one of the top four species in terms of pounds of fish captured for Puerto Rican artisan commercial fisheries.

Aspects of the biology and ecology of adult *Lutjanus analis* have been examined from studies in Florida (Mason and Manooch, 1985), Bahamas (Mueller, 1994, 1995; Mueller et al., 1994), Colombia (Echardt and Meinel, 1977), Cuba (Rojas, 1960; Pozo, 1979; Claro, 1981; Claro, 1983; Claro and Colas, 1987) and Venezuela (Palazón and González, 1986). Assessment of the species reproductive biology was done by Claro (1981) in Cuba and by Figuerola and Torres (2001) in Puerto Rico. Embryological and larval development of *L. analis* seems to occur in the oceanic habitat (Claro, 1981). Clarke et al. (1997) noted that early larval stages of the various snapper taxa are extremely similar and difficult to distinguish. Newly hatched larvae measure 2.2-2.5 mm SL with feeding beginning at 2.6-2.8 mm (24-48 h post-hatch). Notochord flexion starts as 4.4 mm (11-12 d post-hatch) and transformation begins at 10 mm (13-19 d post-hatch) (Clarke et al., 1997).

The depth range of adult mutton snapper is typically from 5-86 m. Fishes reside in diverse habitats of the shelf including natural and artificial reefs, among sponges and gorgonians, algal beds, coastal lagoons surrounded by mangrove and sandy bottoms (Claro, 1981). Juveniles (60-

150 mm) are found in shallow coastal waters associated with algal beds, coral reefs and rocky bottoms, whereas medium size fish (180-400 mm) characteristically prefer regions farther from the coast with sandy bottoms, algal beds, and places with abundant patch reef at depths of 3-10 m (Cervigon, 1993). Large adults (400-700 mm) are usually found at the shelf edge at depths greater than 25 m, but tend to swim to shallower areas in search of food. The difference in habitat according to size is more pronounced in narrow platforms (Claro, 1981).

According to Randall (1967), *L. analis* diet is made up of 44.4% crabs, 29.8% small fishes and 13% gastropods. Maximum recorded size is 86 cm weighing at 16 kg (Mason and Manooch, 1985). When found over sandy bottoms, *Lutjanus analis* body color turns almost white and when encountered over coral bottoms body coloration turns to redish green (Randall, 1967). Generally, they are not found in large groups except during the days previous to spawning where they form large aggregations in certain places along the shelf edge (Thompson and Munro, 1974; Claro, 1981). Mueller (1995) reported limited movement of *L. analis* over artificial unexploited reefs in the Bahamas.

In Cuba, Claro (1981) reported spawning aggregations taking place at an average depth of 20-40 m at the shelf edge over rocky coralline bottoms and sandy bottoms with abundant gorgonians. These aggregations start 3-4 days previous to the full moon (Feb-May) lasting almost seven days after the full moon. The fish do not bite the lines unless there is a strong current, although their presence is detected from the surface.

A study on the reproductive biology of the mutton snapper in Puerto Rico (Figuerola and Torres, 2001) identified April and May as the months when group spawning occurs. They found that during this period 97% of females presented advanced gonad stages. Also, all captured females showing signs of eminent spawning activity coincided with the six days after the full moon of both April and May. Males with advanced gonad stages were also captured during the same two months.

Reef fish spawning aggregations are one of the most impressive biological phenomena found in neritic waters. Despite the importance of spawning aggregations for the conservation and management of the species there is limited information about the biology of such behavior (Sadovy, 1993). Fishermen have long targeted aggregations of some species, since they are predictable with regard to location and timing, but in past decades fishing pressure on aggregations has increased to the point that many commercially important species are threatened throughout most of their ranges (Colin et al., 2003).

The mutton snapper conforms to the majority of coral reef fishes by having a pelagic larval stage (Sale, 1980). Since adults are considered sedentary, the opportunity for long distance dispersal determining the degree of connectivity between populations arises during the planktonic phase (Leis, 1982). Mortality rates are highest during the larval stage delimiting future adult size populations (Richards and Lindeman, 1987; Doherty, 1991; Leis, 1991). Dispersal mechanisms determining spatial and temporal distribution of coral reef fishes are structured by the interaction of specific species capabilities, site and time specific physical oceanography and scale (Sale, 2002).

Initial studies viewed the longevity of some pelagic larvae and the influence of dispersal by currents as evidence favoring open populations (Sale, 1978, 1980; Doherty, 1991). The massive spawning aggregation in oceanic waters have been proposed as a behavioral adaptation for avoidance of predation by neritic zooplanktivorous fishes and for increasing the extent of dispersal (Johannes, 1978). However, recent investigations of water current flow near reefs (Cowen et. al, 2000), larval behavior (Leis and McCormick, 2002; Fisher and Bellwood, 2002), tagging studies (Jones et.al, 1999) and genetic information (Planes, 2002) have questioned the initial open population concept.

The new trend suggests that even though some coral reef fish larvae can last for weeks or months in the pelagic environment, their larvae are capable of actively determining their own dispersal and staying within the vicinity of reefs (Cowen et. al, 2000). Coral reef fish larvae in the latter stages of development have been found to be able of orienting towards different reef stimuli (Leis and McCormick, 2002). Reef sound and smell have been suggested as the most probable stimuli for orientation. Laboratory studies have shown that late stage fish larvae can be very good swimmers, capable of reaching speeds between 5-50 cm/s, with enough duration to cover from 4-200 km before exhaustion depending on species (Dudley and Montgomery, 2000). Fisher and Bellwood (2002) showed that late stage larvae of damselfish *Amphiprion melanous* are capable of swimming at a constant speed of 4.7 cm/s in order to avoid advection for a period of 12-48 h. The average water current speeds for the Mona Channel are of 1.0 cm/s (Rojas, 2002) and 0.7 cm/s for southwestern Puerto Rico (Ojeda, 2002). Furthermore, field observations by Leis et al. (1996) reported individuals swimming shoreward.

The distances necessary to avoid advection from natal reefs are significantly shortened if reef fish larvae were to use vertically stratified flows that facilitate retention. Cowen et. al (2000), suggested that reef fish larvae (6-9 d post-hatch) use a local coastal upwelling circulation that flow shoreward in Barbados by actively swimming to deeper waters (35 m). On the other hand, Sale (2002) questioned the ability of larvae to detect different current directions at different depths. There are other small to mesoscale oceanographic features that provide opportunities for predictable transport of larval fish, such as reduced water circulation due to reef topography, eddies, surface slicks, tidal currents and alongshore currents (Capella, 1999; Sale, 2002).

Colin and Clavijo (1988) observed 11 reef fish families that spawn at the shelf-edge of La Parguera to have peak reproductive season not conforming to tidal currents favoring off shore dispersal. Correspondingly, subsequent work at the same area reports that water currents away from the reefs were greater at non-spawning times than at spawning times for *Thalassoma bifasciatum* (Appeldoorn et al., 1994; Hensley et al., 1994). Both studies suggest physically driven mechanisms, other than tidal currents, potentially capable of retaining eggs and larvae inshore.

Largier (2003) discuses the importance of understanding the interactions between along-shore and cross-shore advection in estimating larval dispersal distances from oceanographic data. When considering dispersal parameters at appropriate population scales, cross-shore circulation is disproportionately more important for recruitment of coral reef fish larvae given that small changes in cross shore dispersal translate into large increases or decreases in along shore dispersal (Gaines et. al, 2003). In neritic environments the shoreline and seafloor combine to make near coastal waters a retention zone for larvae known as the coastal boundary layer. Advection perpendicular to the coastal boundary layer is weak in the absence of a persistent flow structure where surface and bottom waters move in opposite cross-shore directions (Largier, 2003). However, internal tidal waves have recently been discovered by Leicher et. al (1998) and Pineda (1994a) to produce predictable nearshore upwelling, as they break into turbulent cool-water internal bores that travel up the insular slope delivering zooplankton and nutrients into the reef environment.

Coastal seiching events in the south west coast of Puerto Rico lead to the assumption that large amplitude semidiurnal internal waves associated with the spring and neap tides came crashing into the shelf edge. These events are thought to originate when larger than usual tidal currents pass over the shallow bathymetry of the Aves Ridge, 650 km southeast of Puerto Rico (Giese et. al, 1990). Internal tidal waves show both diurnal and semidiurnal periodicity and travel shoreward along the pycnocline at depths of 50 to 80 m breaking once they reach the shallower continental shelf much like a surface wave breaking in a beach (Pineda, 1994b and Leichter et. al, 1998). Maximum activity in the northern Caribbean takes place during spring and summer four days after the full moon and two days after perigee. Large amplitude spring and neap tides related to lunar perigee-zyzyge alignment are necessary but not sufficient alone for development of the internal waves (Pineda, 1994b). It has been suggested that the strength of the water current, mixed layer depth, and stratification of the water column also affect the transfer of energy from tides to waves (Giese et. al, 1990; Pineda, 1994b; Leichter et. al, 1996, 1998).

Ramírez-Mella and Garcia-Sais (2003) reported abundance of coral reef larvae to predominate over oceanic type larvae as far as 29 km off-shore in the southwest coast of Puerto Rico. The horizontal distribution of Caribbean coral reef fish larvae was found to exhibit three basic patterns; one mostly neritic (e.g. Clupeiformes), a widespread oceanic (e.g. Labridae) and one associated with the outer shelf-edge (e.g. Lutjanidae). Very low abundances of coral reef fish larvae were found at 46 km off-shore from the west coast of Puerto Rico, concluding that Mona Passage could be acting as a barrier to larval dispersal from the Puerto Rico shelf (Rojas, 2002). Accordingly, current meter data at the southwest corner of the island platform recorded mean surface flow running northward along the bathymetry of the Cabo Rojo and Mayaguez shelf (García-Sais et. al, 2003).

Ojeda (2002) reported a strong westward current due to faster than usual winds and far-field mesoscale eddies impinging on the coast as a responsible for rapidly dispersing eggs and larvae, but also to have kept larvae near the shelf-edge during the spawning season of the red hind

(*Epinephelus guttattus*) at La Parguera. More importantly, a period of calm currents followed by a current reversal prevailed along the southwest coast during late March and early April. Increments in abundance of pre and post-flexion larvae of various fish taxa collected during this time suggest that these currents influenced a multi-species larval retention near the shelf-edge reef.

Due to the difficulty of directly tracking coral reef fish larvae, mathematical models have proven to be helpful in predicting larval dispersal, as well as to identify the importance of a particular factor influencing dispersal (Sale, 2002). Cowen et al. (2000) developed a physical model of circulation in the eastern Caribbean coupled to estimates of larval mortality and diffusion to predicted that larval concentrations essentially fall to zero at a distance of only 140 km from the larval source. Pagán (2003) used a three-dimensional general circulation model including potential simple swimming behavior with emphasis on the area of La Parguera, southwest Puerto Rico. The model suggests that an almost perennial (November to August) westward flow exists along the near shore waters of southwestern Puerto Rico. Under this flow field the potential for local retention of passive particles in the region is strongly supported due to Ekman transport towards the coast.

METHODS

Study Site - La Parguera is located in the south western coast of Puerto Rico, where the shelf extends offshore to approximately 11km before dropping abruptly from 20 to 3,800 m. To the south the shelf break defines the end of the island platform while to the north, a deeper sandy fringe borders the inner boundary of the shelf edge reef (Figure 1). The shelf edge reef system of La Parguera is considered one of the largest and best developed coral reefs in Puerto Rico.

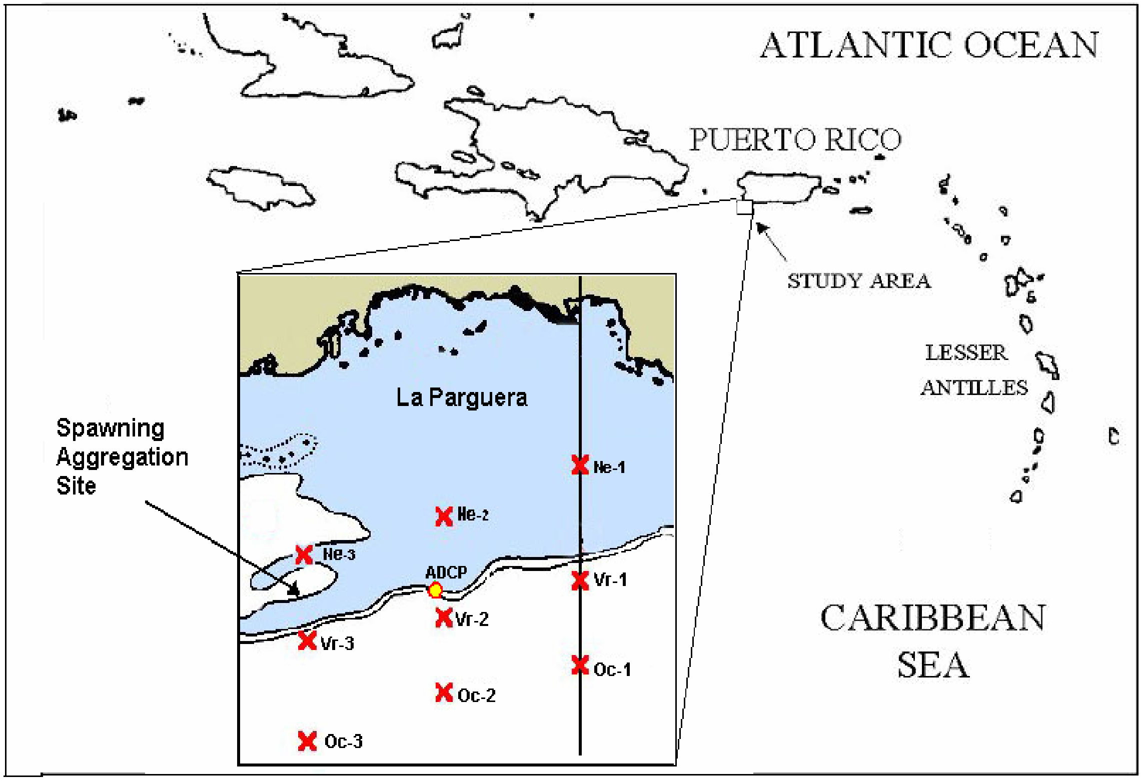


Figure 1. Location of ADCP current meter, larval fish sampling stations and mutton snapper spawning aggregation site at La Parguera.

To the west, this area connects with the Mona Passage and to the east with Guánica and Guayanilla Bays.

Caribbean Sea circulation in the Venezuela Basin to the south of Puerto Rico is affected by intense mesoscale activity, but typically flows westward at a speed of 0.25 m/s (Molinari et al., 1981; Roemmich, 1981; Morrison and Smith, 1990). Average wind direction in La Parguera is from the east-southeast peaking in early afternoon and decreasing towards late afternoon. The trade wind pattern is reflected on subtidal surface current flow, which is channeled along the coastline and is almost entirely westward. Once at the southwest corner of the island platform, the mean surface flow runs along the bathymetry of the Cabo Rojo and Mayaguez shelf in a northward direction (García-Sais et al, 2003). With the exception of passing tropical storms, wind speeds are weaker during the fall. In contrast, springtime brings stronger winds with periods where the wind relaxes and a flow reversal towards the east has been observed (Tyler and Anderson, 1995; Sanderson et. al, 1994; Appeldoorn et al., 1994) as well as reports of deeper currents flowing opposite to the wind stress.

Along shore pressure gradients on the shelf are thought to be responsible for the changes in flow direction during periods where the wind stress drops (Tyler and Anderson, 1995). Trade winds blowing towards the west drive a northward Ekman transport. Tides on the southern coast of Puerto Rico are diurnal with a mean range of less than 10 inches (Kjerfve, 1981). Tide generated internal waves along with wind shear bring about variability in a well stratified water column where the mixed layer ranges from 60-80 m (Capella and Fornshell, 1990).

Larval fish samplings – Ichthyoplankton sampling was designed to cover the period when mutton snapper (*Lutjanus analis*) historically aggregates at known spawning sites in La Parguera. Samples were collected during four cruises: March 21, April 3, April 23 and May 16, 2003 along three meridional (north-south) transects running perpendicular to the coastline at 67.00 W, 67.03 W and 67.06 W (Figure 1). Three bathymetric contours were occupied along each transect, at the shelf edge (Vr 1-3), three kilometers south (Oc 1-3) and three kilometers north (Ne 1-3), forming a nine station (3 x 3) rectangular grid. Station coordinates (Table 1) were determined using a Differential Global Position System (DGPS). The three stations sampled along each contour were considered replicates and averaged to represent three longitudinal (neritic, shelf edge and oceanic) gradient values. Neritic stations were sampled by oblique tows encompassing the entire water column, except for a few meters near the bottom. Shelf edge and oceanic stations were sampled in vertically stratified, step-oblique tows at three discrete depths (0-20, 20-60 and 60-120 m) with a 1 m² Tucker Trawl fitted with three 308 um mesh nets and standard General Oceanic flow meters. Nets were towed during five-minute intervals at a cruise speed of 2 knots for an approximate sampling field volume of 300 m^3. At the 67.03° W transect there was an additional surface neuston tow for all three contours with a 202 um mesh net and standard General Oceanic flow meters.

Table 1. Geographic positions and depths of larval fish sampling stations in La Parguera, March – May, 2003.

