INFLUENCE OF SURFACE CURRENTS IN THE DISPERSAL PATHWAYS OF EGGS OF CUBERA SNAPPER, *Lutjanus cyanopterus* (CUVIER, 1828), AT A SPAWNING AGGREGATION SITE AT GLADDEN SPIT, BELIZE

A Thesis

by

ADRIANA MÉNDEZ-JIMÉNEZ

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

August 2012

Major Subject: Geography

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Approved by:

Chair of Committee,	William D. Heyman
Committee Members,	Steve DiMarco
	Christopher Houser
Head of Department,	Vatche Tchakerian

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ABSTRACT

Influence of Surface Currents in the Dispersal Pathways of Eggs of Cubera Snapper, *Lutjanus cyanopterus* (Cuvier, 1828), at a Spawning Aggregation Site at Gladden Spit, Belize. (August 2012)

Adriana Méndez-Jiménez, B.A., Unversidad de Bogotá Jorge Tadeo Lozano

Chair of Advisory Committee: Dr. William D. Heyman

Most large reef fish use a migratory reproductive strategy and tend to spawn in aggregations that occur at predictable locations and times. Though numerous hypotheses have been formulated to explain the reasons behind this phenomenon, there remain few data to evaluate the relative merits of various hypotheses. Oceanographic variables and lunar cycles are believed to drive the timing and location of this reproductive strategy. However, the dynamics of the interaction between coastal currents, water temperature, biomass concentrations, spawning site selection and gamete transport are still unclear. This study aimed to examine the influence that currents exert on gametes released at spawning aggregations of Cubera snapper *Lutjanus cyanopterus* (Cuvier, 1828) at Gladden Spit, Belize. It was hypothesized that surface currents flowed offshore at the time and location of spawning. However, observations from this study, using Lagrangian and Eulerian methods, indicated that eggs most likely travel westerly towards the reef and into the reef channel. The dispersal rate of eggs appeared to be explained by a power relationship, with buoyant fertilized eggs dispersing horizontally such that the area of the spawning cloud increased with time. Egg density within the spawning cloud generally decreased over time as it dispersed with the predominant surface currents. Most importantly low-cost surface drifters area an appropriate, highly replicable way to monitor surface ocean currents at spawning sides in areas where more sophisticated methods are not available. Understanding how abiotic factors influence the occurrence of multispecies spawning aggregations will lead to better conservation and management strategies in the Western Caribbean.

DEDICATION

To my loving family and close friends

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I. INTRODUCTION

Fish spawning aggregations

Tropical marine conservation depends on understanding the life history of commercially exploited species. Even though all phases of development are crucial to species survival, early life stages are generally overlooked, either because of the inherent difficulty of their study or because generalized assumptions about these stages have been accepted as factually accurate (Shapiro et al. 1988, Colin et al. 2003).

Many ecologically and commercially important reef fish species form spawning aggregations, generally accepted as groups of fish of the same species that have migrated exclusively to reproduce in numbers that 3 times those found in the area outside the reproductive period (Domeier & Colin 1997, Claydon 2004). Spawning aggregations are a fundamental phase in the life cycle of many tropical reef fishes. They serve to replenish natural populations, maintain the health of reef environments and provide resources for local fisheries because large food fish form predictable aggregations (Johannes 1978, Pineda et al. 2007). This reproductive phase therefore has major biogeographic, evolutionary and ecological implications for reef fish populations (Sala et al. 2003). Yet the formation of these aggregations and the subsequent larval transport is far from being well understood.

This thesis follows the style of Marine Ecology Progress Series.

Since aggregated fish are relatively easy and vulnerable targets artisanal fisheries have often capitalized on them to provide food for local human populations (Johannes 1978). However, fishing has lead to declines and even extirpation (Sadovy & Domeier 2005). Precisely because of their importance and vulnerability, fish spawning aggregations need to be extensively studied and carefully managed.

The occurrence of spawning aggregations is mediated by the potential costs and benefits derived from the migration prior to fertilization and the dispersal of eggs and larvae after spawning (Helfman et al. 1997). Site selection for spawning areas has been attributed to a variety of reasons and several explanations have been hypothesized (see Barlow (1981); Shapiro et al. (1988) and Claydon (2004) for reviews). In the Caribbean, many sites share common geomorphological characteristics (Kobara & Heyman 2010) and tend to be used by multiple species (Heyman & Kjerfve 2008). Aggregation periods are highly dependent on the species but their timing is generally associated with various phases of the moon and tidal currents (Johannes 1978, Robertson 1991, Heyman et al. 2001b, Nemeth 2009). Immediately after spawning, viable eggs are fertilized, and their movement is subject to the action of the prevailing currents (Heyman et al. 2005).

Though many hypotheses about the movement of propagules from spawning aggregations have been advanced, few have actually been tested in the field or have been evaluated directly by measuring the movement of propagules in the water (Colin & Bell 1991, Pineda et al. 2007). Some hypotheses argue the importance of long distance egg dispersal, while others suggest that sites are selected that will maximize larval retention near to the spawning site (Johannes 1978, Barlow 1981, Shapiro et al. 1988, Claydon

2004). There is a extensive body of literature that qualitatively describes the characteristics of fish spawning aggregations, their findings are generally site specific and restricted to a particular species (Johannes 1978, Barlow 1981,, Carter 1988, Colin & Bell 1991, Carter & Perrine 1994, Colin 1996, Domeier & Colin 1997, Sala et al. 2001, Claro & Lindeman 2003, Sala et al. 2003, Lindeman & DeMaria 2005, Kadison et al. 2006). In comparison to this encompassing literature, relatively few studies (Doherty et al. 1985, Colin 1992, Appeldoorn 1994, Cowen & Castro 1994, Dahlgren et al. 2001, Domeier 2004, Ezer et al. 2005b, Paris 2008, Ezer et al. 2010) approach egg and larval dispersal from a quantitative perspective, or have used empirical data to examine the influence of currents in the movement of eggs and larvae shortly after spawning. Sampling limitations and logistic challenges, account for this lack of data making it difficult to evaluate the influence of small-scale processes on the transport of propagules, eggs, and early stage larvae (Pineda, Hare, and Sponaugle 2007). Furthermore, most studies base their conclusions on conceptual assumptions (Johannes 1978, Barlow 1981, Shapiro et al. 1988) or models. Some examples of these models include the heuristic computer simulation developed Doherty et al. (1985), they released hypothetical larvae in cell array representing a patchy marine environment and measured the survival rate of these larvae under different scenarios. Using this model they tested the success of two different dispersal strategies: limited dispersal with larvae remaining near their natal reef, and a greater dispersal where larvae abandoned their source reef and developed adaptations to venture into the pelagic environment. Cowen et al. (2000) developed and two-dimensional Eulerian Advection-Diffusion-Mortality model to study the factors that influence larval exchange among coastal fish populations. Based on their findings they suggested that marine populations are not open systems and that larval exchange might not be sufficient to sustain downstream populations. Gilg et al. (2003) used a modification of a two-dimentional surface circulation model to project larval dispersal for mussel populations in South West England. This study related patterns of larval movement with the spatial scale of dispersal. Similarly, Paris et al. (2005) evaluated the dispersal pathways of Cuban snapper larvae, as well as the potential linkages between Cuba and other geographically associated locations, using a high-resolution biophysical transport model. In Gladden Spit, Ezer et al. (2005) used a high resolution three-dimensional model of the West Caribbean Sea (WCS) to examine the variability of the of water flow near the Meso-American Reef System (MBRS) and its impact in the mean trajectory of two surface drifters deployed in the southern part of the reef. Later a similar study, aiming to investigate high-frequeny flow variations was conducted, using a numerical coordinate, terrain-following ocean model (Ezer et al. 2011). This time the impact of topography in water circulation was considered. In spite of this modeling efforts, few studies have empirically and systematically tested the various hypotheses proposed to explain spawning site selection mechanisms (Shapiro et al. 1988, Claydon 2004).