Station	Latitude (°N)	Longitude (°W)	Nets	Tow Depth (m)	Station Depth (m)
Ne-1	17°54.42	67°00.00	1	20-0	20
Ne-2	17°53.59	67°03.00	1	20-0	20
Ne-3	17°53.08	67°06.00	1	20-0	20
Vr-1	17°53.00	67°00.00	1	120-60	>1000
			2	60-20	
			3	20-0	
Vr-2	17°52.176	67°03.00	1	120-60	>1000
			2	60-20	
			3	20-0	
Vr-3	17°51.660	67°06.00	1	120-60	>1000
			2	60-20	
			3	20-0	
Oc-1	17°51.18	67°00.00	1	120-60	>1000
			2	60-20	
			3	20-0	
Oc-2	17°50.04	67°03.00	1	120-60	>1000
			2	60-20	
			3	20-0	
Oc-3	17°49.48	67°06.00	1	120-60	>1000
			2	60-20	
			3	20-0	

Due to break down of the trawling cable, the Tucker trawl system was lost during the crucial second week (May, 7) following the massive spawning event as documented by local commercial landings. After the accidental loss of the Tucker trawl, May, 16 samplings were conducted using a Bongo net, equipped with two 202 um mesh nets and standard flow meters. The two samples collected in each bongo net were pooled, and the total volume filtered was calculated by adding the readings of both flow meters. Subsequent samplings at shelf edge (Vr) and oceanic stations (Oc) consisted of two oblique tows; one from 120 m to the surface, and a second one from 60 m to the surface. This differed from the Tucker trawl ability to sample at three vertical discrete depths for the March 23, April 3 and April 21 cruises.

Ichthyoplankton samples were fixed in 5% buffered formalin and later preserved in 95% ethanol. Entire samples were sorted for total fish larvae. Larval snappers (Lutjanidae) were identified and enumerated. Taxonomic identification of snapper larvae to the lowest taxonomic level possible was done according to Clarke et. al (1997). Larval fishes were classified as pre-flexion or post-flexion based on the upward flexion of the urostyle, which comes before the formation of the caudal fin. Reports of total fish larval abundance include both pre-flexion and post-flexion stages as water column means (0-60 m) of three stations occupied within each distance contour, normalized to Ind/100m^3.

Two-way Analysis of Variance (2-way ANOVA) tests were performed on log transformed abundance data for total larvae in order to examine potential differences of larval abundance between distance contours on each cruise. When ANOVA tests were statistically significant at $p < 0.05$, Student-Newman-Keuls (SNK) multiple mean comparison tests were performed to further elucidate which distance contours were statistically different from others (at $p < 0.05$). In order to provide a snapshot characterization of temporal differences in horizontal distribution of larvae, abundance contour maps for each cruise were prepared for both total larvae and snapper larvae.

Assessment of adult gonad maturity was determined according to definitions and criteria from García-Cagide et. al (1994). Adult samples were obtained from local port surveys during the massive spawning aggregations of mutton snapper at the shelf-edge of La Parguera. Description of the fishing vessels and fishing gear was documented. Interviews with the fishermen provided additional information about timing, location and duration of the aggregation. All data obtained for the preliminary documentation of the fisheries was done according to Colin et. al (2003).

Currents – Water current measurements at La Parguera were obtained during two deployments of an upward looking RD Instruments (RDI) 600 kHz Acoustic Doppler Current Profiler – Workhorse Sentinel (ADCP) mounted on the bottom at station Vr-2 (67°.03 W) at a depth of 21.8 m, approximately 35 m off from the seaward end of the shelf break. The deployment period extended from March 3 through May 16, 2003, encompassing the entire group spawning aggregation of the mutton snapper. The ADCP measured the vertical velocity profile of currents at 15-minute sampling intervals with 300 pings per interval and a bin size of 0.5m. The shelf edge bottom contours are aligned east to west with a slight southwest to northeast component (approximately 250° – 70° true). The RDI Sentinel ADCP has a beam angle of 20 degrees, which restricts useful data to depths greater than 6% (=1 – cos(20)) of the transducer depth. Thus, the ADCP did not provide good data close to the sea surface. Wind speed and direction measurements from a tower at Isla Magueyes were used to verify and correct the suspect data from the upper bins. Along with the vertical velocity current profile, the ADCP also provided continuous temperature measurements near the bottom of the shelf edge reef.

Hydrography - Oceanographic data were collected using a CTD (SBE 19 form Sea-Bird Electronics, Inc.) with an integrated fluorometer (Wet Labs, Inc.) in order to provide salinity, temperature, sigma-t and chlorophyll-*a* data. During each of the four sampling cruises, CTD casts were performed at stations Oc-2 and Vr-2 down to 120 m. A third cast was performed at station Ne-2 measuring the entire water column (20 m). Station time series contour plots were produced by interpolation between cast dates with the contouring program Surfer (Golden Software, Inc.)

RESULTS

Port Survey - Port surveys and fishermen interviews revealed that 2003 was a year of record mutton snapper landings. Due to bad weather, only one of the fishermen left port the night before the full moon of April 16. This fisherman reported a small catch of only seven individuals, three of them females with hydrated gonads. The weather got worst and there was no fishing done by any of the boats from the surrounding area during the first three days after the full moon. By the fourth day after the full moon a total of 500 lbs were reported. The following day 1,020 lbs were brought in. April 22 was the day of the biggest catch with approx. 4,000 lbs of mutton snapper landed. Three fishing boats caught more than a hundred individuals each. The fishermen with the largest catch had 140 individuals, weighing in at 1,300 lbs. Fishermen interviewed agreed that most of the fish where caught when the clouds covering the moon dispersed from 4:30am to 6:00am. Outing periods when the current slacked no mutton snappers would bite the lines, instead yellowtail snappers with hydrated gonads where caught. This suggests that more than one species of snapper were aggregated at the spawning site. On April 23, the catch reported was of 2,000 lbs and of 1,500 lbs on April 24. One week after the full moon the aggregation was over. All of the 126 sampled fish had mature gonads, or showed signs of recent spawning. Fish weights ranged between 7 and 18 lbs. The average standard body length was 55 cm.

Sampling effort only included landings from the fishing village of La Parguera. Members of other nearby fishing villages also targeted the aggregation, adding to a total of sixteen boats out fishing the aggregation site each night. On average, six members of the surveyed fishery were out at the aggregation site every night. The largest fishing boats from La Parguera were two 30 footers with 3 fishermen each. The smallest boat was a 17 ft artisan boat (yola) with one fisherman.

All fishermen used hand lines and all the fishing was done between dusk and dawn. Bait was thrown in the water in order to keep the aggregation localized and closer to the surface. For this particular year, as well as for the previous one, the site of most activity remained the same, just at the self-edge, south of Margarita Reef (67°.00 west) (Figure 1.)

Larval fish samplings - The total collection of larval fishes during the four sampling cruises included 10,396 individuals, of which 75 larvae were identified as Lutjanids. Water column mean abundances for total larvae and snapper larvae are reported for each distance contour in Table 2 and Figures 2 a-d. Pre-flexion total larvae represented 90% of the total larval collection, whereas the remaining 10% were flexion and post-flexion stage larvae. Form the total collected snapper larvae, pre-flexion larvae were 55% and post-flexion 45%.

Differences of larval fish abundance during spring 2003 were not statistically significant between sampling dates at any station (2-way ANOVA, $P > 0.05$). This was probably related to the high within contour variability of larval fish abundance. Water column mean abundance of larvae at the neritic station varied between 50-298 Ind/100m^3. Mean abundance at the shelf edge ranged from 19-85 Ind/100m^3 and between 73-80 Ind/100m^3 at the oceanic station. The abundance contour maps provide a snapshot characterization of temporal differences in horizontal distribution for both total larvae and snapper larvae during each cruise (Figures 3 a-d, 4 a-d).

Statistically significant differences of mean total larval abundance were found between distance contours during April 3, April 23 and May 16 dates (2-way ANOVA, $P > 0.05$). A pairwise multiple comparison procedure (Student Newman Keuls Method) identified the neritic station as significantly different from the rest. Peak total larval abundance (298 Ind/100m^3) was observed at the neritic station on April 3, followed by a comparable second peak of 261 Ind/100m^3 on April 23. Conversely, April 23 marked the minimum abundances at the shelf-edge and oceanic stations. Larval abundance at neritic, shelf-edge and oceanic stations were within the range previously reported by Ramírez-Mella and García-Sais (2003).

Two peaks of total larval abundance were evidenced in April, 2003 (Figure 4-a). The first peak was influenced by the maximum post-flexion larval abundance of 63 Ind/100m^3 on April 3 at the neritic station. This single noticeable increase in abundance of post-flexion larvae occurred two weeks following the full moon of March, during which a yellowtail snapper aggregation was detected at the shelf-edge (Figure 4 c). Unusually calm seas with multiple surface slicks were present during the April 3 cruise. Post-flexion larval abundance decreased on April 23 (2.3 Ind/m^3) and remained low on May16 (2.8 Ind/m^3). Different to the observed increase of abundance after the full moon of March, there was not such pattern following the full moon of April, during which the massive mutton snapper spawning aggregation took place.

Table 2. Monthly variations of water column mean (WCM, Ind/100m^3) larval abundance from sampling stations at inner and outer sections of the shelf-edge; La Parguera, March-May, 2003.

Total Larvae

Dates	Oceanic	Shelf-edge	Neritic
3/21/2003	52.82	19.42	50.63
4/3/2003	32.68	43.28	298.00
4/23/2003	23.23	25.80	261.33
5/16/2003	79.78	83.53	128.34

Snapper Larvae

Dates	Oceanic	Shelf-edge	Neritic
3/21/2003	1.55	0.66	0.26
4/3/2003	0.32	1.25	2.42
4/23/2003	0.20	0.28	0.00
5/16/2003	0.37	0.83	2.09

Total Pre-flexion Larvae

Dates	Oceanic	Shelf-edge	Neritic
3/21/2003	46.25	14.52	41.80
4/3/2003	27.24	36.06	256.00
4/23/2003	19.52	22.06	259.00
5/16/2003	73.54	70.90	122.92

Snapper Larvae Pre-flexion

Dates	Oceanic	Shelf-edge	Neritic
3/21/2003	0.28	0.42	0.30
4/3/2003	0.14	0.73	2.15
4/23/2003	0.07	0.07	0.00
5/16/2003	0.00	0.00	1.25

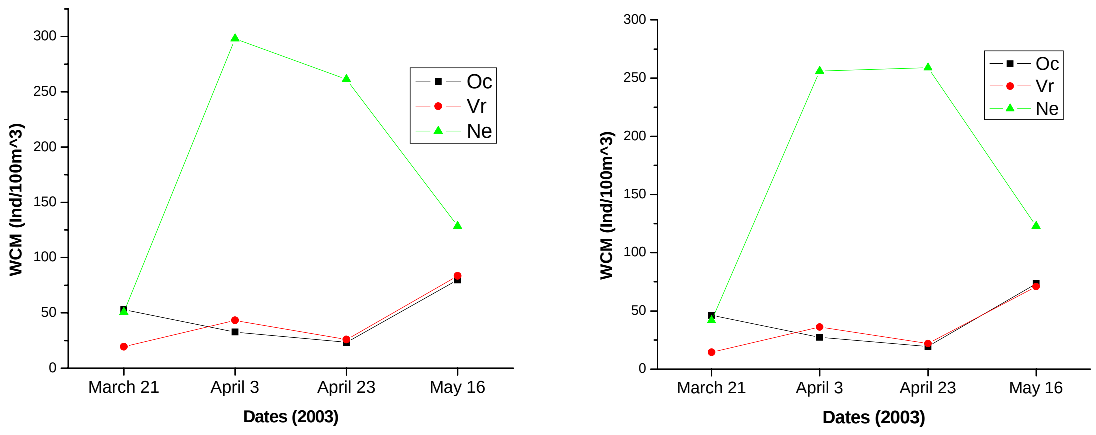
Total Post-flexion Larvae

Dates	Oceanic	Shelf-edge	Neritic
3/21/2003	6.56	2.93	8.83
4/3/2003	5.44	7.22	63.00
4/23/2003	3.72	3.74	2.33
5/16/2003	5.06	4.19	2.77

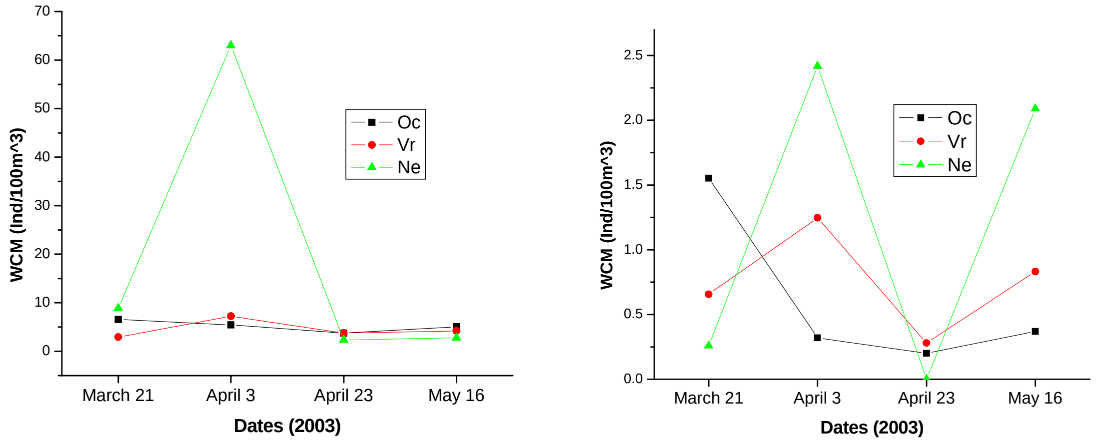
Snapper Larvae Post-flexion

Dates	Oceanic	Shelf-edge	Neritic
3/21/2003	0.38	0.09	0.00
4/3/2003	0.05	0.30	0.27
4/23/2003	0.07	0.07	0.00
5/16/2003	0.20	0.80	0.84

a) Total larvae b) Total larvae pre-flexion



b) Total larvae post-flexion d) Snapper larvae



e) Snapper larvae Pre-flexion f) Snapper larvae post-flexion

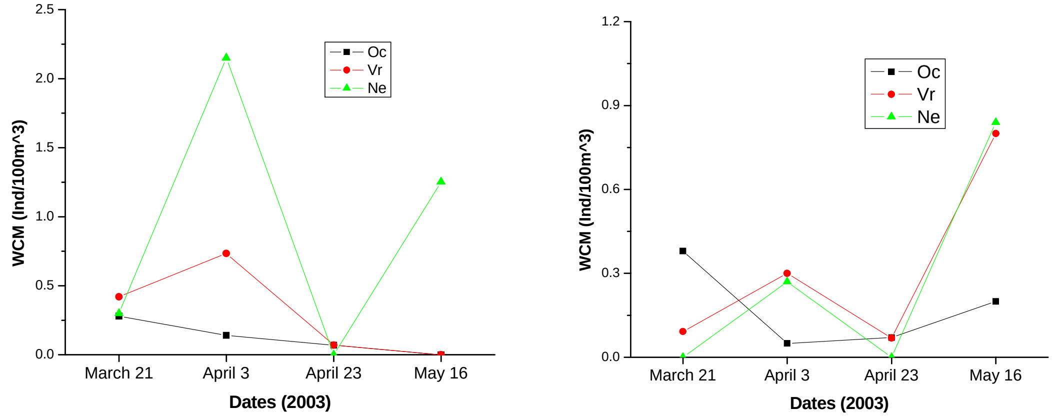
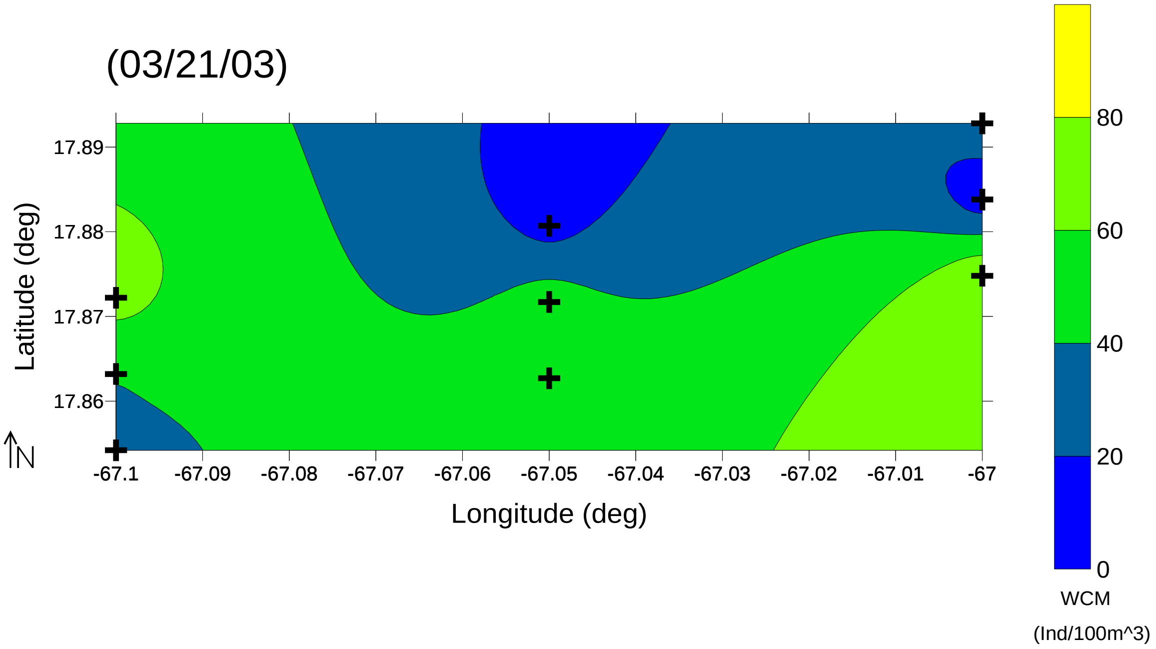