The present study examines the hypothesis that prevailing currents transport freshly released eggs offshore. This hypothesis was tested by tracking the dispersal pathways of freshly released eggs of Cubera snapper, *Lutjanus cyanopterus,* at a spawning aggregation site in Belize. Models related to this hypothesis have been developed (Ezer et al. 2005b, Paris et al. 2005, Treml et al. 2008, Karnauskas et al. 2011), but few direct observations exist (Colin 1992, Cowen & Castro 1994, Dahlgren et al. 2001, Domeier 2004, Paris & Cowen 2004) to verify model predictions for particular areas or species. Some examples include the heuristic computer simulation developed Doherty et al. (1985), they released hypothetical larvae in cell array representing a patchy marine environment and measured the survival rate of these larvae under different scenarios. Using this model they tested the success of two different dispersal strategies: limited dispersal with larvae remaining near their natal reef, and a greater dispersal where larvae abandoned their source reef and developed adaptations to venture into the pelagic environment. Cowen et al. (2000) developed and two-dimensional Eulerian Advection-Diffusion-Mortality model to study the factors that influence larval exchange among coastal fish populations. Based on their findings they suggested that marine populations are not open systems and that larval exchange might not be sufficient to sustain downstream populations. Gilg & Hilbish (2003) used a modification of a two-dimentional surface circulation model to project larval dispersal for mussel populations in southwest England. This study related patterns of larval movement with the spatial scale of dispersal. Similarly, Paris et al. (2005) evaluated the dispersal pathways of Cuban snapper larvae, as well as the potential linkages between Cuba and other geographically associated locations, using a high-resolution biophysical transport model. In Gladden Spit, Ezer et al. (2005) used a high resolution three-dimensional model of the West Caribbean Sea (WCS) to examine the variability of the of water flow near the Meso-American Reef System (MBRS) and its impact in the mean trajectory of two surface drifters deployed in the southern part of the reef. Later a similar study, aiming to investigate high-frequency flow variations was conducted, using a numerical coordinate, terrain-following ocean model (Ezer et al. 2011). This time the impact of topography in water circulation was considered.

More studies coupling spawning timing and location with the localized physical oceanographic features (Thresher 1984, Doherty et al. 1985, Leis 1987, Heyman & Kjerfve 2008, Nemeth 2009, Kobara & Heyman 2010) are needed.

Although models are useful tools, their predictive power is limited by the quality of the data and the assumptions on which they depend. Until reliable *in situ* data are collected and analyzed on small-scale egg and larval dispersal patterns from spawning aggregation sites, fundamental questions about dispersal and recruitment will remain unanswered. Simply put, modeling has little meaning without observation-based knowledge.

Water flow and propagule dispersal

Some of the most common terms used to describe propagule movement are: drift, dispersal, dispersion, export, retention, advection and transport. Understanding these terms is essential when studying the spatial dynamics of fish populations. Conversely, most of these terms are nonoperational, meaning that they cannot be measured, because they involve multiple variables most of which cannot be recreated in models or controlled during field experiments. In addition, results from studies about the subject are difficult to compare due to the diverse methodologies employed.

In ocean waters, current velocity is variable in time and space. Water masses carry different suspended particles from numerous origins to equally numerous destinations. This physical process of the movement of water and associated particles is known as dispersion. It is defined as the motion of water parcels and particles from a source zone as a function of distance. Dispersion is determined by multiple oceanographic conditions, but in general it is defined as the mean square particle displacement from its starting position. One of the generic tendencies of dispersion is that it implies constant diffusivity (LaCasce & Bower 2000). Particles separate from each other and from their point of origin over a period of time covering a certain distance. In ocean waters this process is forced by a combination of advection and eddy diffusion (Largier 2003). Dispersal, on the other had, refers to the movement and distribution of living organisms by oceanic currents. Eggs, embryos, and larvae, collectively called propagules, are in many cases incapable of movement. Therefore, their transport is dictated by the speed and direction of the prevailing ocean currents as they drift passively (Arnold 1981). When dealing with fish eggs or larvae that are incapable of overcoming the predominant water flow, and they drift passively with the predominant currents, dispersal is entirely determined by diffusion. Hence, these two terms are commonly used as synonyms in early life cycle studies. When dealing with fish spawning aggregations, advection is the mean transport of a group of free drifting particles and refers to the way in which the spawning cloud moves in the water column, independently of the movement of individual fertilized eggs. Finally, transport is understood as the horizontal translocation of eggs and larvae from point X_1,Y_1 to point

X_2, Y_2. Both x and y are considered to be horizontal axes, perpendicular and parallel to the shoreline (Pineda et al. 2007). Particles released in ocean waters move along and spread out as they move, the mean movement is caused by advection, while the spread out is caused by diffusion. They are transported by the currents and this movement determines their dispersal (Largier 2003, Pineda et al. 2007). In the case of passively drifting particles, (e.g. recently fertilized fish eggs) dispersal can be inferred from water dispersion (Gilg & Hilbish 2003, Pineda et al. 2007).

In this study the term dispersal will be used to refer to the spread of eggs from the spawning site towards the settlement area. Spawning is the trigger of dispersal; hence the importance of understanding the oceanographic conditions at the time and location it occurs. Such conditions may influence the occurrence of spawning will determine the initial transport of the recently fertilized eggs. It is during the minutes and hours after spawning, and within sub-kilometer scale that physical oceanographic processes appear to have the greatest dispersal potential (Lee et al. 2001, Pineda et al. 2007). Dispersal determines the probability that propagules will settle in an appropriate environment over a certain distance, the dispersal distance. As demonstrated by prior studies the spatial scale of larval transport can be quite small, tens to hundreds of kilometers (Cowen et al. 2000, Gilg & Hilbish 2003, Buston et al. 2011), indicating that physical process near the coast are much more important in egg and larval transport than previously thought (Pineda 2007).