Figure 2 a-d. Monthly variations of larval abundance from sampling stations at inner and outer sections of the shelf-edge, La Parguera, March – May, 2003.

a) March 21, 2003



b) April 3, 2003

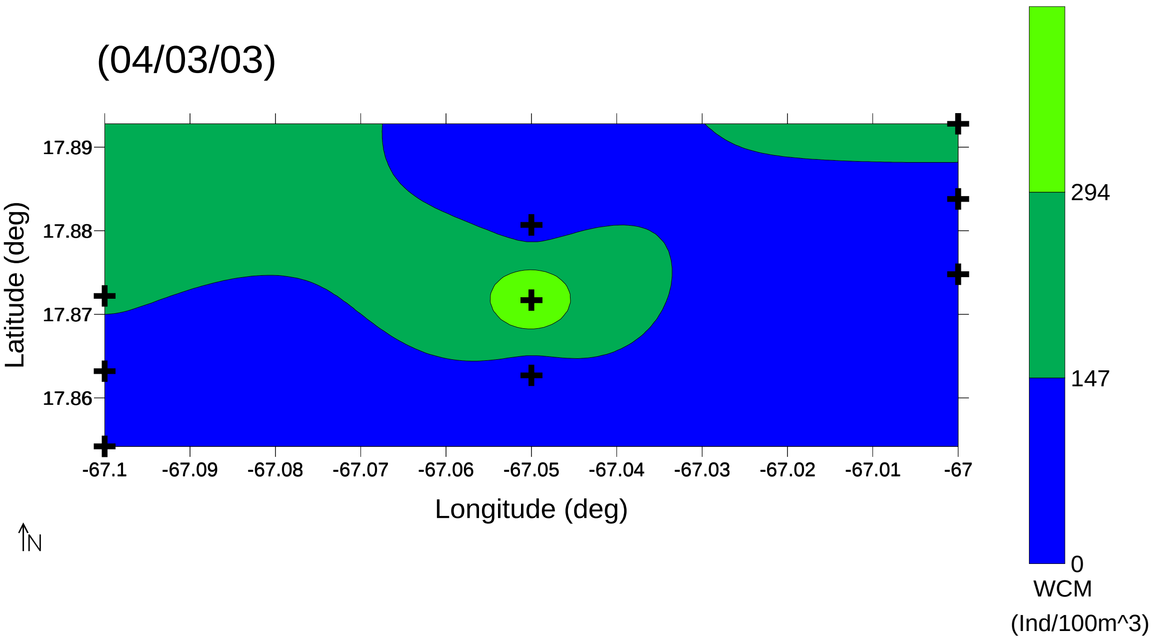
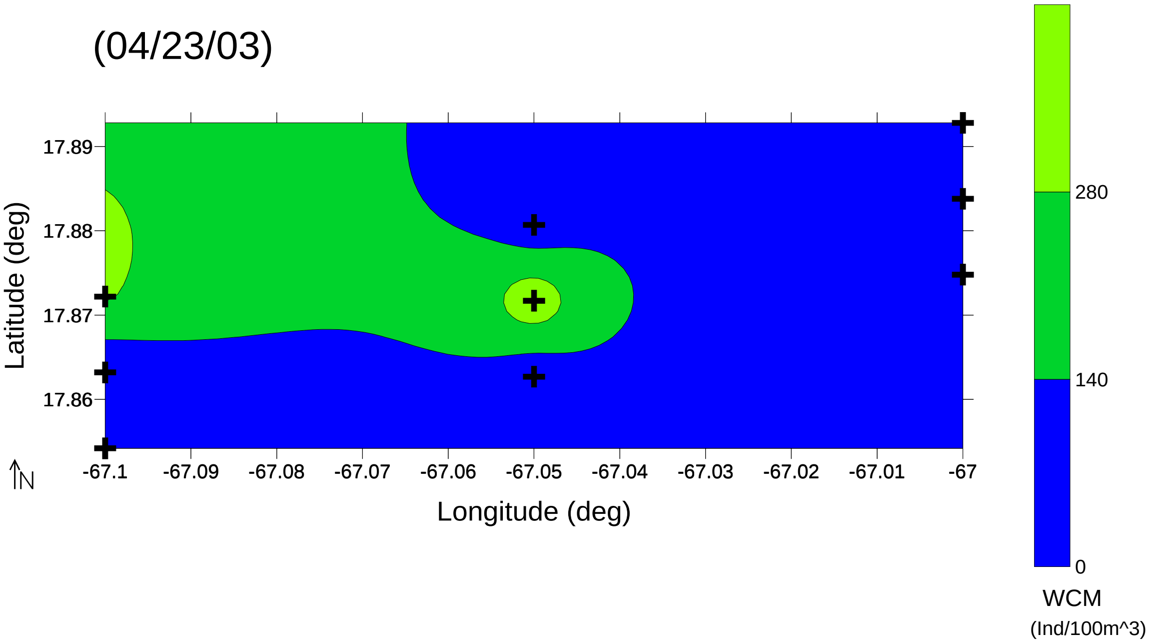


Figure 3 a-d. Contour maps of water column mean abundances (WCM) of total larvae collected during four cruises off La Parguera, Puerto Rico.

c) April 23, 2003



d) May 16, 2003

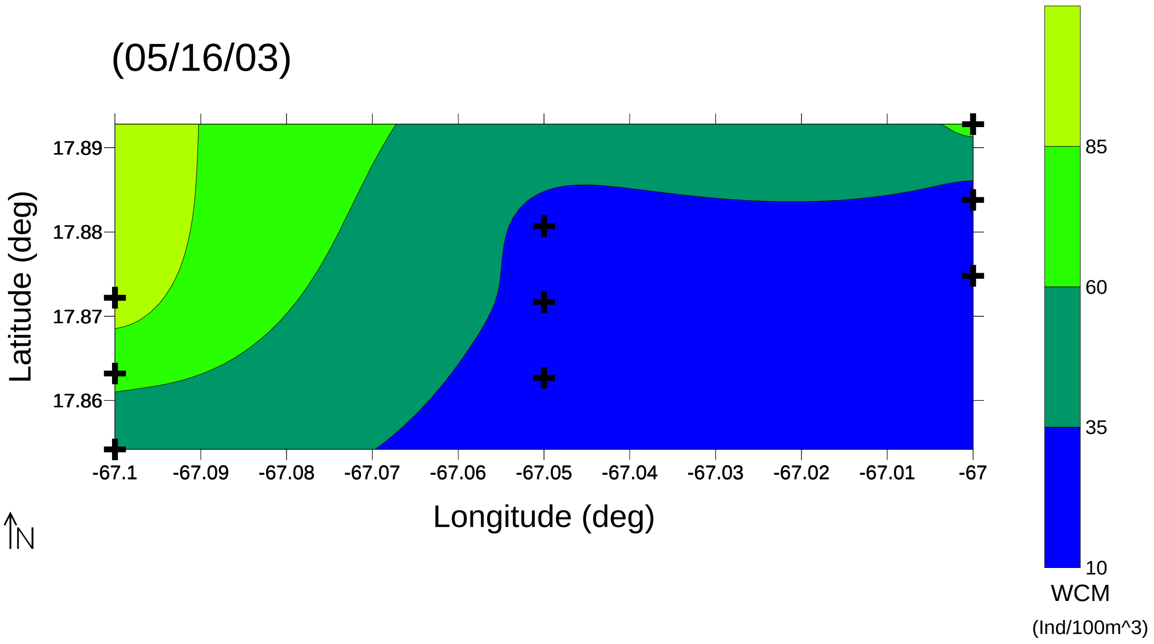
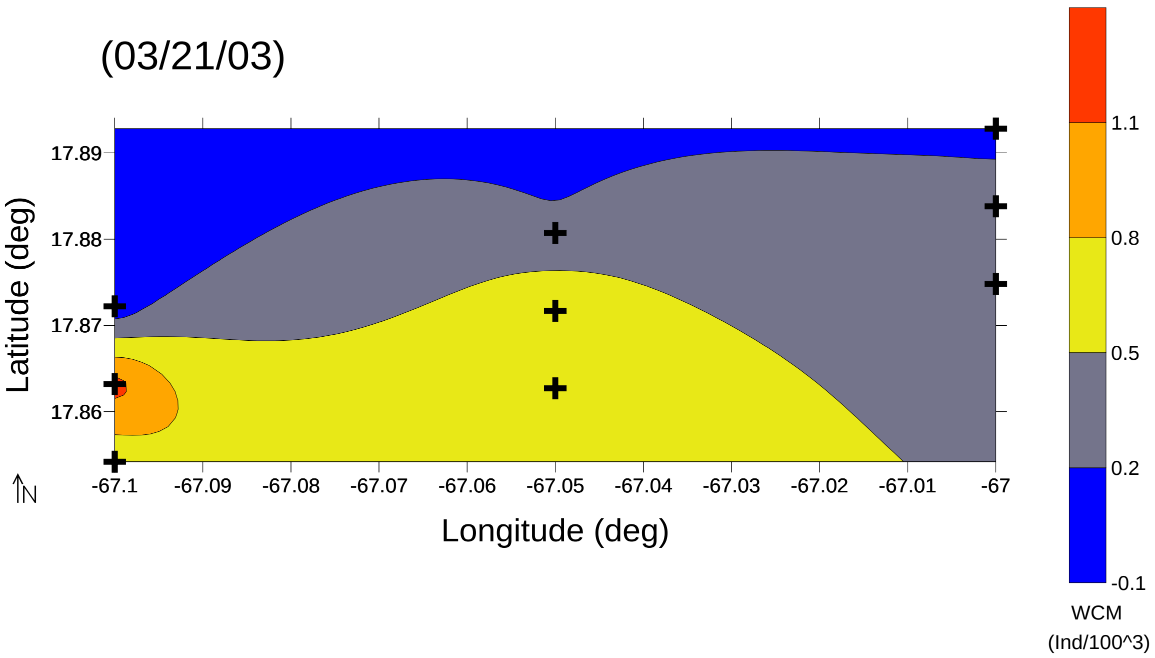


Figure 3. (cont.).

a) March 21, 2003



b) April 3, 2003

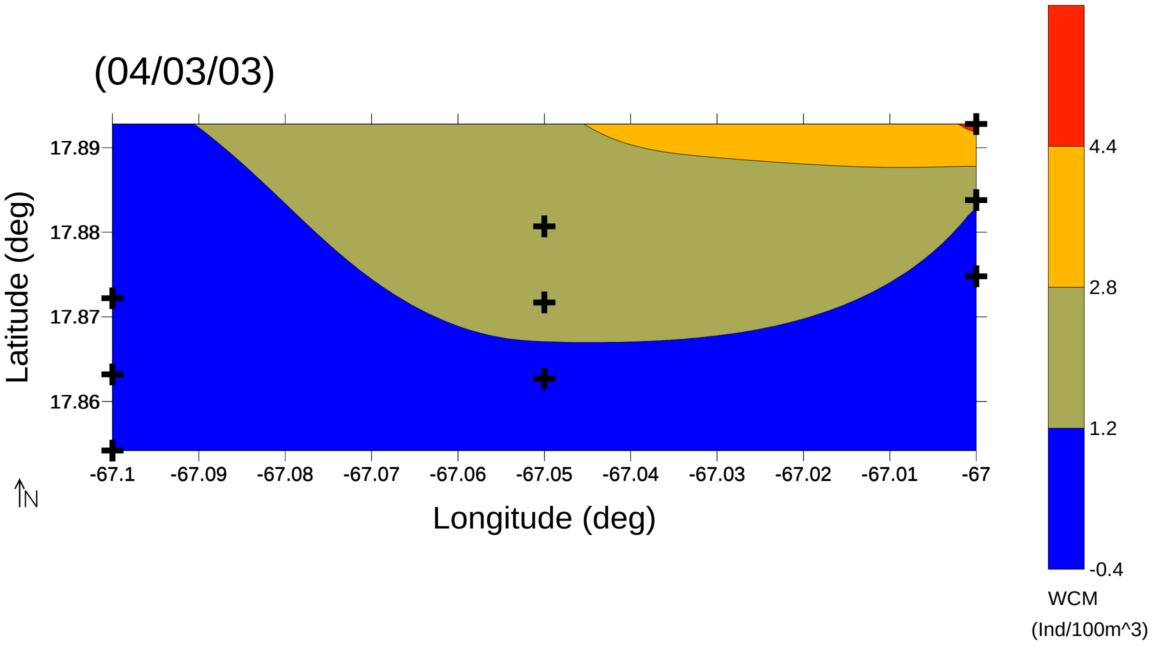
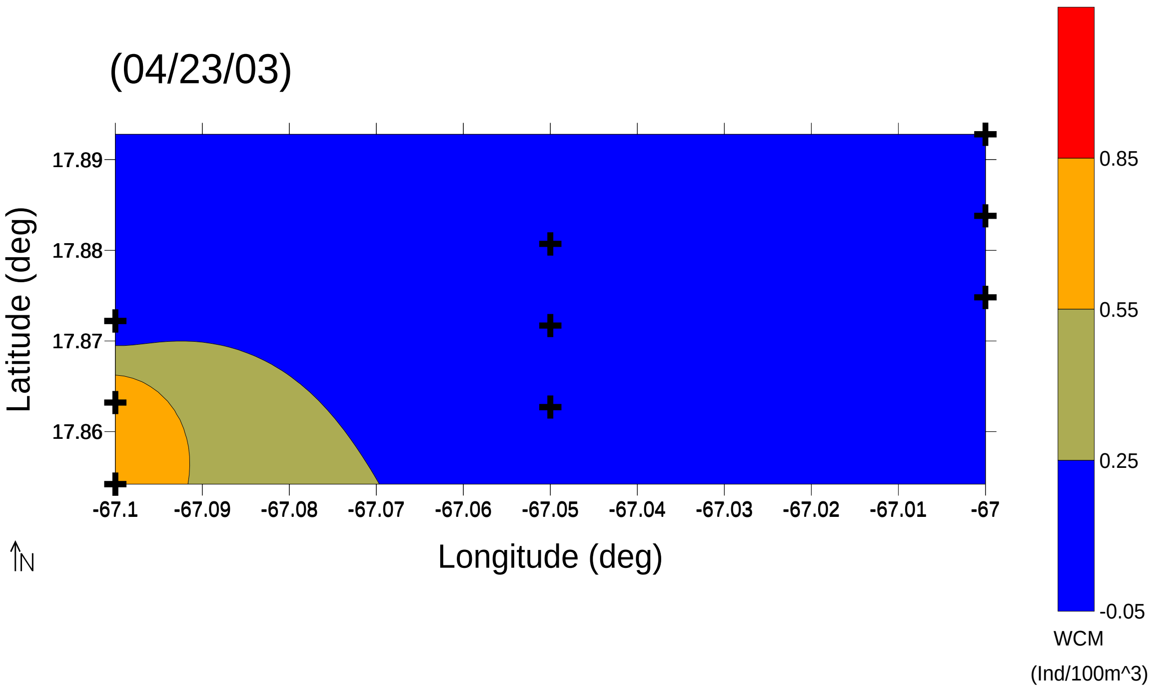


Figure 4 a-d. Contour maps of water column mean abundances (WCM) of snapper larvae collected during four cruises off La Parguera, Puerto Rico.

c) March 23, 2003



d) May 16, 2003

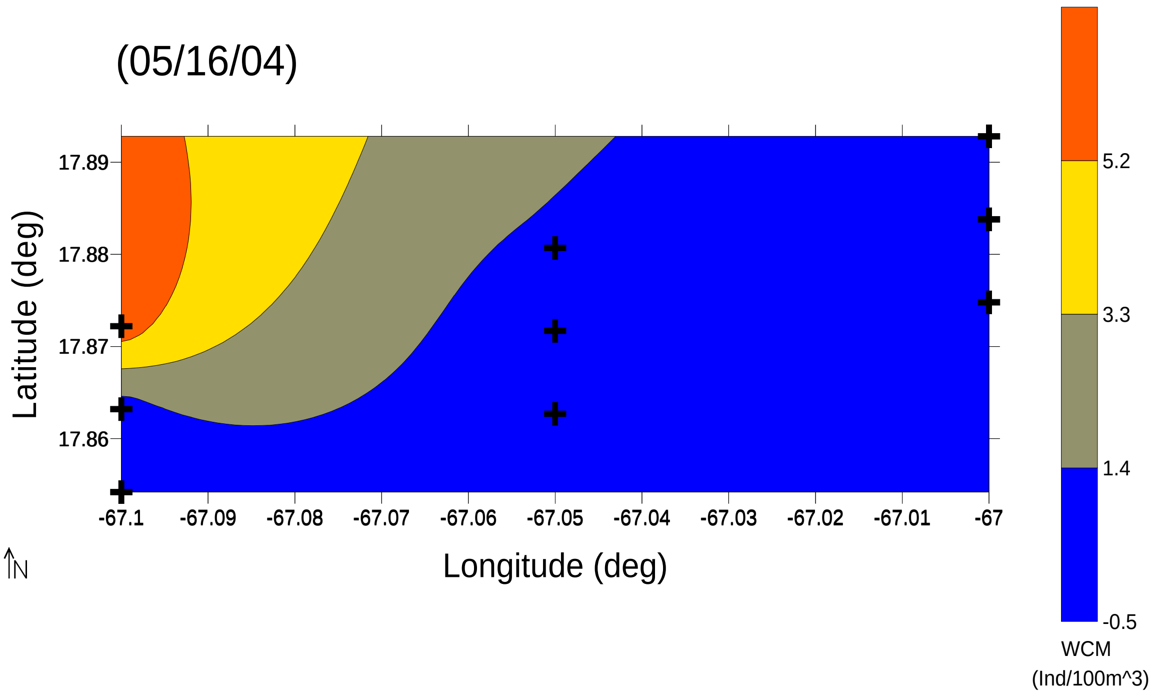


Figure 4. (cont.)