This study will focus on egg dispersal based on what has been called the "off-reef transport hypothesis" (Claro & Lindeman 2003). This hypothesis is a compilation of ideas proposed by Johannes (1978), Barlow (1981) and Doherty et al. (1985). Johannes stated that spawning aggregations happen where eggs will be taken offshore to reduce the risk of predation. Barlow (1981) built upon that idea suggesting that offshore spawning also guarantees gamete dispersal and Doherty et al. (1985) made this even more significant by specifying that spawning favors offshore dispersal which is advantageous in a patchy marine environment where food resources are scarce and distributed throughout great distances (Lee & Wong 2001, Claro & Lindeman 2003). In sum, the offshore transport hypothesis suggests that spawning sites seem to provide an evolutionary advantage transporting propagules off the reef to reduce predation, promote dispersal and set larvae in suitable current regimes that may increase the likelihood of encountering food and will ultimately enhance their survival (Claro & Lindeman 2003).

Egg sampling studies have traditionally been conducted using oceanographic cruises, typically disregard diffusion and drifting patterns. Due to the logistical challenges involved in tracking water parcels to explain biological processes, few studies undertake oceanographic topics from a biological perspective or attempt to test biological hypotheses. Little work has been done to track planktonic eggs immediately after spawning, while they drift passively with the currents (Pineda et al. 2007). The current study proposes to assess egg dispersal during actual spawning conditions and times.

Although, pre-flexion larvae of most reef species already possess swimming capabilities, studies on the swimming abilities of other Perciformes show that they might lack the critical swimming speed or endurance that would allow them to completely surmount the strength of the currents (Fisher et al. 2000, Clark et al. 2005, Fisher 2005). The movement of eggs and larvae as a function of water flow must to be addressed to better understand connectivity in marine environments, to comprehend the interactions between fish and the marine environments at the ecosystem level, and ultimately to support the design of biologically significant marine protected areas (Cowen et al. 2006, Pineda et al. 2007, Heyman et al. 2008, Nemeth 2009).

Studies exclusively using satellite oceanographic imagery tend to overestimate the importance of meso and large scale processes on larval transport, completely disregarding the importance of near shore processes that can only be measured directly (Pineda et al. 2007). Shipboard sampling is logistically difficult and not always available. Remotely-tracked drifters measure ocean currents from a Lagrangian perspective, i.e. the device registers the magnitude and direction of the current as it is left to drift freely with it. This measuring technique is relatively inexpensive and simple, and facilitates the study of individual parcels of water without continued involvement of the researcher (Okubo & Ebbesmeyer 1976, Emery & Thomson 1997). Low cost tropical Drifters (LCD) were first designed and built in the 1980s by the Atlantic Oceanographic and Meteorological Laboratory (AOML), the Massachusetts Institute of Technology (MIT) and the Scripps Institutions of Oceanography (SIO). Their intention was to lower the cost of individual drifters while being able to generate reliable information. In general these devices consisted of inexpensive drifting buoys with position and sensor information related to satellite telemetry (Bitterman & Hansen 1986, Bitterman et al. 1990, Bitterman & Hansen 1993). Simple drifters such as bottles and cards have been used to study the influence of ocean current variability in the spawning season of reef fishes in Hawaii (Lobel 1989) and most recently to study the potential dispersal routes of fish larvae in the Florida Keys (Dahlgren et al. 2001). Several designs of drogued surface drifters have been suggested as an idoneous technique in the characterization of reef fish spawning aggregations (Colin et al. 2003, Ezer et al. 2011). More technically sophisticated drifters have been used to assess the relationship between environmental conditions and reproduction of Nassau groupers in the Bahamas (Colin 1992), the potential recruitment pathways of larvae in Florida (Domeier 2004), and the orientation of fish larvae in Key Largo, Florida (Paris 2008).

Ocean currents have long been studied as accompanying factors in ecological processes, but their role in phenomena such fish spawning aggregations remains open to discussion. Different hypotheses have been proposed to explain the influence of ocean currents on spawning site selection. These hypotheses can be classified in three groups: predation hypotheses, reproduction hypotheses, and the egg dispersal larval retention hypotheses. According to the predation hypotheses spawning aggregations reduce predation on adult fish and their eggs by means of predator satiation. In terms of reproduction spawning aggregations increase the degree of mate selectivity and allows the assessment of sex ratios of populations to change sex accordingly. Likewise, spawning aggregations enhance the survival of larvae during the pelagic phase and increase the probability of settlement (Claydon 2004). This current study centered on the dispersal of propagules on a small spatial scale (10 to 100 m) during short periods of time, minutes and hours after spawning, as determined by localized surface currents at the time and location of spawning. This study examines the potential dispersal routes of the freshly released eggs of Cubera snapper as mediated by surface currents at Gladden Spit, Belize. Furthermore, there has been little research studying the role of currents and other oceanographic features in biological connectivity and dispersal at Gladden Spit or other areas along the Belize Barrier Reef (BBR) (Heyman & Kjerfve 2008). Oceanographic insight into egg dispersal processes is necessary to develop credible dispersal models at the population level (Largier 2003). Observations of egg distribution and dispersal, combined with circulation models, have been conducted for species from temperate regions and for industrialized fisheries (Colin & Bell 1991, Mountain et al. 2003, Mountain et al. 2008), but few comparable studies exist for tropical and artisanal fisheries (Paris et al. 2005, Ezer et al. 2010). Nevertheless, it is possible to sample restricted domains for short periods of time to provide an indication of actual movement and thus inform population models that describe connectivity at larger scales. Monetary constraints common to the Caribbean and other tropical regions, where massive spawning aggregations occur, provide motivation to develop creative, low cost, replicable research techniques that can be easily implemented by local research teams.

The multispecies spawning aggregation in Gladden Spit has been monitored over an extended period of time (Heyman & Kjerfve 2008) and preliminary attempts to track surface currents have been conducted (Heyman unpublished data, Ezer et al. 2005, Ezer et al. 2011). The present study focuses on one of the better-studied species of massive spawners in the Caribbean, Cubera snapper *Lutjanus cyanopterus*. Like many other Lutjanids, Cubera snappers migrate considerable distances to spawning sites where they form massive spawning aggregations and release their gametes around dusk (Thresher 1984, Leis 1987, Heyman et al. 2005a, Nemeth 2009).

Cubera snapper is an ecologically and commercially important species, reaching a mass of 57 kg and a total length of 160 cm. It is the largest species of snapper in the Western Atlantic (Allen 1985, Robins & Ray 1986). It is among the most important food fishes in the Caribbean (Munro et al. 1973, Allen 1985, Nelson 1994). Even though the condition of regional stocks for Cubera snapper across the Caribbean is unknown due to lack of data, it has been listed as a vulnerable species by the International Union for the Conservation of Natural Resources (IUCN) (Kadison et al. 2006).

Aggregation periods for Cubera snapper correspond to times of the year when water temperatures are rising (March to September) and are determined by the phase of the moon, with peak spawning activity occurring between 3 and 8 days after the full moon and continuing 12 days after the full moon (Heyman et al. 2005). After spawning, fertilized eggs float to the surface and drift with the currents. They hatch about 18 h about 24 to 45 h after spawning and reabsorb the yolk sac in 3 to 4 d after hatching (Thresher 1984, Leis 1987). Lutjanid larvae undergo caudal flexion 14 to18 d after hatching at lengths of 4.8 to 6 mm (Paris et al. 2005), at which time they are finally able to swim at speeds that will overcome the current (Fisher et al. 2000, Clark et al. 2005, Fisher 2005). While eggs are passively drifting, their dispersal pathway is most likely determined by two forces: the surface currents and the prevailing winds (Heyman et al. 2005a, Ezer et al. 2010).

Cubera snapper reproductive biology

Fertilized eggs of Cubera snapper are 0.75 to 0.78 mm in diameter (Leis 1987, Heyman et al. 2001) and are less dense than sea water (density of 0.8 g cm^{-1}). As a result they rise to the surface at a rate of 0.14 to 0.31 m s^{-1}. Assuming that they are released at depths between 2 and 10 m in the water column they should reach the surface within 10 min to 2 h after spawning (Heyman et al. 2001). According to studies on the vertical distribution of tropical fish larvae, more that 50% of Lutjanid larvae stay at depths between 0 and 25 m, and within the top meter or two during the first 18 h after spawning (Cha et al. 1994, D'Alessandro et al. 2010, Ezer et al. 2010). Tracking surface currents during this period will serve as a measure of potential dispersal routes and rates for eggs and early larval stages. Cubera snapper like other large migratory fish spawn at specific locations at predictable times, though this behavior has been assumed to maximize larval survival, the effect of spawning location on dispersal is still under debate (Pineda et al. 2007).

Research purpose

The purpose of this study is to examine how surface currents influence the dispersal of freshly released eggs from a spawning aggregation site at Gladden Spit, Belize. This purpose is formalized in three research hypotheses:

I: Surface currents at Gladden Spit flow offshore at the time and location of Cubera snapper spawning.

II: Eggs disperse at a constant rate from the time and location of spawning such that the horizontal area of their spawning cloud increases at a constant rate.

III: Egg density within the spawning cloud decreases over time as it disperses with the predominant surface currents.

The following objectives were designed to address the hypotheses:

I: Measure the speed and direction of dispersal of freshly released eggs of Cubera snapper by evaluating the mean transport of drogued surface drifters from the time and location of spawning.

II: Measure how the area of water parcels tracked from the location of spawning changes through time, by determining the change in size of triangular areas formed by 3 surface drifters over successive time intervals.

III: Determine egg density, using quantitative plankton tows, within the spawning cloud at the time of spawning and at intervals as the water parcels disperse.

II. MATERIALS AND METHODS

Study site

Gladden Spit (16°35′N, 88°00′W), a reef promontory along the Belize Barrier Reef (BBR) (See Appendix A: Fig. A1), the longest continuous barrier reef in the Western hemisphere, is an area of great ecological and economic importance (Burke 1982, Heyman & Kjerfve 2001). Several reef fish species gather every year in this location and to reproduce in massive spawning aggregations (Heyman et al. 2001a, Graham & Castellanos 2005, Heyman et al. 2005a, Heyman & Kjerfve 2008). Counting on this predictable food source, Whale sharks *Rhincodon typus* and other oophagous (egg eating) and ichthyophagous (fish eating) fishes gather annually to feed on the gametes or on the mature individuals (Heyman et al. 2005), displaying a fascinating array of trophic and ecological interactions. Because of its importance as a multispecies spawning and feeding area Gladden Spit was included in the Gladden Spit Gladden Spit and Silk Cayes Marine Reserve (GSSCMR) in May 2000 (Government of Belize 2000, 2003).

This ecologically complex reef feature is considered to be the border between the central and southern physiographic provinces of the BBR (Burke 1982). The promontory is characterized by a moderate-relief spur and groove zone, and abundant *Acropora palmata* rubble (40 to 60%). The reef crest is dominated by *Millepora complanata* and *Palythoa sp*., while *Acropora palmata* and *Agaricia agaricites* dominate the spur margins. The back reef is shallow (1 to 2 m), has a relatively low relief, and is mostly covered by coralline mounds and rubble. From the reef crest, the reef slopes gently reaching an average depth at the outer fore-reef of 30 m. Coral density is generally greater along the shelf edge and on the reef crest. Close to the reef promontory the reef opens forming a narrow sand channel, 5 to 15 m deep and 4.5 km long, connects the open sea reef with the inner barrier reef lagoon known as the Victoria Channel (Burke 1982, Heyman et al. 2005).

Gladden Spit is adjacent to the 1,000 m isobath, approximately 46 km away from the mainland (See Appendix A: Fig. A1, A2) (Heyman et al. 2001). It has a tropical climate with sea surface temperatures varying from 27 to 31°C, the mean tidal range is 0.2 m (Kjerfve 1981, Stoddart et al. 1982) and average salinity values of 36 to 37 all year round. The Northeasterly trade winds are predominant from December to May, interrupted by occasional frontal systems from North America from November to April. Water flow at the site is determined by winds and temporary meso-scale eddies, flowing parallel to the reef at mean speeds of 3 to 15 cm s^{-1} (Heyman & Kjerfve 2001, Heyman et al. 2005b, Graham & Roberts 2007, Heyman & Kjerfve 2008).

Deep water currents at Gladden Spit generally run from north to south along the reef with occasional reverse flow near the reef due to meanders of the Caribbean Current (CC) and the westward propagation of meso-scale eddies (Ezer et al. 2005b, Heyman et al. 2008, Ezer et al. 2010). Surface currents inside the barrier reef are predominantly southerly and seaward of the main reef crest and atolls.

Data collection and analysis

Mean current flow

In order to examine the hypothesis that currents at Gladden Spit flow offshore at the time and location of Cubera snapper spawning, a 2-week *in situ* experiment was conducted at Gladden Spit, the known location of spawning in May at the expected peak of the spawning season for this species (Heyman et al. 2005). Full moon occurred on May 17, 2011. Sampling took place between May 16 to 29, 2011; from one day before full moon to 11 d after full moon, encompassing the entire peak spawning time for the month from before the spawning period began (3 d after full moon) until after was completed (Heyman et al. 2005a, Heyman & Kjerfve 2008). Low cost drogued surface drifters were used to estimate the dispersal routes of fertilized eggs immediately after spawning.