The second peak of total larval abundance occurred during April 23, three weeks after the first one. This second peak was propelled by the highest mean abundance of early stage larvae (259 Ind/100m^3) at the neritic station. Maximum mean abundance of early stage larvae occurred one week after the detection of cold water associated with the breaking internal wave at the shelf edge. Pre-flexion larval abundance then decreased to (123 Ind/100m^3) on May 16 (Figure 4-b).

Abundance of snapper larvae ranged from 0.2 to 2.4 Ind/100m^3 at the neritic, shelf-edge and oceanic stations respectively during sampling cruises of March through May 2003 (Figure 4-d). Mean abundances of snapper larvae at the neritic shelf-edge and oceanic stations was below the range previously reported by Ramírez-Mella and García-Sais, (2003) of 5 – 7 Ind/100m^3. Maximum snapper larvae abundance (2.4 Ind/100m^3) was found at the neritic station on April 3rd. The lowest abundance of snapper larvae for all three stations was recorded on April 23, 2003. The April 23rd cruise took place during the last day of the mutton snapper massive spawning aggregation and was characterized by high relative abundance of unidentifiable early stage larvae. This large number of yolk-sack stage larvae may have been mutton snapper larvae.

At least two species of snapper larvae are included in the total collection and appear to share a similar distribution range within the array of stations sampled (Plates 1 and 2). During the March 21 cruise, a very large aggregation of yellowtail snapper (*Lutjanus chrysurus*) was detected at the shelf-edge area known as “El Hoyo”, and fishermen landed thousands of pounds. Thus, it is possible that the early pre-flexion larvae collected during the initial cruise of March 2003 were indeed yellowtail snappers.

Plate 1. Type A (pre-flexion stage)

Plate 2. Type B (post-flexion stage)

Currents – The vertical flow variability profile at the shelf-edge reef system off La Parguera was monitored to gain insight about the initial direction of fish eggs and larvae transport during the period of the mutton snapper spawning aggregation. Summarized statistics for the ADCP data are presented in Tables 2 and 3. Surface reflection of the acoustic signal and wind driven surface wave activity make the near surface measurement questionable. Wind direction and magnitude obtained from a tower at Isla Magueyes were used to estimate surface velocities.

Mean speed was always strongest at the surface (2.5-3.0 m deep) and then decreased linearly with depth due to constant vertical shear until a depth of 18 m, where the bottom friction slows it down, eventually bringing it to a stop (Figure 5 a-b). Mid-water (11 m) mean speed was 10.5 cm/s and peaked at 31.9 cm/s. Mean current direction was due west at the surface and southwest below the surface.

Tidal currents were the main source of flow variability, with typical semidiurnal amplitude of 15 cm/s in spite of the diurnal nature of tides in the northern Caribbean. Westward flow was strongest when in phase with the high tide. Eastward flow peaked when in phase with the low tide. The maximum recorded speed resulted from the addition of a 20 cm/s tidal current amplitude to a westward low frequency flow of 10 cm/s. Contrary to observations at the site during the previous year (Figure 6 a-b), where flow oscillated due to tidal effects, a persistent westward flow accelerated or slowed down according to the tidal component rather than reversing the direction.

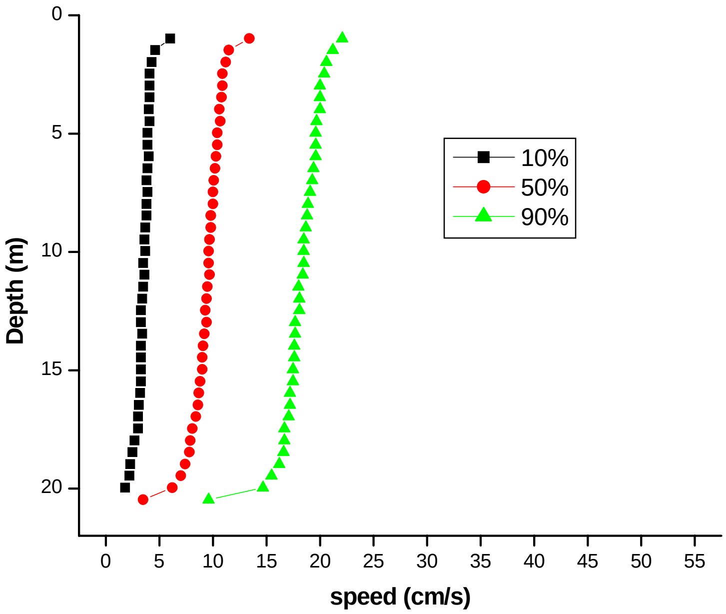
Table 3. ADCP mean statistics and percentiles at “El Hoyo”, La Parguera during 3/21/03 – 4/08/03. Depth in meters and speeds in cm/s. Scalar = scalar speed average, Res = magnitude of the resultant vector, Dir = direction of the resultant vector, R/S = Res/Scalar ratio, u = average of the u (east-west) component, v = average of the v (north – south) component. Data at 10%,50% and 90% depth are highlited in bold.

Depth	Scalar	Res	Dir	R/S	U	V	10	50	90	max
0.97	30.9	29.0	289.0	0.9	-27.5	9.3	13.9	31.0	46.9	71.2
1.47	13.8	10.7	276.0	0.8	-10.7	1.2	6.0	13.4	22.1	36.1
1.97	**12.4**	**8.4**	**264.0**	**0.7**	**-8.3**	**-0.8**	**4.6**	**11.5**	**21.2**	**35.4**
2.47	12.0	7.7	263.0	0.6	-7.6	-1.0	4.3	11.2	20.6	35.6
2.97	11.8	7.5	262.0	0.6	-7.4	-1.0	4.1	10.9	20.4	32.9
3.47	11.6	7.3	261.0	0.6	-7.2	-1.1	4.1	10.9	20.0	33.7
3.97	11.5	7.2	260.0	0.6	-7.1	-1.2	4.1	10.8	20.0	33.8
4.47	11.4	7.1	260.0	0.6	-6.9	-1.2	4.0	10.6	20.0	31.8
4.97	11.4	7.0	260.0	0.6	-6.9	-1.3	4.1	10.7	19.7	33.8
5.47	11.3	6.8	259.0	0.6	-6.7	-1.3	3.9	10.4	19.6	32.9
5.97	11.2	6.8	259.0	0.6	-6.7	-1.3	3.9	10.4	19.6	33.8
6.47	11.2	6.7	258.0	0.6	-6.6	-1.4	4.0	10.3	19.6	32.3
6.97	11.0	6.7	258.0	0.6	-6.5	-1.4	3.9	10.2	19.4	31.8
7.47	11.0	6.6	257.0	0.6	-6.4	-1.5	3.8	10.1	19.3	31.8
7.97	10.9	6.5	257.0	0.6	-6.3	-1.5	3.9	10.0	19.1	30.9
8.47	10.8	6.4	256.0	0.6	-6.2	-1.5	3.8	10.0	18.9	31.4
8.97	10.7	6.4	256.0	0.6	-6.2	-1.6	3.8	9.8	18.8	31.8
9.47	10.6	6.3	256.0	0.6	-6.1	-1.5	3.7	9.8	18.7	30.0
9.97	10.6	6.2	255.0	0.6	-6.0	-1.6	3.6	9.7	18.5	31.7
10.47	10.5	6.1	255.0	0.6	-5.9	-1.6	3.7	9.6	18.5	33.0
10.97	10.5	6.1	255.0	0.6	-5.9	-1.6	3.5	9.6	18.5	31.9
11.47	10.4	6.0	254.0	0.6	-5.8	-1.6	3.6	9.7	18.4	31.2
11.97	10.3	6.0	254.0	0.6	-5.8	-1.6	3.5	9.5	18.0	33.6
12.47	10.2	5.9	254.0	0.6	-5.7	-1.7	3.4	9.4	18.1	30.7
12.97	10.1	5.9	254.0	0.6	-5.6	-1.6	3.3	9.3	18.1	30.0
13.47	10.1	5.8	254.0	0.6	-5.6	-1.6	3.3	9.4	17.7	30.8
13.97	10.0	5.7	254.0	0.6	-5.5	-1.6	3.4	9.2	17.7	28.8
14.47	9.9	5.7	253.0	0.6	-5.5	-1.6	3.3	9.1	17.6	30.3
14.97	9.9	5.6	253.0	0.6	-5.4	-1.6	3.3	9.0	17.6	28.9
15.47	9.8	5.6	253.0	0.6	-5.4	-1.7	3.3	9.0	17.5	29.2
15.97	9.7	5.5	253.0	0.6	-5.3	-1.7	3.3	8.8	17.5	29.2
16.47	9.6	5.6	252.0	0.6	-5.3	-1.7	3.2	8.7	17.2	30.4
16.97	9.5	5.5	252.0	0.6	-5.2	-1.7	3.1	8.6	17.2	29.0
17.47	9.3	5.5	252.0	0.6	-5.2	-1.7	3.0	8.4	17.1	29.3
17.97	9.1	5.5	252.0	0.6	-5.2	-1.7	3.0	8.1	16.7	29.5
18.47	8.9	5.5	251.0	0.6	-5.2	-1.8	2.7	7.9	16.7	31.7
18.97	8.7	5.5	250.0	0.6	-5.2	-1.8	2.5	7.8	16.6	27.9
19.47	**8.4**	**5.4**	**250.0**	**0.6**	**-5.1**	**-1.9**	**2.3**	**7.4**	**16.2**	**28.3**
19.97	8.0	5.3	248.0	0.7	-4.9	-2.0	2.2	7.0	15.5	27.1
20.47	7.3	4.9	245.0	0.7	-4.5	-2.0	1.8	6.2	14.7	27.6

Table 4. ADCP mean statistics and percentiles at "El Hoyo", La Parguera during 3/21/03 – 4/08/03.. Same parameters as in Table 3.

Depth	Scalar	Res	Dir	R/S	U	V	10	50	90	max
0.96	17.4	15.9	291.0	0.9	-14.9	5.6	7.4	16.8	28.0	49.5
1.46	14.8	13.3	272.0	0.9	-13.3	0.5	6.7	14.4	23.1	40.8
1.96	**14.4**	**12.7**	**257.0**	**0.9**	**-12.4**	**-3.0**	**5.2**	**13.9**	**23.8**	**47.1**
2.46	12.9	11.0	254.0	0.9	-10.6	-2.9	4.6	12.3	21.7	45.1
2.96	12.6	10.7	254.0	0.8	-10.3	-3.0	4.5	11.9	21.4	44.4
3.46	12.5	10.6	254.0	0.8	-10.1	-3.0	4.4	11.7	21.2	43.4
3.96	12.2	10.4	253.0	0.9	-10.0	-3.0	4.3	11.6	20.7	41.3
4.46	12.1	10.3	253.0	0.8	-9.8	-3.0	4.2	11.3	20.7	44.7
4.96	11.9	10.1	253.0	0.8	-9.7	-2.9	4.1	11.2	20.3	40.4
5.46	11.7	9.9	253.0	0.8	-9.5	-2.9	4.1	11.3	20.0	39.4
5.96	11.5	9.7	253.0	0.8	-9.3	-2.8	4.0	10.9	19.8	39.8
6.46	11.4	9.6	253.0	0.8	-9.2	-2.8	3.8	10.8	19.6	39.1
6.96	11.2	9.4	252.0	0.8	-9.0	-2.8	3.6	10.7	19.3	39.3
7.46	11.1	9.3	252.0	0.8	-8.9	-2.8	3.7	10.6	19.3	36.9
7.96	11.0	9.2	252.0	0.8	-8.8	-2.9	3.6	10.5	19.3	37.6
8.46	10.9	9.1	252.0	0.8	-8.6	-2.8	3.5	10.4	18.9	34.8
8.96	10.8	9.0	252.0	0.8	-8.5	-2.8	3.4	10.2	19.0	33.1
9.46	10.7	8.9	251.0	0.8	-8.4	-2.9	3.4	10.1	18.6	32.0
9.96	10.7	8.8	251.0	0.8	-8.3	-2.8	3.4	10.1	18.6	32.0
10.46	10.6	8.7	251.0	0.8	-8.2	-2.8	3.4	10.0	18.6	33.1
10.96	**10.5**	**8.6**	**251.0**	**0.8**	**-8.1**	**-2.8**	**3.4**	**9.9**	**18.4**	**33.7**
11.46	10.5	8.4	251.0	0.8	-8.0	-2.7	3.4	9.7	18.3	32.5
11.96	10.4	8.4	251.0	0.8	-7.9	-2.7	3.4	9.9	18.4	31.5
12.46	10.4	8.2	251.0	0.8	-7.8	-2.6	3.5	9.8	18.2	32.2
12.96	10.3	8.1	251.0	0.8	-7.7	-2.6	3.3	9.8	18.0	30.4
13.46	10.3	8.0	251.0	0.8	-7.6	-2.6	3.3	9.7	18.0	31.4
13.96	10.2	7.9	252.0	0.8	-7.5	-2.5	3.2	9.7	17.8	31.1
14.46	10.1	7.8	252.0	0.8	-7.4	-2.4	3.2	9.7	17.8	29.9
14.96	10.1	7.7	252.0	0.8	-7.3	-2.4	3.3	9.5	17.6	32.6
15.46	10.0	7.5	252.0	0.8	-7.2	-2.4	3.1	9.5	17.4	29.5
15.96	9.8	7.4	252.0	0.8	-7.0	-2.3	3.0	9.4	17.3	28.9
16.46	9.8	7.3	252.0	0.7	-6.9	-2.2	3.0	9.1	17.1	31.1
16.96	9.6	7.1	253.0	0.7	-6.8	-2.1	3.0	9.0	17.1	30.3
17.46	9.6	7.0	253.0	0.7	-6.7	-2.0	2.9	9.0	17.0	28.8
17.96	9.4	6.8	253.0	0.7	-6.5	-2.0	2.9	8.8	16.9	28.0
18.46	9.3	6.6	253.0	0.7	-6.3	-1.9	2.8	8.6	16.7	30.6
18.96	9.1	6.3	254.0	0.7	-6.0	-1.8	2.8	8.4	16.2	27.6
19.46	8.8	6.0	254.0	0.7	-5.8	-1.7	2.6	8.2	16.0	27.2
19.96	**8.4**	**5.6**	**253.0**	**0.7**	**-5.4**	**-1.7**	**2.5**	**7.7**	**15.3**	**26.8**
20.46	7.6	5.0	251.0	0.7	-4.7	-1.6	2.1	6.8	13.8	25.2

a) 3/03 – 4/08, 2003



b) 4/08 – 5/16, 2003

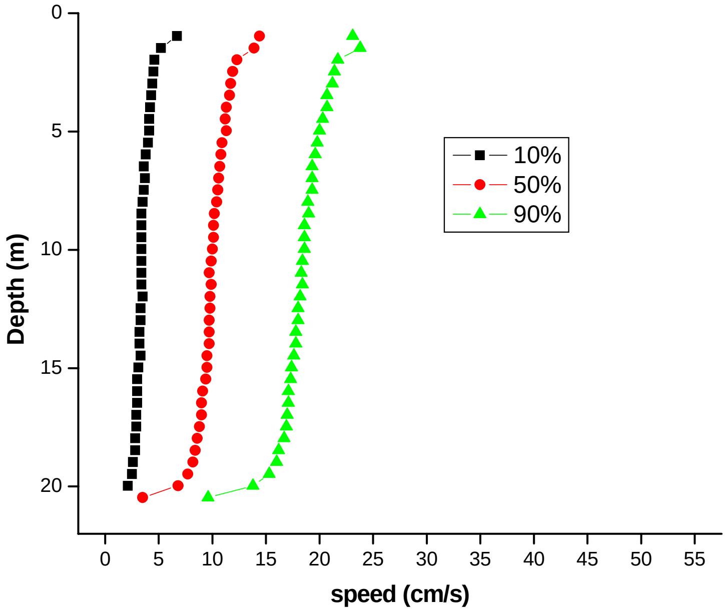
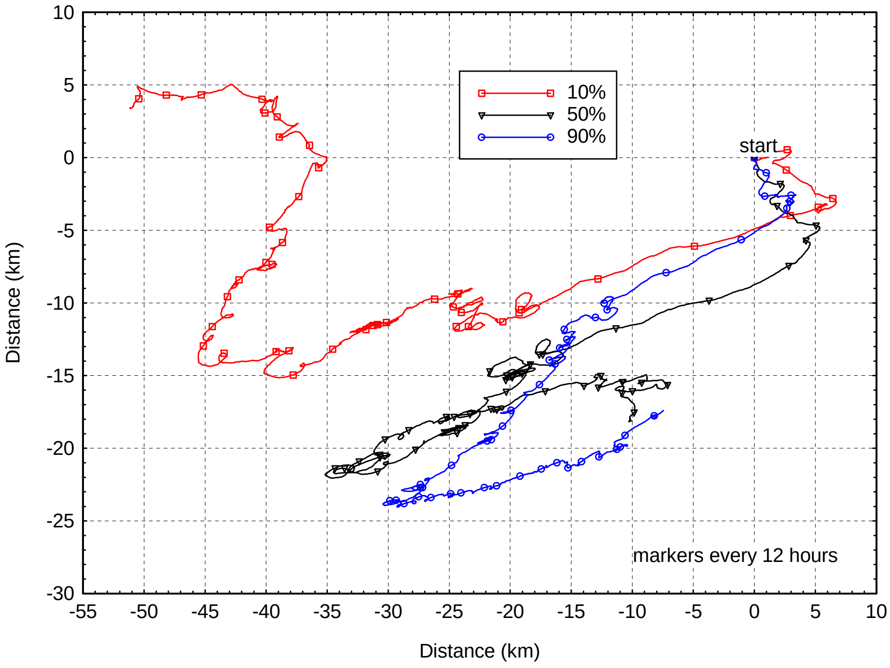