Numerous designs of surface drifters have been previously used to investigate potential routes for egg and larval dispersal in the Caribbean (Colin 1992, Appeldoorn 1994, Dahlgren et al. 2001, Sala et al. 2002, Paris & Cowen 2004, Ezer et al. 2010), and though attempts for standardization have been made (Colin et al. 2003, Heyman et al. 2004) no single method has been universally adopted. The drifters used in this study are a modification of the design proposed by Heyman et al. (2004). The buoy is designed to track rip currents in Florida (Houser, unpublished data). The buoys were built using low cost materials easily accessible across the Caribbean.

Surface drifters design and construction

Each drogue consists of a styrofoam buoy for flotation and stability and a drogue that drifted ~30 cm below the water surface, to estimate the movement of surface water currents (Colin et al. 2003, Heyman et al. 2004). Only a small portion (<2.5cm) of the styrofoam buoy broke the surface, allowing little wind resistance. Thus, it was assumed that the drifter is measuring surface currents (See Appendix A: Figs. A2, A3).

The drogue was made from a single 1x1.20 m cloth vane (40% polyester, 60% cotton) fastened on both ends to 1.27 cm diameter PVC tubes that were capped at both ends. The bottom tube was weighted with fine beach sand, to provide a vertical orientation of the tube while drifting. The caps of the top tube were pierced to allow water to fill the pipe during deployment and to prevent undesired buoyancy. Each flag was connected to a 12.7 cm diameter hemispherical styrofoam buoy with 0.5 cm diameter polyester rope such that the top of the drogue generally was ~30 cm below the water surface (See Appendix A: Figs. A2, A3).

Buoys were constructed using 15.2 cm (6 in) diameter PVC sewer pipe cut into 1 m lengths and capped at both ends with standard commode flanges, using a modified design of buoys previously used to track rip currents in Florida (Houser, unpublished data). The center of the top flange was drilled to allow a fiberglass rod (1.27 cm diameter) to pass through. This rod was inserted until it touched the bottom flange. The rod extended 50 cm above the flange and served as a stem to attach both a waterproof survival flashlight with a blinking red light-emitting diode (LED) and a GPS tracking device (dog collar) (See Appendix A: Fig. A2).

After the fiberglass rod was put in place, the bottom third of each buoy was filled with coarse beach sand and seawater to moisten the sand and add to additional weight. The remainder space inside the PVC pipe was filled with a combination of boat foam core pieces and approximately 100 ml of expanding spray foam insulation that filled all of the remaining air space. The space between the fiberglass rod and the flange was sealed with water resistant silicone. Prior to sealing, drogue buoyancy was tested to verify buoyancy was the same for all drogues. About a third of the buoys floated above the water surface. Finally the vane and the buoy were attached with floating, water-resistant polyester rope (0.5 cm in diameter) and tied such that they were separated by 80 cm. The total mass of the drifting buoy and drogue out of the water was 9.3 kg.

To aid in recognition during deployment, drifters were marked with visual identifiers using 1, 2, or 3 rings of electrical tape around the stem. Finally, to facilitate tracking and retrieval at night, each drifter was equipped with a LifeGear waterproof survival flashlight with a blinking red LED (light-emitting diode) light. One drifter of each set of three was also equipped with a dog-tracking collar with a built-in GPS unit (Garmin DC 40). The DC 40 is not salt water-resistant so it was placed inside a dry bag for protection. DC 40s transmit real time position data to a handheld Garmin Astro 220, allowing the recording of the exact location of the drifter and aiding retrieval after long deployments and under conditions of low visibility.

Tracking surface currents using low cost surface drifters

In order to test the hypotheses that surface currents at Gladden Spit flow offshore at the time and location of Cubera snapper spawning, mean transport of drifting particles from the time and location of spawning was measured using the GPS-tracked surface drifters described above.

Cubera snapper spawning events generally occur between 40 min before sunset and 10 min after sunset (Heyman et al. 2005). The standard deployment scheme, therefore, consisted of releasing one set of drifters every day approximately 1 h before sunset, i.e., ~18:15 local time. Deployments lasted as long as environmental factors permitted safe sampling conditions and were generally retrieved 1 h after initial deployment. Wind speed tended to increase in the afternoon, creating bigger (2 to 3 m high) waves, reducing visibility and making boat maneuvering more challenging. Additional drifters were deployed opportunistically at various times in the afternoon, during seven days of the field study (May 16 to 18, 20, 23, 25 and 27).

One overnight deployment occurred between May 28 and 29, drifters were deployed at 17:06 h and retrieved at 9:11 next morning (See Appendix A: Table A1). Battery power was diminished but the signal continued transmitting 16 h after deployment, and all drifters were located and retrieved.

For each deployment, three drifters were placed about 2 m apart and aligned with the prevailing wind. To prevent entanglement, drogues were left in the water to drift for at least 2 min before their initial position was recorded (Heyman et al. 2004). Approximately every 15 min all deployed drifters were located and their position recorded using a hand held Garmin GPSMAP 76. The deployment scheme was kept constant all sampling days and the drifters remained in the water for at least 1h insofar as environmental conditions allowed it. The drifter outfitted with a dog collar tracking device, recorded real-time position data every second (1 Hz) and was turned on <2 min before deployment.

Geospatial analysis of drifter data

The coordinates recorded with the handheld GPS for each drifter at every time step where transferred and logged as “Point Features” in ArcGIS Desktop version 10 (ESRI 2011). A “Point Feature” represents a geographic location of interest; in this case the position of the drifters throughout deployment, and it is identified on a map by a point symbol (Ormsby et al. 2010).

For every day the drifters were deployed an individual shape file, a digital vector storage format, was created and edited using the “Editor” toolbar and “Create Features” window from ArcMap 10. These tools allow the geospatial analysis of geo-referenced data points, including measuring distances and areas between points. Shape files are commonly used to store geometric location as well as other associated attribute information about spatial features (Ormsby et al. 2010).

Two approaches were considered to determine the mean transport of the surface drifters. Initially, the dispersion pathways for drifters deployed in the early afternoon and at sunset were considered individually. A total of 54 drifters were deployed in the early afternoon and 63 at sunset from May 16 to 27. Visual examination of the tracks showed that the travel direction of the drifters during May 17 during both deployments differed from the general trend. Because of this, date from May 17 in the early afternoon and at sunset were removed from the analysis and N = 55 for sunset deployments and N = 43 for the early afternoon. All drifters move inshore towards the reef, either NW or SW.

Because oceanic diffusion is better represented by the observation of water parcels, observation of the motions of drifter clusters were made using the Area Rate of Change (ARC) a method outlined by Molinari and Kirwan (1975). For this purpose, the areas of the triangles determined the 3 drifters at each time step were considered. For 90 of the 98 individual drifts, unique locations were recorded for each drifter on the set. Using these 3 specific “Point Features” a triangle was created using the “Feature Construction” toolbar and its area computed using the “Calculate Geometry” option. Then, the centroid (mean center of the triangle) was calculated using the "Feature To Point" option from the “Features” menu under the "Data Management" toolbox. Centroid calculation in ArcMap 10 is based on the weighted average of X and Y coordinates of a polygon, and it is a useful way to summarize the locations of a set of points (Ormsby et al. 2010).