Figure 5 a- b. Current speed vertical profiles at “El Hoyo”, La Parguera during 2003.

a) 2/26 – 3/20, 2002



b) 3/25 – 4/05, 2002

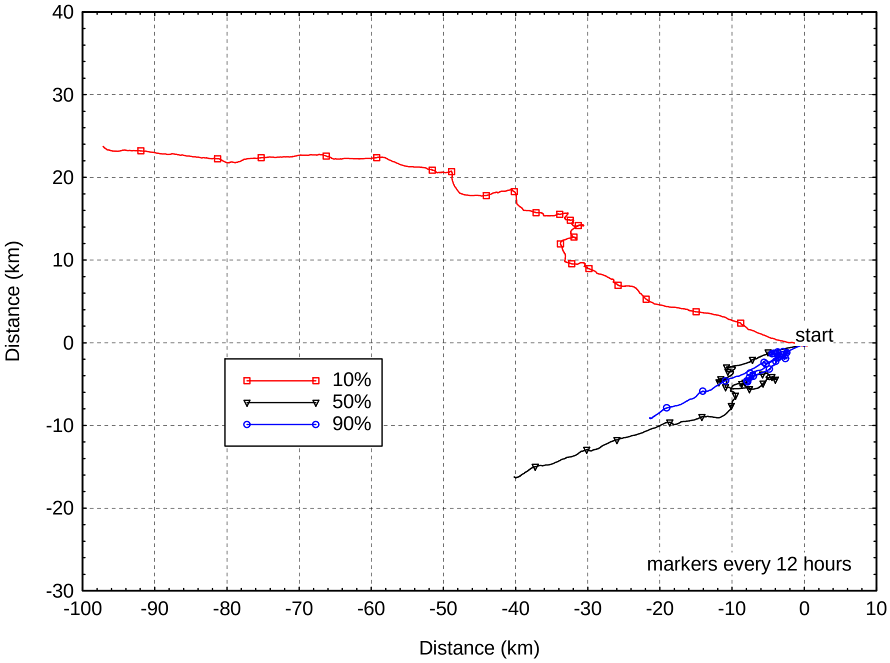
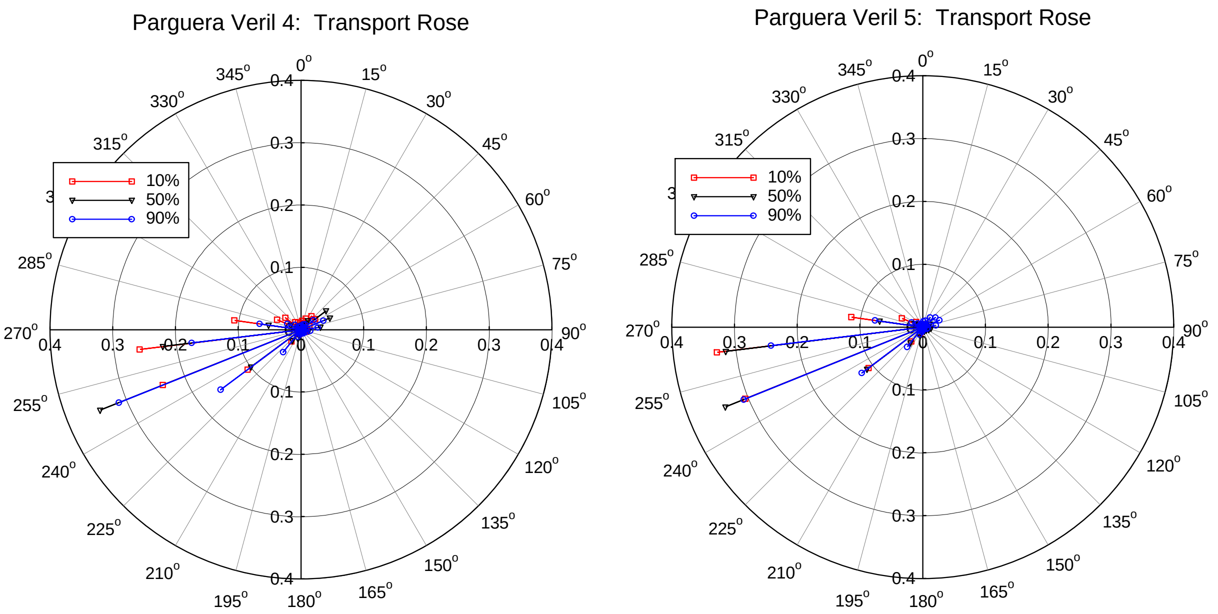


Figure 6 a-b. Progressive current vector time series at "El Hoyo", La Parguera during a) 2/26 – 3/20, 2002. b) 3/25 – 4/05, 2002.

Flow oscillations were measured by the mean resultant magnitude to mean ratios (Tables 2 and 3). Linear flow patterns generated high ratios. Oscillatory flow behavior during the monitoring period is best appreciated in the progressive vector (PV) pseudo-trajectories presented in Figure 6 and in the directional distributions of transport-per-unit-area (Figures 7a-b). Assuming uniform along-isobath velocities similar to those observed at the mutton snapper spawning aggregation, the positively buoyant larvae would have been transported westward 7.3 km per day. Figures 8 a-b show the spring 2003 east-west current components as a persistent westward flow accelerated or slowed down, rather than reversing direction according to the semidiurnal tidal cycle. This suggests that the pelagic eggs and larvae sampled during the corresponding cruises resulted from fishes spawning upstream of the study area; the magnitude and consistency of the flow is indicative of how far these larvae could have been transported. Similarly, any eggs and recently hatched larvae spawned from La Parguera would have had low probabilities of local retention, at least until developing swimming capabilities

Rapid cooling near the bottom was detected on April 17, 2003. Northward (shoreward) flow near the bottom accompanied the drop in temperature with maximum velocities reaching 10 cm/s. A simultaneous offshore flow with velocities of up to 35 cm/s on the upper seven meters of the water column indicated surface waters moving offshore as deep water surged on to the reef slope. Color contours of the zonal (east-west) and meridional (north-south) velocity components from April 14 to April 23 are presented in Figures 9 and 10. The cross shelf velocity burst of the April 17 event stood out from the otherwise nearly homogeneous structure of the internal layer.



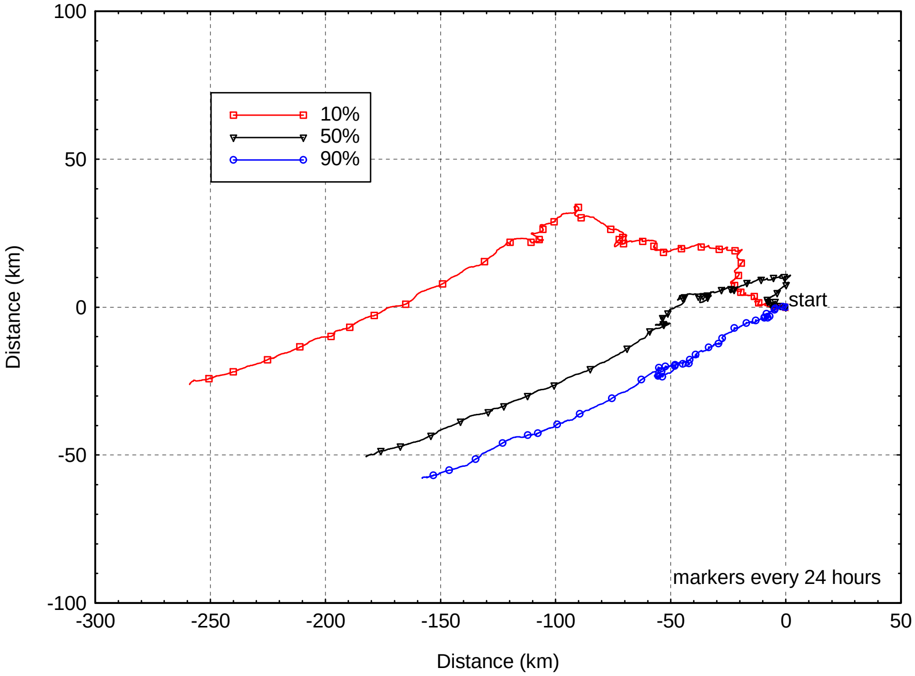
a) 3/21/03 – 4/8/03.

b) 4/8/03 – 5/16/03.

Figure 7 a-b. Directional distributions in percentiles of transport-per-unit-area. a) 3/21/03 – 4/8/03. b) 4/8/03 – 5/16/03.

A return to previous conditions started approximately 7 days after the initial cooling. The water column rapidly warmed up from 27.45 C to 28.23 C from April 25 to April 27 signaling to the possibility of cooler water being trapped on the deeper sand ridge behind the shelf-edge reef at La Parguera. This pattern of cool water flowing inshore near the bottom accompanied by warm surface water flowing offshore is typical of events where internal waves bring deeper cooler water to the shelf platform as described by Leichter et al. (1996). Flow during non-internal wave periods was predominantly along shore with linear westward flow accelerating and decelerating according to tidal influence and reaching peak velocities of ~30cm/s.

a) 3/03 – 4/08, 2003



b) 4/08 – 5/16, 2003

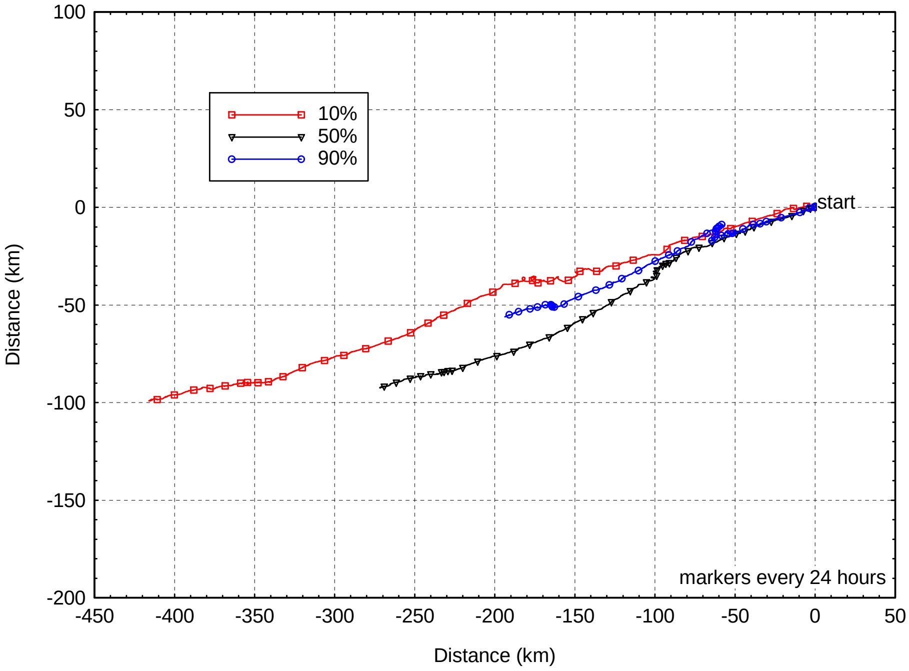


Figure 8 a- b. Progressive water current vectors at "El Hoyo", La Parguera during a) 3/03 – 4/08, 2003. b) 4/08 – 5/16, 2003.

Hydrography – Water column hydrographic profiles of Oc-2, Vr-2 and Ne-2 stations during the fall of 2003 are shown in Figures 11- 19. On all four sampling dates the water column showed stable density stratification typical of springtime thermocline with a warmer mixed surface layer overlying cooler subsurface water. During March 21 and May 16 stratification of the mixed layer was strong and the thermocline was located near a depth of ~80 m. However, in April 3 and April 23 the stratification was weaker with a less sharply defined thermocline. At station Ne-2, the 20 m water column 3 km shoreward from the shelf-edge was completely homogeneous for the April 3 and the May 16 sampling dates. A progressive increment of water temperature approaching the summer was measured at all stations, except during the April 23 profile. This anomaly of the April 23 profile was more pronounced at the Ne-2 and Vr-2 stations, where a warmer temperature layer was detected in the first 10 meters of the water column. Fluorescence showed marked subsurface peaks indicating well-defined chlorophyll-*a* maximum layers associated with the thermocline. However, on April 23, chlorophyll-*a* concentrations peaked at Vr-2 at a depth of 17 m. That same day, the highest recorded chlorophyll-*a* concentration was measured at 10 m in Ne-2.

The eroded thermoclines, observed during April 3 and April 23 appear to be associated with breaking internal waves that also transported cooler waters on to the shelf. Chlorophyll-*a* concentrations above the shelf were comparatively low during periods before and after the internal wave event. When warm waters prevailed over the shelf, chlorophyll-*a* concentrations remained below 1.3ug/l. The arrival of a single isolated cold (deeper) water event on April 17, 2003 may explain the sharp increase in fluorescence recorded during the April 23 cast at stations Ne-2 and Vr-2.

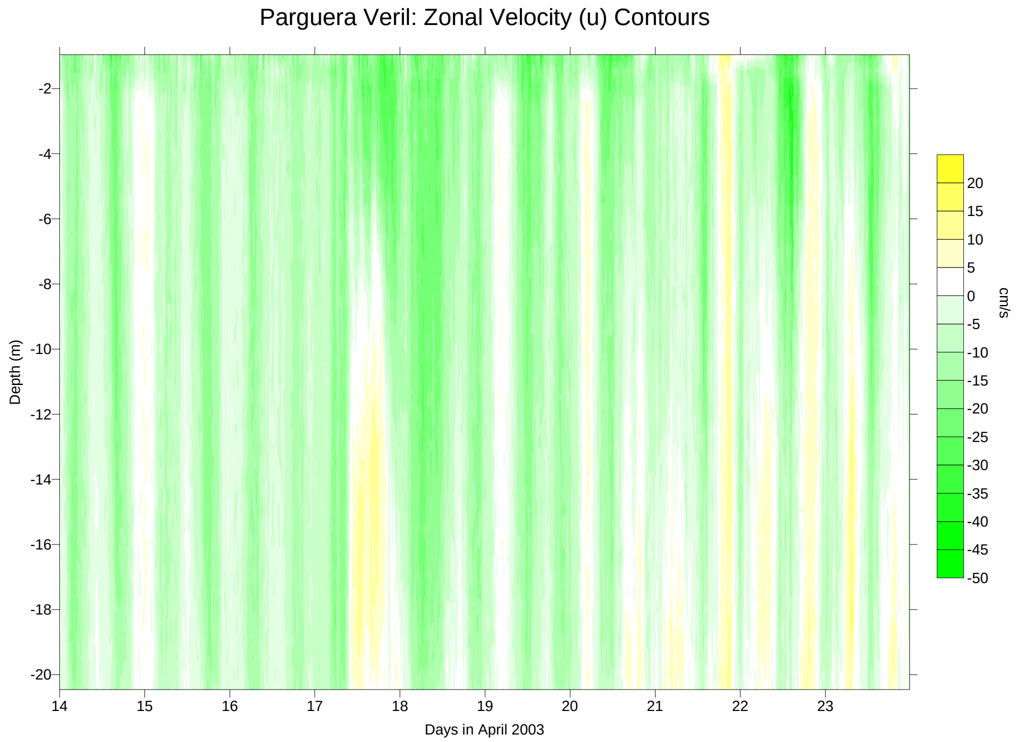


Figure 9. Zonal water current velocity u (east-west) contours at La Parguera.

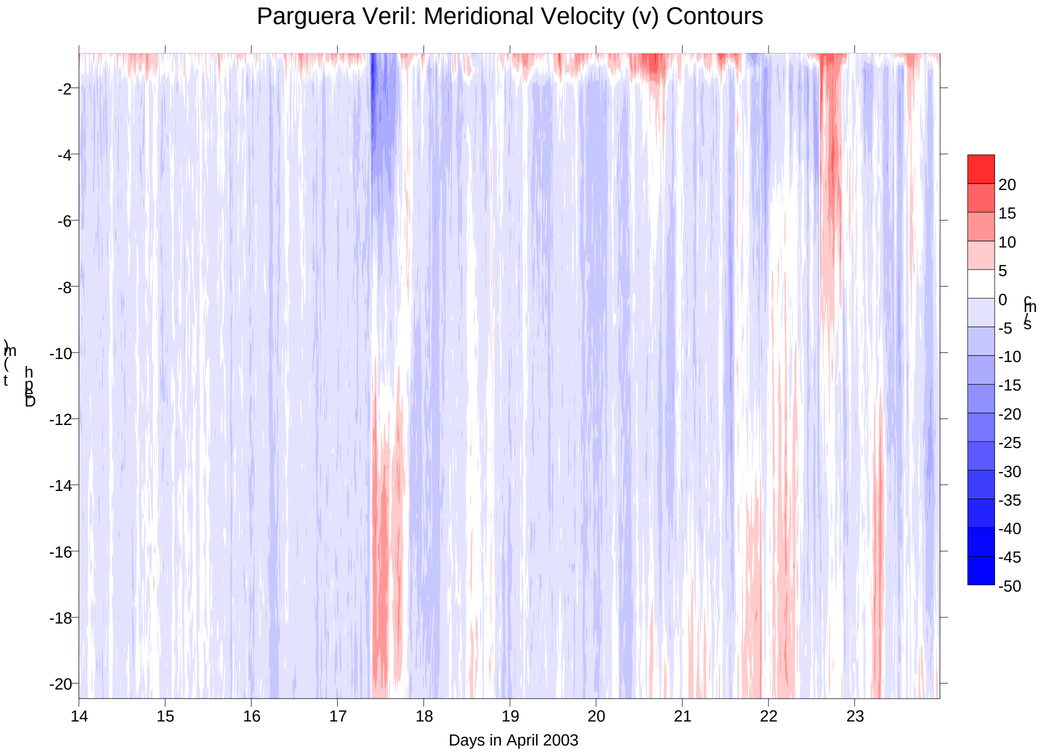


Figure 10. Meridional water current velocity v (north-south) contours at La Parguera.