In 6 cases, May 19 (third time step), May 20 (second time step), May 21 (third time step), May 22 (first and second time steps), and May 27 (first time step), due to performance limitations of the instrument, only 2 unique coordinates were recorded. This happened when the drifters came within proximity of each other and the Wide Area Augmentation System (WAAS) (position < 3 m, velocity 0.05 m sec^{-1} steady state) and GPS accuracies (position< 15 m, velocity accuracy of 0.05 m sec^{-1} steady state), did not allow for the instrument to register 2 separate locations. In these cases, a “Point Feature” equidistant between the 2 points recorded, was created on the map using the “Midpoint” tool from the “Feature Construction” toolbar in ArcGIS 10. This tool assumes the earth to be locally flat and uses the arithmetic mean between the latitude and longitude of 2 known points the estimate the midpoint between them (Ormsby et al. 2010). In May 16 and 18, at the beginning of deployment, when only 1 location was registered for the 3 drifters, this single point was used to represent the position of the 3 drifters for that time step.

Finally, when a centroid, midpoint or single point” was available for every time step for every all daily deployments, all points for the deployment were connected using the “Feature To Line” tool, and all drift tracks were plotted over a bathymetric map of the area using ArcGIS 10 (ESRI 2011). The resulting line showed the drift route and mean total distance traveled by the drifters. The time elapsed and distance between the first and the last Feature Point of a track, were used to calculate the mean drift speed for each of the drifters’ tracks (Okubo & Ebbesmeyer 1976).

The direction of travel, i.e., bearing, was calculated using the latitude and longitude coordinates for the initial and final points of each drift. After calculating displacement, the shortest distance between the final and initial points of a drift, the angle of travel was calculating using a the arctangent function (atan2):

$$\text{atan2}\,(y,x) = 2 * \arctan\,(y, (x^2 + y^2) + x)^{-1/2}) \qquad (1)$$

Using this equation the direction in which the drifters were moving was calculated as a function of the latitude and longitude of the starting and ending points for each drift. The results represent the compass angle in the range 0° to 360°. The overnight drift (17:06 h May 28 to 9:11 h May 29) was considered separately, but special analysis was conducted the same way.

Acoustic Current Profiler (ACP) measurements

From 7 June 2009 to 10 December 2011, a Nortek AS 600 KHz AWAC Acoustic Wave and Current Profiler (ACP) was deployed on the sea bottom at the spawning site, directly below the location where surface drifters were released in this experiment (16° 30' N, 87° 57' W). The AWAC is designed to monitor coastal environments and it is suitable for long deployments, ensuring data accuracy and precision. This instrument has four transducers, one larger placed at the center surrounded by three equally spaced transducers angled 20°off the vertical axis. Due to acoustic contamination, and sidelobe interference, data recorded within the first meters of the water column are presumed to be spurious (Gordon1996, Emery & Thomson 1997, Pedersen & Lohrmann 2004).

The ACP was mounted at a depth of ~30 m, ~1.50 m above the bottom, and measured current speed and direction in 1 m depth bin layers from the bottom to the surface. To allow for possible increases in sea level due to tides (mean tidal range 0.2 m), and tropical storms, the instrument was set to record data in 35 bins. This *in situ* current meter provided a time-series of current speed and direction at a fixed location, from a Eulerian perspective, at the same time and location that drifter experiments were conducted.

This acoustic current profiler uses a continuous wave burst technique, and short and high frequency (600 KHz) sound pulses. This instrument determines the Doppler frequency shift (time delay) of the return signal scattered from drifters in the water column. Absolute velocities, east-west (*u*) and north-south (*v*), are calculated using measurements from an internal magnetic compass, while the relative frequency shift is derived from the observed frequency and the resulting echo.

The unit is designed to measure the current profile. Instead of providing current time-series at a fixed point, they provide time-series profiles of the average flow at a range of depths (Brumley et al. 1991, Emery & Thomson 1997). Throughout the deployment the instrument was operated in autonomous, or internally recording, mode such that raw data were stored to the internal data logger. Power was provided by an external battery pack. The ACP recorded speed and direction of the eastward (*u*) and northward (*v*) components of the horizontal velocity in 1 m depth layers, every 10 min averaging 2 MHz pings. The instrument also recorded pressure and temperature data at ~30 m.

This thesis only considers the current profile data corresponding to the times of the drogue deployments, May 16 and 31, from 17:00 h to 19:00 h. For each sampling day the vector current speed was calculated using the eastward (*u*) and northward (*v*) daily average speed was calculated from individual vector components. Current measurements from the days during which the experiment was conducted were compared against the surface drifter velocities.

Egg dispersal as a function of divergence

Divergence of the water masses at the time and location of spawning can be used to infer how the spawning cloud would move under localized oceanographic conditions set times of the day. To assess whether eggs disperse from the time and location of spawning at a constant rate, horizontal divergence at the spawning site was estimated from data collected with a set of 3 surface drifters. Divergence measures the change in the area of water parcels without considering changes in orientation or shape (Molinari & Kirwan 1975).

Once the drogues were placed in the water, they drifted from the release site and from each other. Drifters were labeled A, B and C and were easily identified using individual visual markers. By recording the location of each drifter approximately every 15 min, each set of points formed the vertices of a triangle, whose area could be calculated to estimate divergence. Drifter position was always registered in the same order (A, B, and C) to guarantee that the time interval between measurements was held constant.

Divergence is a measure of the horizontal motion of water parcels. There are 2 methods to calculate divergence: least squares and area rate of change. In this study, the latter method for ocean drifter data was used (Molinari & Kirwan 1975). Horizontal divergence can be expressed as a fractional Area Rate of Change (ARC) of the horizontal area of a water parcel. First the horizontal area of each triangle formed by the triplet of surface drifters was estimated using the "Geometric Calculator" of ArcMap 10. Then, the time rate of change was evaluated by taking the difference in the area described by the drifters at a given time and the area of the triad from the previous time step (Molinari & Kirwan 1975).

The location of each surface drifter at each time step corresponds to the vertices of a triangle, the area of which was estimated using the "Editor" toolbar and "Create Features" window from ArcMap 10. The area of each triangle at each time step provided an estimate of how much the water parcel spread. Divergence was evaluated as the time rate of change of the horizontal area using the equation:

$$ARC = (A_{ii} - A_{i})/(t_{ii} - t_{i}) \quad (2)$$

where ARC is the area rate of change of the triangular areas, A_i is the initial area, A_{ii} is the area of the same water parcel during the next time step, T_i is the initial time and T_{ii} is time registered at the next time step. $A_{ii} - A_i$ gives the difference in the area of the water parcels between consecutive time steps while $T_{ii} - T_i$ corresponds to the time elapsed between consecutive time steps (Molinari & Kirwan 1975).

Egg abundance in space and time

When spawning was observed, distinguishable from the boat by the presence of large bubbles that rapidly expanded into milky-white circles at the surface (Heyman et al. 2005), quantitative ichthyoplankton tows were taken inside the gamete cloud. The first plankton tow was conducted <1 min after spawning was first observed, and subsequent tows were carried out at ~6 min intervals until the cloud was visible from the boat. As reported by Heyman et al. (2005), the spawning cloud expanded rapidly in three-dimensions and remained clearly visible for at least 8 min. Additionally, the coordinates for the star and end locations of each tow were recorded using a hand-held GPS.

To test the third hypothesis, that egg density within the spawning cloud decreased over time as the cloud dispersed, egg density was estimated. Egg density estimations were based on the number of eggs present in a volume of water filtered across the surface of the spawning cloud at ~6 min intervals as the cloud dispersed. The location of spawning clouds was estimated using a single drifter deployed at the estimated center of the spawning cloud within one minute of its appearance at the surface. These experiments were attempted every day that spawning was observed (See Appendix A: Table A1). Tows were intended to cross the cloud, however, environmental conditions limited the boat's maneuverability and perpendicular tows were only achieved during 19, 23 and 24 May (Appendix A: Table A8, Figs. A13, A14, A15, A16) and so only these data were used to address the hypothesis. During May 20 the cod end of both nets was completely full thus the sample was deem uncountable and the total number of eggs was estimated based on the volume one egg of Cubera snapper and the volume of the cod end (Appendix A: Table A8).

In order to estimate how egg density changed through time across the spawning cloud, the tows were conducted perpendicular to the direction of dispersion. Egg samples were obtained using a Hydrobio bongo net, equipped with two 500-µm nets (30 cm diameter mouth x 90 cm deep). The nets were connected by an aluminum frame and had separate cod ends where the plankton samples were concentrated. A mechanical General Oceanics 2030R flowmeter with a standard rotor was attached to the aluminum frame to measure the volume of water filtered through the nets (Colin & Bell 1991). The net was deployed near the bow and out of the wake of the boat to avoid the turbulence from the boat, using a 3-m long aluminum pipe mounted in the bow of the boat for stability. Nets were towed at a speed of ~0.8 -1 m s^{-1} just bellow the surface (~30 cm deep) for 1 min.

Total volume, speed, and tow distance were calculated using the equations provided by the flowmeter manufacturer on the operators manual:

$$D = ((c\mathit{ii} - c\mathit{i}) * r)/999999 \tag{3}$$

$$S = (D * 1000)/t \tag{4}$$

$$V = ((3.14 * d^2) * d)/4 \tag{5}$$

where *D* is the distance of the tow, $(cii - ci)$ is the difference in counts from the flowmeter's rotor, *r* is the rotor's constant, *S* is speed at which the tow was conducted, *t* is the time the tow lasted, *V* is volume and *d* is mouth diameter of each individual net.

Thought multiple spawning events can happen per night, only 1 spawning event was observed and sampled during this experiment. Because the conditions under which spawning happens are site specific and temporally bounded, each spawning cloud seem was considered to be a separate sampling unit. For each tow of each net, the plankton sample collected in the cod end was transferred to a labeled sample bottle. To prevent post-collection predation, the content of each bottle was fixed with 20 ml of 100% ethanol. The final volume of the concentrated samples was variable, so as to unify the total water volume of all samples, seawater was added to each bottle until a total volume of 1000 ml was reached. Prior to counting, the content of the bottle was manually homogenized using eight-figured gentle shakes for 1 to 3 min to guarantee uniform distribution of eggs throughout the sample. Then, to calculate egg density for each tow, four replicate 5-ml aliquots were taken from the 100 ml sample. In order to facilitate counting, only 1 ml of the 5-m aliquot was taken each time and all eggs present were counted using an AmScope 10x-20x-30x Student Binocular Stereo Microscope and a CST/Berger 30-100 4-digit mechanical counter.

The distance of each tow was determined using the flowmeter readings and the distance formula provided by the flowmeter manufacturer (Eq. 3), except for May 19 (tows 2 and 3) and May 20 (tow 1). For these days, the calculated values were inexplicably high and presumed to be unauthentic. These values were replaced with tow distances determined using ArcGIS 10 “Spatial Analyst” tools to measure the straight-line (Euclidean) distance from the start to the end point each tows for these 2 days.

III. RESULTS

Mean current flow and egg dispersal

Surface drifters measurements

To test the first hypothesis, that surface currents at Gladden Spit flow offshore at the time and location of Cubera snapper spawning, a 2-week in situ experiment was conducted (May 16 to 28, 2011) to evaluate the mean transport of surface currents. The mean speed and direction of dispersal of freshly released eggs were estimated by recording the tracks of 95 surface drifters released from the location of spawning. Drifters were released in sets of 3 either 1 h before sunset or in the early afternoon (See Appendix A: Table 1). During most deployments, both in the early afternoon and at sunset, surface drifters traveled largely westward towards the reef, with angles of travel ranging between 217° (SW) and 305° (NW), and a mean direction of travel of 255° (SW). Visual assessment of the drifter's tracks showed that May 17 differed from the trend showed by the other drifters. This appreciating was corroborated with the bearing was estimate. Because of this May 17 was considered separately or was removed from parts of the analysis. The tracks of 82 individual drifters were considered to analyze the mean dispersal routes. Their mean speed and direction was determined using the centroid a set of 3 drifters for every day of the experiment (See Appendix A: Tables A2, A3, Figs. A3, A5). The direction of travel for early afternoon and sunset drifts carried out the same day showed a strong positive correlation based on Pearson's product moment correlation analysis ($r = 0.8 > 0.707$, $N = 6$, $p < 0.05$).

The only three drifters that did not fit this pattern drifted first to the NE or SE but changed direction and curved back westward towards the reef, before the deployment was completed (See Appendix A: Figs. A3, A4). Specifically, on May 17, drifters were released at 15:45 h and retrieved at 19:08 h. During this time, the surface drifters moved E at a 70° angle, coinciding with the estimated wind direction. However, around 18:30, the drift direction changed and the drifters started to move NW, curving towards the reef. Likewise, on 18 May drifters were released at 13:07 h and retrieved at 16:44 h and initially traveled SE at a 165° angle but at approximately 14:45 the track curved to a southwesterly direction towards the reef (See Appendix, Table A3, Fig. A4). Similarly the set of drifters deployed overnight, 1 h before sunset at 17:06 h May 28 and retrieved at 9:11 h on May 29, traveled towards and through the reef channel, covering a distance of 7,032 m at a mean speed of 12 cm s^{-1} (See Appendix A: Table A2, Fig. A6).