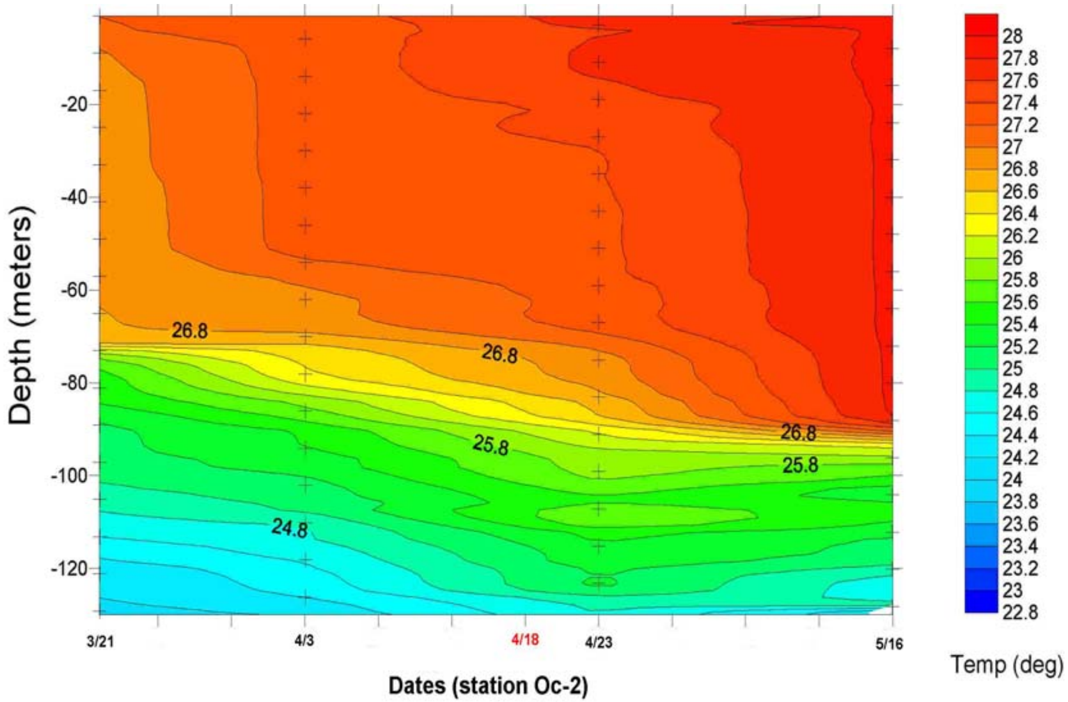


Figure 11. Water temperature contours at station Oc-2, La Parguera.

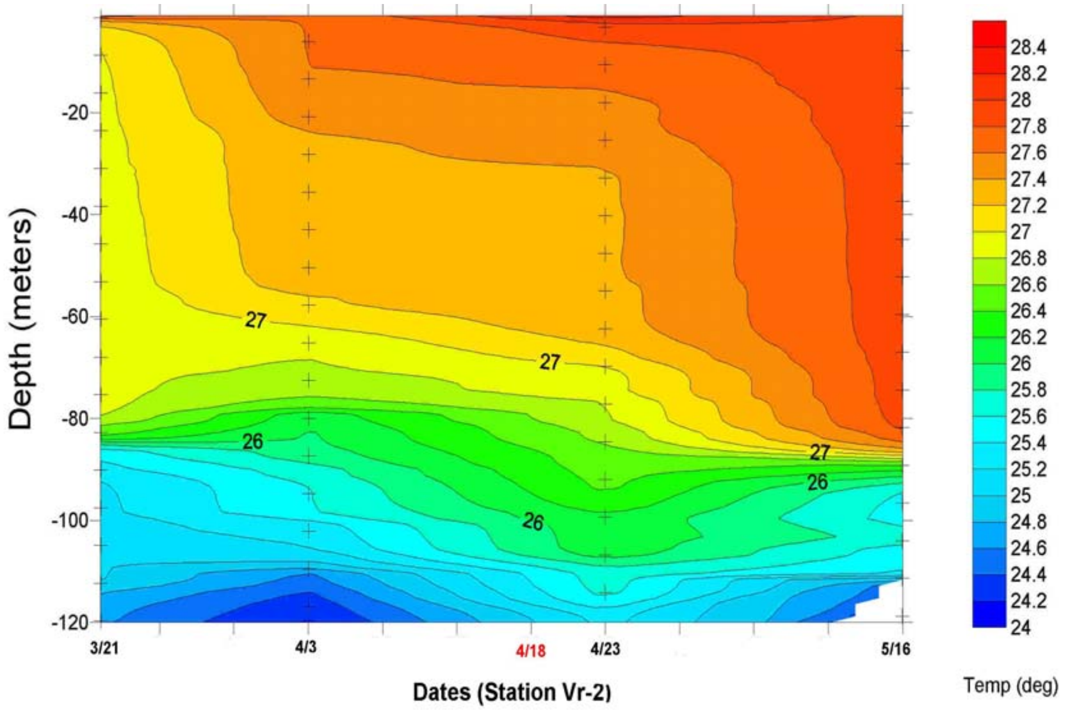


Figure 12. Water temperature contours at station Vr-2, La Parguera.

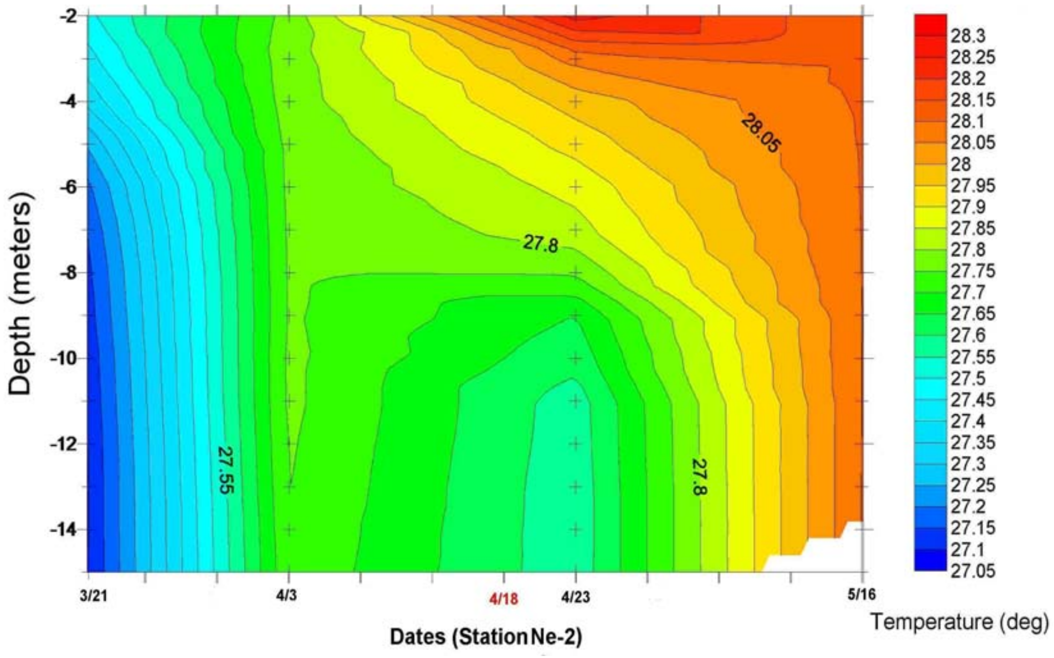


Figure 13. Water temperature contours at station Ne-2, La Parguera.

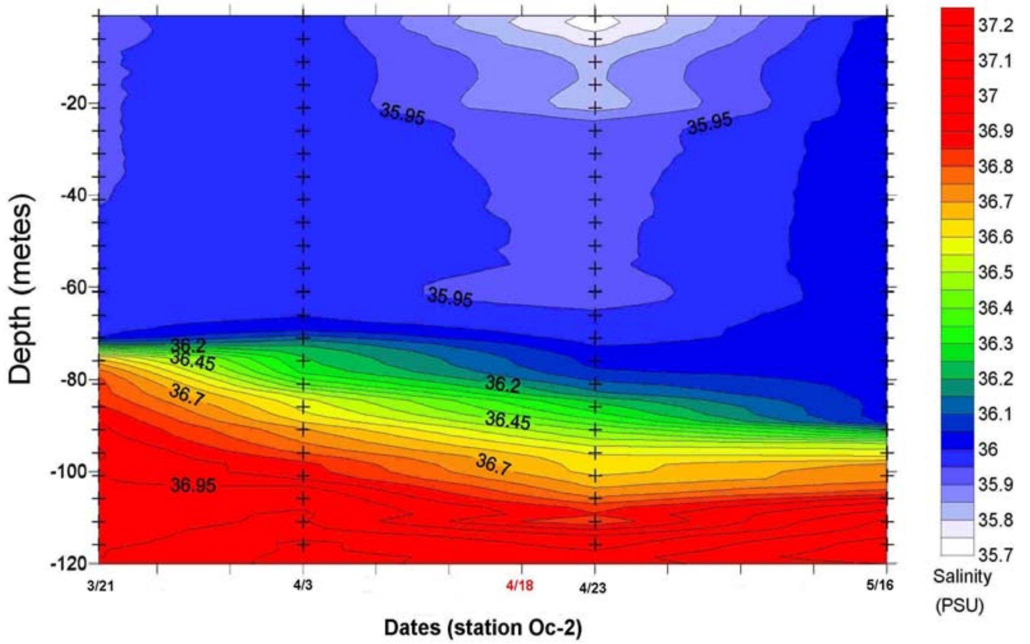


Figure 14. Water salinity contours at station Oc-2, La Parguera.

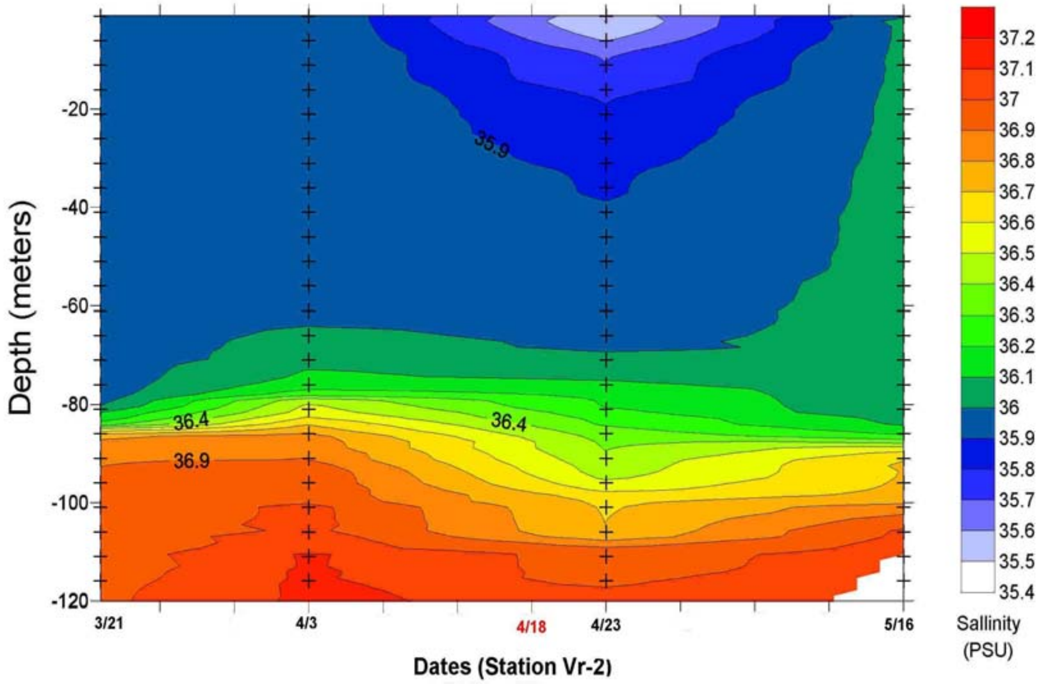


Figure 15. Water salinity contours at station Vr-2, La Parguera.

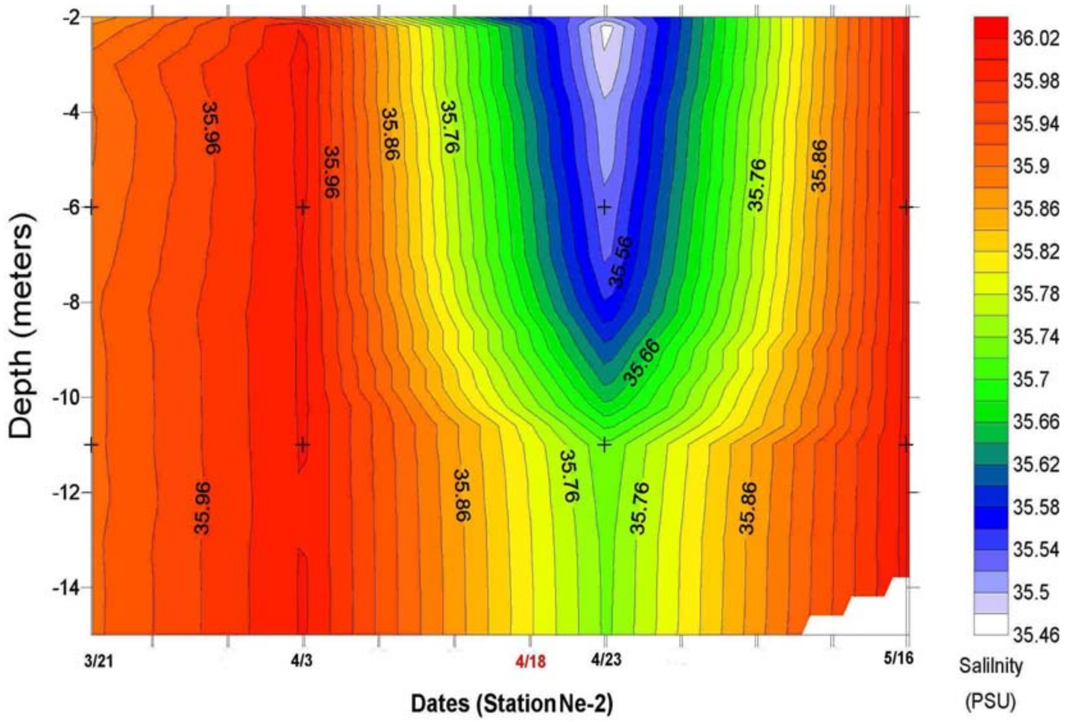


Figure 16. Water salinity contours at station Ne-2, La Parguera.

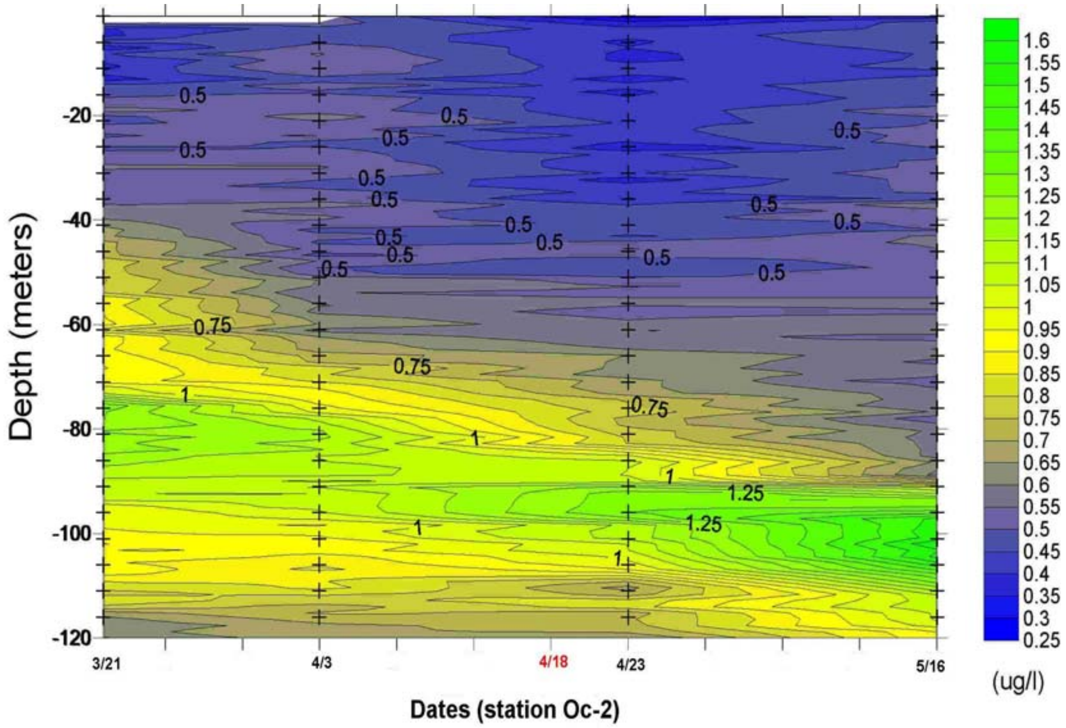


Figure 17. Chlorophyll-*a* concentration contours at station Oc-2, La Parguera.

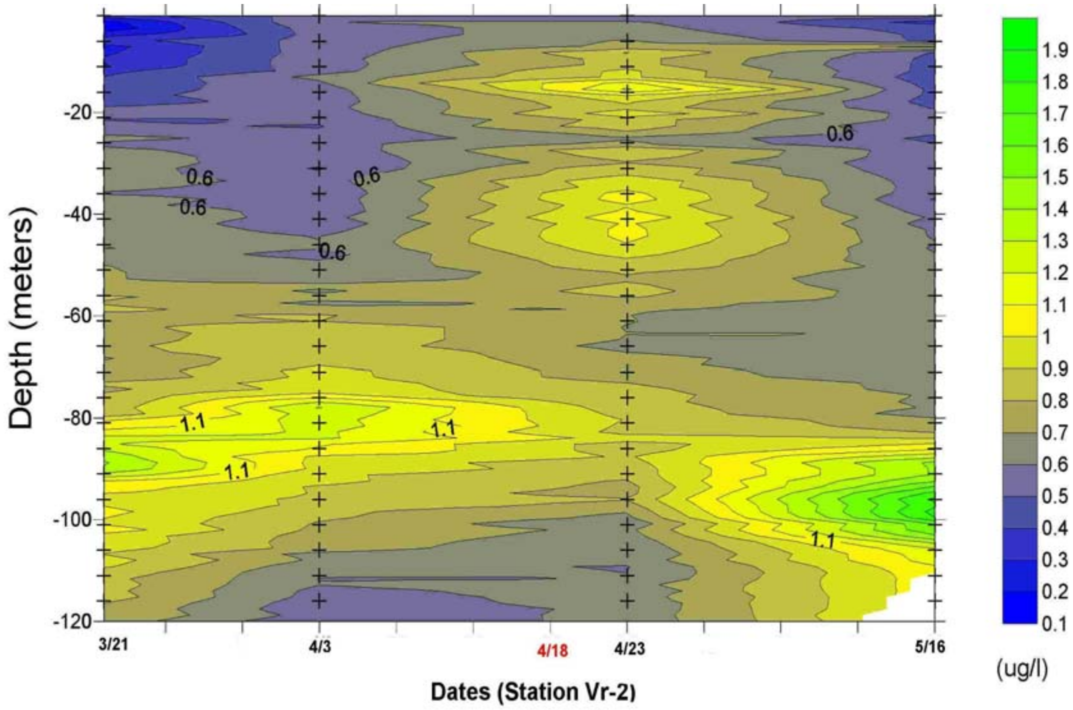


Figure 18. Chlorophyll-*a* concentration contours at station Vr-2, La Parguera.

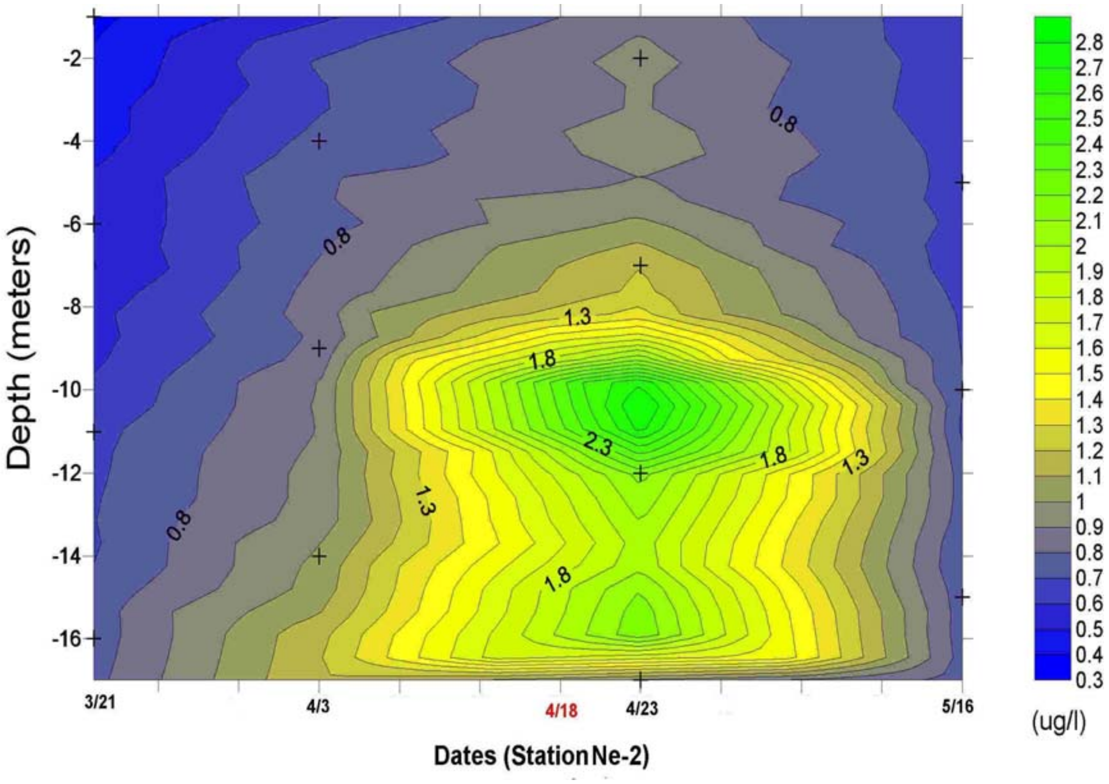


Figure 19. Chlorophyll-*a* concentration contours at station Ne-2, La Parguera**.**

Heavy rains affected the southwest coast of Puerto Rico during the first three days of the mutton snapper spawning aggregation of April 2003. This influx of fresh water explains the minimum near surface salinity readings during the April 23 sampling at all three stations. Rainfall events may have also provided nutrient inputs via runoff which may explain the observed increase in fluorescence (chl-a) during April 23. The apparent increase of phytoplankton, as suggested by the higher chlorophyll-a concentrations may have also represented an improvement in food availability for first feeding fish larvae.

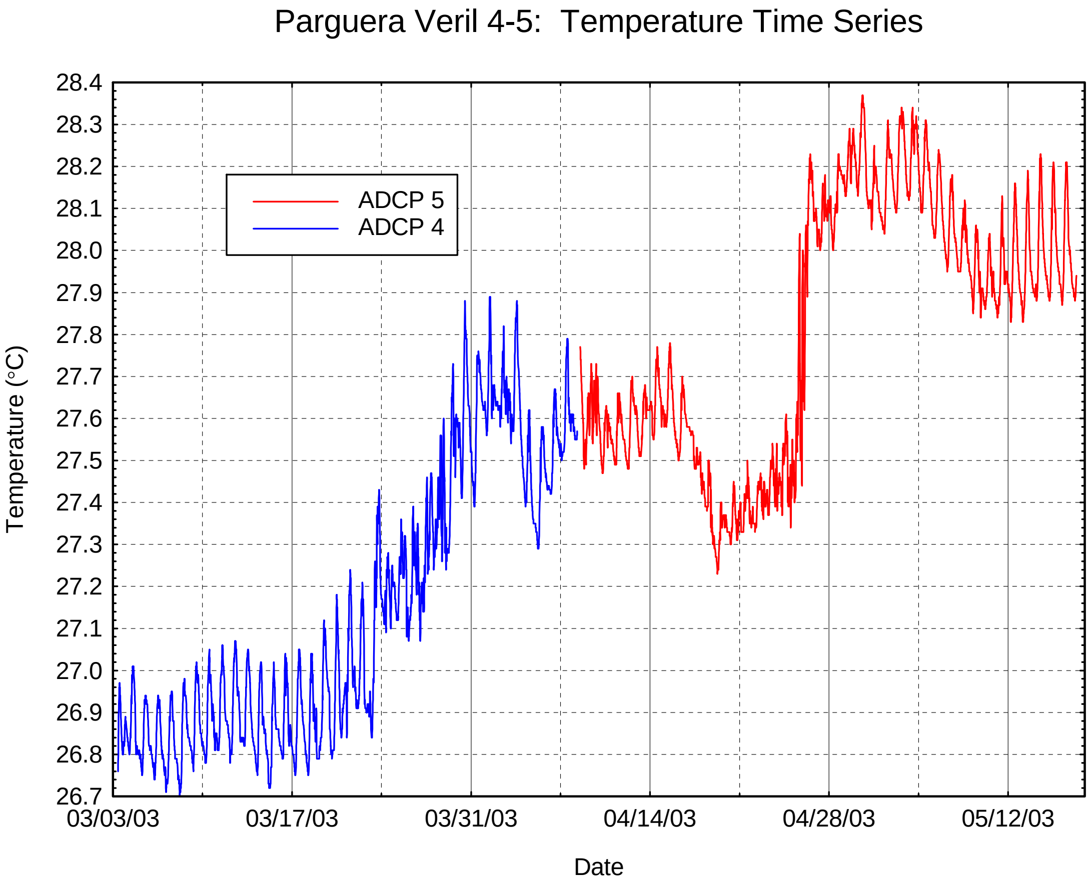


Figure 20. Temperature time series at “El Hoyo”, La Parguera.

Temperature – The bottom temperature time series from the ADCP varied by 1.70 °C from March 3 through May 16, 2003 (Figure 20). The minimum temperature of 26.70 °C was recorded during March 8, 2003. Daily oscillations of water temperature (e.g. 0.2 °C) reflect the diurnal heating/cooling effect superimposed on the seasonal increase of temperature during the sampling period. From March 24 to April 4, 2003 water temperature gradually increased from 27.09 °C to 27.89 °C. Then, an interval of relatively large variability began with the first of two pronounced temperature drops occurring on April 5, 2003. The second and largest temperature drop was recorded on April 17, 2003. Cooler waters remained over the shelf-edge reef for approximately seven days. Water rapidly warmed up from 27.45 °C to 28.23 °C from April 25 to the 27, reaching the maximum recorded measurement of 28.40 °C on April 31, 2003.

Warm temperatures remained until the end of the sampling period. Relatively large temperature variations during April 16-26, 2003 (Figure. 14) could be related to the perigge-syzygy of April 16 as the variability pattern is similar to that described in Leichter et al. (1996) as due surges of cold water forced inshore by internal waves.

DISCUSSION

Assessment of the local fisheries during the sampling period of March trough May indicate that the mutton snapper aggregated to spawn at a specific site (67.06 W, south of Margarita Reef) on the shelf-edge of La Parguera the week following the full moon of April 16, 2003. Dispersal of the newly released larvae is determined by multiple factors, including adult spawning location and timing, hydrography, topography, vertical distribution of larvae, horizontal swimming and larval behavioral capabilities (Sale, 1980). Mutton snapper adult behavior promoted off-shore dispersal by injecting a large number of fertilized eggs where the bathymetry favors advection rather than diffusion and observed flows ran parallel to the sharp break contour at the outer shelf-edge of an extensive insular platform during a rather short spawning season. Fertilized eggs, as well as early stage pre-flexion larvae resemble passive planktonic particles vertically distributed within the top meters of the water column and with limited behavioral and swimming capabilities (Sale, 2002). As a result of narrowing down the complex constituents determining dispersal, spawning aggregation of mutton snapper at the shelf-edge reef in La Parguera Bay presented an ideal scenario to examine the prevailing oceanographic conditions influencing dispersal of fertilized fish eggs and to propose initial dispersal patterns of the early pre-flexion larvae during the snapper spawning season.

The full moon of April 17 marked one of two lunar perigee-syzygy events that occurred in 2003 and which were particularly important due to their timing in relation to snapper spawning aggregations. Variability of the oceanographic data conforms to the theory of peak tidal flows near the shelf-edge generating large internal waves that propagate inshore. A weakly stratified shallow mixed layer preceded a sudden decline in the water temperature profile, as the current magnitude and direction measurements at the shelf-edge demonstrated cool water flowing inshore along the bottom while displacing warm surface water seaward. Chlorophyll-*a* concentrations above the shelf were comparatively lower during periods before and after the event of the breaking internal wave. Previous studies show that larger amplitude internal waves when formed where the thermocline is relatively shallow can move cooler, nutrient rich sub-thermocline waters into shallow depths (Leichter et. al, 1996, 1998). Accordingly, short-term changes of 2 - 5 °C can be indicative of internal waves and associated cross-shelf horizontal water advection (Pineda, 1994).

Seiching events along Puerto Rico’s insular margins and tidally forced internal waves in the Caribbean basin may be important factors for larval recruitment, or for triggering spawning events with the intrusion of subsurface cooler waters. A similar pattern of temperature variation coincided with the group spawning of the red hind (*Epinephelus guttatus*) during 1997 (Ojeda, 2002). Also, since the temporal pattern of planktonic larval settlement occasionally resembles a pulse, it has been correlated to the vertical transport and water displacements during the pass of internal waves (Pineda, 1994). Such sources of increased nutrients, and associated potential for increased zooplankton biomass, may serve as an important food source for the entire reef community and may have triggered the mutton snapper spawning aggregation of April, 2003 by creating conditions that would favor high adult reproductive success and larval survival.

The pattern of total fish larval mean abundances between the inner and outer portions of the shelf-edge suggests that the sharp geographic boundary of the island platform serves as a transition point for the coral reef ichthyoplankton communities off La Parguera as proposed by Ramírez-Mella and García-Sais (2003). The shelf-edge transition point was very pronounced during two April cruises, but less evident during the first (March 21) and last (May 16) sampling dates. Mean abundance of early stage larvae peaked at the neritic station on April 23 (259 Ind/100m^3) a week after the arrival of cooler waters brought by the breaking internal wave. Cross shelf advective processes, such as internal waves could have had direct implications on position and definition of the neritic oceanic transition point. The presence of such advection could also add up to the many possible cues affecting adult reproductive behavior

Ramírez-Mella and García-Sais (2003) have recently reported the taxonomic structure and distribution of larval fishes across a neritic-oceanic gradient off La Parguera. A total of 51 coral reef and 25 oceanic type fish larvae were identified from a distance contour encompassing 16 kilometers offshore from the shelf-edge at La Parguera. Larval snappers (Lutjanidae) displayed a dispersion pattern associated with the shelf-edge, in which pre-flexion larvae tend to concentrate along the interior margin of the shelf-edge and the post-flexion larvae were more abundant along the outer section. The highest abundance of larval snappers was observed during February and May, a period that encompasses their group reproduction near the shelf-edge.

In this study, larval snapper mean abundances during the four sampling cruises of March through May 2003 were lower than those reported by Ramírez-Mella and García-Sais (2003). The overall lower abundances can be attributed to the constant westward current present at the time of the study. Two types of snapper larvae were found which correspond to the observations of yellowtail snapper being present during the mutton snapper spawning aggregation. The difficulty of identifying early stage larvae may also help explain the low snapper larvae abundance at the time of the aggregation.

Acoustic Doppler Current Profiler water current measurements showed essentially homogeneous vertical speed profiles with slightly higher surface velocities and deceleration towards the bottom (20 m). The velocity time series were characterized by a dominant west-southwest flow parallel to the shelf overriding a primarily semidiurnal tidal current. Vertical profile time series during the nine days previous to each of the four ichthyoplankton sampling dates showed a constant west-southwest flow for the entire water column. This pattern suggests that eggs and planktonic larvae spawned at the shelf-edge would be transported offshore in a westward direction towards Mona Passage, eventually turning north as the flow follows the bathymetry along the Cabo Rojo – Mayaguez shelf (Figure 21). However, for those larvae that get transported farther west, the dominant southeasterly subsurface undercurrent prevalent at depths between 20 and 150 m in Mona Passage (Rojas 2003) may act to retain and/or return larvae competent for vertical placement within that subsurface layer towards La Parguera.

The current speed vertical profiles and the resulting progressive vector time series at the shelf-edge during the mutton snapper spawning aggregation season were atypical and may have had relevant implications for the dispersal and recruitment of fish larvae spawning during the period between March through May off La Parguera shelf-edge. First, the wind driven pattern of higher velocities at the surface that characterized the vertical profiles of March and April 2002 were virtually absent in 2003 due to a prolonged slack of wind velocity. Also, the oscillating effect of tides upon the prevailing southwesterly transport was not evident in 2003, contrary to 2002 when tidal currents were the main source of variability in the flow time series.

The absence of strong trade winds implies a weak potential for offshore transport of eggs and non-swimming larvae. This may have implications of higher mortality due to the high abundance of zooplankton predators at the shelf-edge, resulting in low recruitment success for any given population.   Also, the presence of a wind driven strong surface offshore flow may act as a necessary cue for the activation of group spawning by mutton snapper. The lack of current reversals associated with the diurnal tidal regime is counterintuitive in a scenario of low wind conditions, such as that prevailing during the spring season of 2003 in La Parguera. Although no explanation is here advanced for such phenomena, the implications for pelagic fish larvae at the shelf-edge are that of a faster travel away from natal reefs.

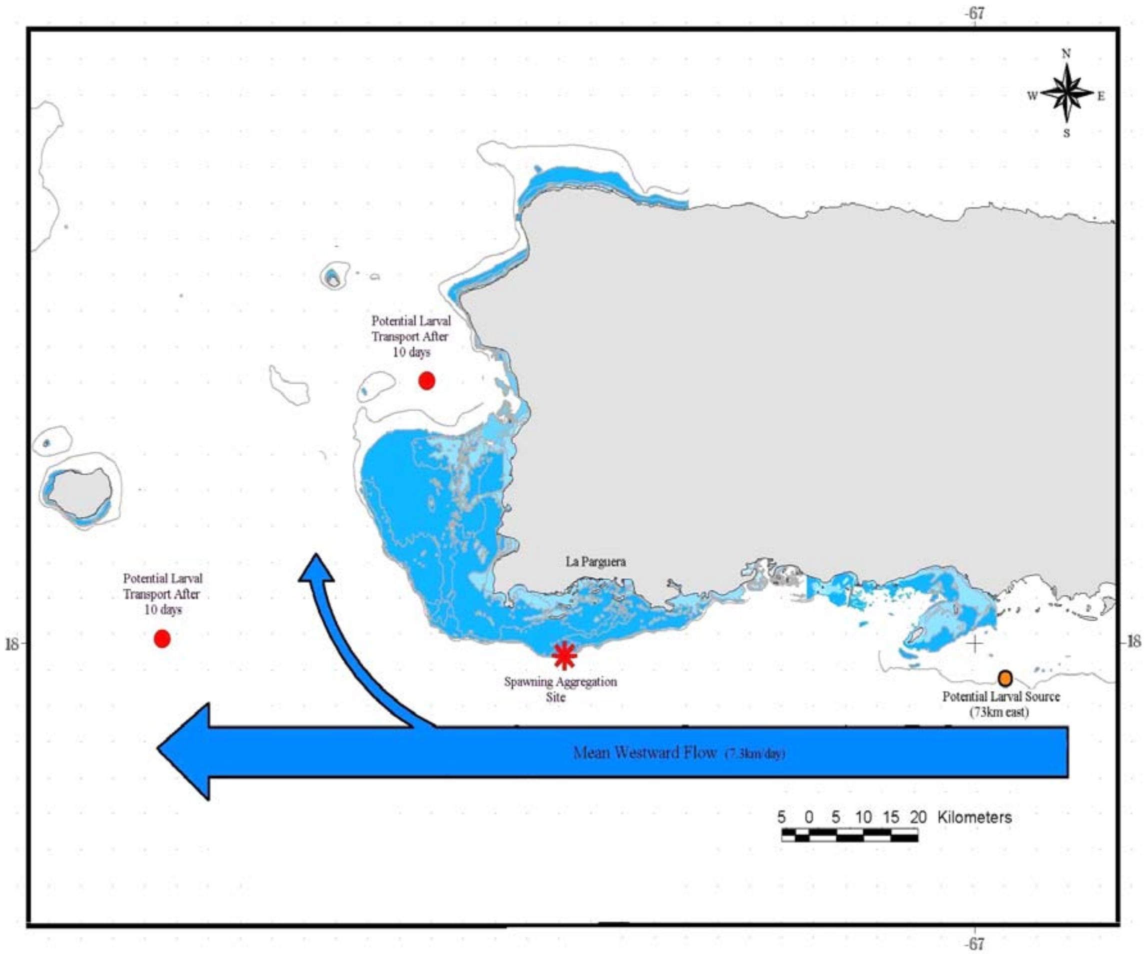


Figure 21. Proposed dispersal trajectories of larvae spawned at La Parguera following the mutton snapper massive spawning fish event of April, 2003.

A specific combination of physical processes could favor diffusion rather than advection from one year to the next, thus influencing the recruitment success of a particular cohort of larvae. The oscillating effect of the semidiurnal tides favors diffusion of passively buoyant particles such as recently spawned larvae. On the other hand, when the variability due to the semidiurnal tidal effect is dominated by a constant flow regime such as the one present during the spring of 2003, there is a better chance for advection and long distance transport of larvae. The capacity of adult individuals and larvae to respond to such physical processes which fall within spatial-temporal scales relevant to the ecological sustainability of the population may be an important contributor to the success of the spawned larvae.

Atypical water current velocity profiles in spring 2003, combined with short duration local nutrient pulses by internal waves represent small mesoscale processes which introduce considerable variability to the dispersal of mutton snapper larvae. Contrary to recruitment of fishes that reproduce over a long period, the short spawning season of the mutton snapper is more likely to be influenced by inter-annual variability of the physical processes acting over the larvae. Not enough evidence is here provided for understanding the implications of inter-annual variability on dispersal of the mutton snapper spawning aggregation at La Parguera. However, it could be so that such atypical conditions are necessary for a truly successful recruiting class to replenish the population.

The ability of reef fish larvae behaviorally influencing their dispersive fate becomes increasingly more important during late stages of development. The possibility of such behavior providing the opportunity for recruitment back to natal reefs is subject to the “how far” the larvae traveled as a passive planktonic particle during its early stages of development. When considering a mean along shore flow of 7.3 km per day on a southwestward direction away from the spawning site possibilities for self-recruitment of the population are not likely.

Conclusions

Mutton snappers aggregated and spawned in very large numbers during the week following the full moon of April 17, 2003 at the shelf-edge of La Parguera. The time and place of the aggregation coincided with those of previous years.

Vertical velocity structure and temperature variations during the April 17 lunar perigee-zizygy event suggest that an internal wave collided with the shelf, resulting in an influx of deeper cooler and probably nutrient rich water over deep sections of the shelf-edge displacing near-surface waters out to the Caribbean Sea.

The mean flow of 7.3 km per day promoted fish eggs and early stage larvae to be dispersed away from the shelf-edge of La Parguera on a west south-west direction towards Mona Passage during the time of mutton snapper spawning aggregation in 2003. However, the surface flow follows the bathymetry northward along the Cabo Rojo–Mayaguez shelf; potentially leading to final recruitment destinations along the west coast of the island during this particular spawning year.

BIBLIOGRAPHY

Appeldoorn, R. S., D. A. Hensley, D. Y. Shapiro, S. Kioroglou, and B. G. Sanderson. 1994. Egg dispersal in a caribbean coral reef fish, *Thalassoma bifasciatum*. Dispersal off the platform. Bull. Mar. Sci., 54:271-280.

Capella, J., G. S. Giese, D. C. Chapman and P. G. Fornshell. 1990. Causation of large-amplitude coastal seiches on the Caribbean coast of Puerto Rico. J. Phys. Oceanogr., 20:1449-1458.

Capella, J. E. 1999. Cross-Shelf distribution patterns of larval fishes in a Caribbean coral reef environment and adjacent waters: Physical Oceanography Component. Dept. of Mar. Sci., U.P.R., Sea Grant Report 6 pp.

Cervigón, F. 1993. Los peces marinos de Venezuela. Vol. 2. Fundación Cientifíca Los Roques, Caracas, Venezuela. 497p.

Clarke, M., M. L. Domeire, and W. A. Laroche. 1997. Development of larvae and juveniles of the Mutton snapper (*Lutjanus analis*), Lane Snapper (*Lutjanus synagris*) and Yellowtail Snapper (*Lutjanus chrysurus*). Bull. Mar. Sci., 61(3):511-537.

Claro, R. 1981. Ecología y ciclo de vida del pargo criollo, *Lutjanus analis* (Cuvier), en la plataforma cubana. Acad. Cienc. Cuba, Inf. Cient. Inst. Oceanol., 186:1-83.

Claro, R. 1983. Dinámica estacional de algunos indicadores morfofisiológicos del pargo criollo, *Lutjanus analis* (Cuvier), en la plataforma cubana. Rep. Invest. Inst. Oceanol. Acad. Cienc. Cuba, 22:1-14.

Claro, R. and I. Colas. 1987. Algunos elementos del balance energético del pargo criollo, *Lutjanus analis* (Cuvier), en condiciones experimentales. Rep. Invest. Inst. Oceanol. Acad. Cienc. Cuba, 12:1-11.

Colin, P. L. and I. E. Clavijo. 1988. Spawning activity of fishes producing pelagic eggs on a shelf-edge coral reef, southwestern Puerto Rico. Bull. Mar. Sci., 43 (2):249-279.

Colin, P. L., Y. Sadovy and M. Domeier. 2003. Manual for the Study and Conservation of Reef Fish Spawning Aggregations. Soc. for the Cons. of Fish Agg., Special Publication No. 1: 1-92.

Cowen R. K., K. M. M. Lwiza, S. Sponaugle, C. B. Paris and D. O. Olson. 2000. Connectivity of marine populations: open or closed? Science, 287:857-859.

Doherty, P. J. 1991. Spatial and temporal patterns in recruitment. In: P. F. Sale, (ed.) The Ecology of Fishes on Coral Reefs. p. 261-292. Academic Press, Inc., N.Y., USA.

Dudley, B., N. Tolinieri and J. Montgomery. 2000. Swimming ability of the larvae of some reef fishes from New Zeland waters. Mar. Freshw. Res., 51:783-787.

Echardt, H. and W. Meinel. 1977. Contribution to the biology of *Lutjanus analis* (Cuvier-Valenciennes, 1828) (Lutjanidae, Perciformes, Pisces) on the Colombian Atlantic Coast. Inst. Rev. Ges. Hidrolbiol., 62(1):161-175.

Figuerola, M. and W. Torres. 2001. Aspectos de la biología reproductiva de la sama (*Lutjanus analis*) en Puerto Rico y recomendaciones para su manejo. Dept. Rec. Nat. Puerto Rico/NMFS Final Report. 48p.

Fisher, R. and D.R. Bellwood. 2002. The influence of swimming speed on sustained swimming performance of late-stage reef fish larvae. Mar. Biol., 140:801-807.

Gaines, S. D., B. Gaylord and J. L. Largier. 2003. Avoiding Current Oversights in Marine Reserve Design. Ecological Applications. 13(1):32-46.

García-Cagide, A., R. Claro and B. V. Koshelev. 1994. Reproducción. In R. Claro (ed.) Ecología de los peces marinos de Cuba. p. 187-262. Inst. Oceanol. Acad. Cienc. Cuba.

García-Sais. J., J. E. Capella, J. Rojas and R. Esteves. 2003. Dispersal of reef fish larvae from known spawning sites in Mayaguez and La Parguera. Dept. of Mar. Sci. U.P.R./NMFS Final Report. 97p.

Giese, G. S., D. C. Chapman, P. G. Black and J A. Fornshell. 1990. Causation of large-amplitude costal seiches on the Caribbean coast of Puerto Rico. Journal of Physical Oceanography, 20:1449-1458.

Hensley, D. A., R. S. Appeldoorn, D. Y. Shapiro, M. Ray and R. G. Turingan. 1994. Egg dispersal in a Caribbean coral reef fish *Thalassoma bifasciatum*. Dispersal over the reef platform. Bull. Mar. Sci., 54:256-270.

Johannes, R. E. 1978. Reproductive strategies of costal marine fishes in the tropics. Envir. Biol. Fish., 3:65-84.

Jones, G. P., M. J. Milicich, M. J. Emslie and C. Lunow. 1999. Self-recruitment in a coral reef fish population. Nature, 402:802-804.

Kjerfve, B. 1981. Tides of the Caribbean Sea. J. Geophys. Res., 86 (C5):4243-4247.

Largier, J. L. 2003. Considerations in estimating larval dispersal distances from oceanographic data. Ecological Applications, 13(1):71-89.

Leichter, J. J., S. R. Wing , S. L. Miller and M. W. Denny. 1996. Pulsed delivery of subthermocline water to Conch Reef (Florida Keys) by internal tidal bores. Limnol. Oceanogr., 41(7):1490-1501.

Leichter, J. J., G. Shellbanrger, S. J. Genovese and S. R. Wing. 1998. Breaking internal waves on a Florida (USA) coral reef: a plankton pump at work?. Mar. Ecol. Prog. Ser. 166:83-97.

Leis, J. M. 1982. Nearshore distributional gradients of larval fish (15 taxa) and planktonic crustaceans (6 taxa) in Hawaii. Mar. Biol., 72:89-97.

Leis, J. M. 1991. Vertical distribution of fish larvae in the Great Barrier Reef Lagoon, Australia. Mar. Biol. 109:157-166.

Leis, J. M. and McCormick, M. I. 2002. The biology, behavior, and ecology of the pelagic larval stage of coral reef fishes. In: P. F. Sale (ed.) Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem, p. 171-199, Academic Press. N.Y., USA.

Leis, J. M., H. P. A. Sweatman, and S. E. Reader, 1996. What the pelagic stage of coral reef fishes is doing out in blue water: daytime field observations of larval behavioral capabilities. Mar. Freshwater Res., 47:401-411.

Mason, D. L. and C. S. Manooch, III. 1985. Age and growth of mutton snapper along the east coast of Florida. Fish. Res., 3:93-104.

Matos-Caraballo, D. 2000. Puerto Rico/NMFS Cooperative Fisheries Statistics Program, April 2000 - January 2001. Dept. Rec. Nat. Final Report to the NMFS, 52pp.

Molinari, R.L., M. Spillane, I. Brooks, D. Atwood, and C. Duckett. 1981. Surface currents in the Caribbean Sea as deduced from larangian observations. J. Geophys., Res. 86:6537-6542

Morrison, J.M. and O. P. Smith. 1990. Geostrophic transport variability along the Aves Ridge in the eastern Caribbean Sea during 1985-1986. J. of Geophys. Res., 95:699-710.

Mueller, K. W. 1994. Gregarious behavior in mutton snapper in the Exuma Cays, Bahamas. J. Sci., 1(3):17-22.

Mueller, K. W. 1995. Size structure of mutton snapper, *Lutjanus analis*, associated with unexploited artificial reefs in the central Bahamas. Fish. Bull., 93(3):573-576.

Mueller, K. W., G. D. Dennis, D. B. Eggleston and R. I. Wicklund. 1994. Size-specific social interactions and foraging styles in a shallow water population of mutton snapper, *Lutjanus analis* (Pisces:Lutjanidae), in the central Bahamas. Env. Biol. Fishes., 40:175-188.

Ojeda, E. 2002. Ontogenic development of the red hind *Epinephelus guttatus*, a spatial and temporal ichthyoplankton distribution study during a spawning aggregation off La Parguera, Puerto Rico. Ph.D. dissertation, U.P.R., Mayaguez, 190 p.

Pagán, F. 2003. Modeling egg and larval dispersal in the nearshore waters of southwestern Puerto Rico. Ph.D. dissertation, U.P.R., Mayaguez. 185p.

Palazón, J. L. and L. E. González. 1986. Edad y crecimiento del pargo cebal, *Lutjanus analis* (Cuvier,1828) (Teleostei, Lutjanidae) en la Isla Margarita y alrededores de Venezuela. Invest. Pesq. (Barc.), 50(2):151-165.

Pineda, J. 1994a. Internal tidal bores in the nearshore: warm-water fronts, seaward gravity currents and the onshore transport of neustonic larvae. J. of Mar. Res., 52:427-458.

Pineda, J. 1994b. An internal tidal bore regime at nearshore stations along the western U.S.A.: predictable upwelling within the lunar cycle. Cont. Shelf Res., 15(8):1023-1041.

Planes, S. 2002. Biogeography and larval dispersal inferred from population genetic analysis. In: P. F. Sale (ed.) Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem. p.201-220, Academic Press, N.Y., USA.

Pozo, E. 1979. Edad y crecimento del pargo criollo (*Lutjanus analis* Cuvier, 1828) en la plataforma noroccidental de Cuba. Rev. Cub. Invest. Pesq., 42(2):1-23.

Ramírez-Mella, J. T.and J. García-Sais. 2003. Offshore dispersal of Caribbean reef fish larvae: how far is it? Bull. Mar. Sci., 72 (3):997-1017.

Randall, J. E. 1967. Food habits of reef fishes of the West Indies. Stud. Trop. Oceanogr., 5:665-847.

Richards, W. J. and K. C. Lindeman. 1987. Recruitment dynamics of reef fishes: planktonic processes, settlement and demersal ecologies, and fishery analysis. Bull. Mar. Sci., 41:392-410.

Roemmich, D. 1981. Circulation in the Caribbean Sea. A well resolved inverse problem. J. Geophys. Res., 86:7993-8005.

Rojas, E. L. 1960. Estudios estadísticos y biológicos sobre el pargo criollo, *Lutjanus analis*. Cetr. Invest. Pesq., Notas Invest., 2:1-16.

Rojas, J. 2002. Caracterización del ictioplancton a traves del Canal de La Mona, con énfasis en familias arrecifales. M.S. Thesis, U.P.R., Mayaguez, 45p.

Sadovy, Y. 1993 The Nassau Grouper, endangered or just unlucky? Ref. Encounter, July. Pp. 10-12.

Sale, P. F. 1978. Coexistence of coral reef fishes, a lottery for living space. Env. Biol. Fish., 3:85-102.

Sale, P. F. 1980. The ecology of fishes on coral reefs. Oceanogr. Mar. Biol. Rev., 18:367-421.

Sale, P. F. 2002. Are populations of coral reef fish open or closed? Trends in Ecol. and Evol., 17(9):423-428.

Sanderson, B. G., A. Okubo, I. T. Webster, S. Kiorglou and R. Appeldoorn. 1994. Observations and idealized models of dispersion on the southwestern Puerto Rican insular shelf. Math. Comput. Modeling., 21(6):39-63.

Shanks, A. L., B. A. Grantham and M. H. Carr. 2003. Propagule dispersal distances and the size and spacing of marine reserves. Ecol. Appl,. 13(1):159-169.

Thompson, R. and J. L. Munro. 1974. The biology, ecology and bionomics of the snapper, Lutjanidae. In: J. Munro (eds.) Carribbean Coral Reef Fishery Resources. p. 94-110. International Center for Living Aquatic Resources Management (ICLARM), Manila, Phillippines.

Tyler, R. H. and B. G. Anderson. 1995. Wind-driven pressure and flow around an island. Cont. Shelf Res., 16(4):469-488.