Drifter's measurements compared to ACP measurements

Surface current measurements from two separate bins from the ACP were used to compare against measurements from the surface drifters. Data quality was assessed determining the standard deviation of the mean *u* and *v* components for all bins. These standard deviations were plotted as a function of distance from the bottom. Visual examination of these plots revealed that for bins 1, 2, and 28 to 35 the standard deviations increased, and were up to 2 times greater than those recorded for the other bins. Based on this, all data between 3 to 28 m above the bottom were considered reliable. All other surface bins were discarded, and information derived from bin 27 was cautiously considered.

Measurements from bin 27 represent the current speed and direction 2 to 3 m below the water surface, while bin 26 represents the average of the horizontal velocities 3 to 4 m below the water surface. Since the instrument was deployed at ~30 m and examination of the standard deviations per sampling day showed that data up to 28 m above the bottom were reliable, information derived from bin 27 was considered with caution. During the peak of the spawning season (May 16 to 28), water masses 2 to 3 m below the surface (bin 27) moved onshore either NW or SW (See Appendix A: Table A5). After comparing the drifter's mean speed and traveling direction against the measurements recorded with the ACP, the drifters' direction of travel coincides with the current direction registered by the ACP 27 m above the bottom. Nonetheless, the magnitude of both measurements exhibits no correlation ($r = -0.09 < 0.557$, $N = 10$, $p < 0.05$) (See Appendix A: Table A5, Figs. A5, A6, A7). In most cases, the ACP's current speeds were higher than those computed from the drifter's tracks (See Appendix A: Table A5, Fig. 8a, 8b).

Similarly, the drifters' traveling direction coincides with the direction observed by the ACP at 26 m above the bottom, except for May 20. In this case the correlation between the magnitudes of both measurements is greater than at 27 m above the bottom ($r = 0.60 > 0.553$, $N = 10$, $p < 0.05$), indicating that 36% of the variation in the drifter's speed is explained by the observed speed measured with the ACP. One meter deeper, as recorded by bin 25, water parcels moved offshore 7 of the 11 sampling days (NE or SE), during May 16, 17, 19 and 20 currents at this depth moved inshore (Table 5). For the single overnight drift conducted from May 28 to 29, the drifters moved onshore into the reef channel.

Divergence: dispersion rate at the spawning aggregation site

To test the second hypothesis, that eggs disperse at a constant rate from the time and location of spawning such that the horizontal area of their spawning cloud increases at a constant rate, the triangular area of water parcels bounded by a set of 3 drifters was measured starting at the location of spawning. The rate of change in size of these triangular areas was also calculated over successive time intervals as a quantitative measure of divergence over time.

The area of the water parcels increased with time, but not at a constant rate as hypothesized (See Appendix A: Figs. A9, A11). Triangular areas showed a rapid size increase over time on May 23, going from 19 m^2 to 3499 m^2 in the first hour and from 5310 m^2 to 15732 m^2 in the following 40 min. May 23 was a day of relatively strong winds (See Appendix A: Fig. A9). The relationship between area sizes over time is better explained by a square-power dependence:

$$A = 100t^2 \tag{6}$$

where y is the area, x is the time elapsed, and 100 and 2 are constant real numbers (r^2 = 0.98 > 0.602, =N 60, $p < 0.05$). The power trend line shows how well the model fits the data and indicates that area sizes increased as a function of time. The size of the triangular area was determined by time multiplied by the scaling factor 100 and raised to the 2nd power. The scaling factor makes x^2 increase, while 2 indicates the rate of growth of the area every time step, as the time doubled the area increased 4 times (See Appendix A: Fig. A11).

No consistent pattern is observable in the Area Rate of Change (ARC) (See Appendix A: Table A7, Fig. A11). The ARC stayed relatively constant in May 17, 19, 21, 24 and 27, with values ranging from -48960 to 57754. Increased on May 18 from 13237 to 117076, and from 28104 to 200271 on May 23. ARC values fluctuated considerably on May 25, starting at -4770, increasing to 196920 and dropping sharply to -76985. Negative values of the ARC indicate that the area of the triangle was reduced in size from one time step the next. In most of these cases, 2 drogues drifted apart, but the third moved inwards, flattening the triangle and reducing its area. This support the idea that 3 drifters are not sufficient to quantify the ARC, since 3 points are not enough to reflect the changes in the water parcels area or orientation. During May 17, 21 and 25 the ARC values showed the greatest variations. On May 17 the initial ARC value was 4230, the lowest value -1800, and the final and highest value was 17550. Likewise, in May 21 values fluctuated from -48960 to 27360, and from -76985 to 196920 in May 25 ARC ranged. During these days the triangles expanded and contracted from one time step to the next (See Appendix A: Table A7, Fig. A9, A12). On 23 May both the areas and the ARC continued to increase over time. The initial area, 15 min after deployment, was 19 m^2 and it increased to 3499 m^2 after 75 min after of deployment. Like wise the initial ARC value was 28104 between t_2 and t_1, and increased to 200271 between t_5 and t_4. May 23 was the only day this occurred (See Appendix A: Fig. A9, A12). Days with strong winds and high waves generally had the highest variability in area rate of change, indicating that wind is a driving factor of surface current variability.

Egg density: egg abundance through space over time

Egg density decreased as time passed for May 19 (from 1402 to 139 egg m^{-3}), 23 (from 41332 to 19990 egg m^{-3}) and 24 (form 41571 to 16275 egg m^{-3}). Spawning was observed from May 19 to 25, throughout the spawning season egg densities increased. Egg density values registered for May 23 and 24, close to the end of the spawning period, were considerable higher (e.g. May 23 = 41571 egg m^{-3} and May 24 = 41332 egg m^{-3} for the first tow) than those registered for May 19, the first day of spawning, (1402 egg m^{-3} for the tow 1) (See Appendix A: Table A8, Fig. A13).

Visual analysis of the paths followed by the set of drifters deployed before sunset and the single drifter placed at the estimated center of the spawning cloud showed that water parcels flow in the same general direction before sunset and while spawning events were taking place. The diminishing egg densities calculated from egg counts from tows taken perpendicular to the direction of cloud dispersion could indicate that the spawning cloud disperses as time passes, but other diminishing factors such as scavenging (Heyman et al. 2001b) and the sinking of non-viable eggs should be considered.

IV. DISCUSSION

Mean current flow and egg dispersal

The results of the present study do not support the hypothesis that surface currents at Gladden Spit flow offshore at the time and location of Cubera snapper spawning. Surface drifters moved inshore during the early afternoon, around sunset and during the overnight drift. These results coincide with the results presented by Ezer et al. (2011). Using a high-resolution numerical ocean model, this study compared simulated and real surface drifters to study high-frequency flow variations in Gladden Spit. The most common travel direction for the simulated drifters was SW, corresponding with the direction followed by drifters deployed near the spawning site at various times.

Based on daily observations around sunset and the overnight drifter observation, surface currents tend to flow along the edge of the reef, and into the channel, corroborating Ezer et al. (2011) conclusions. In their study, the observed and the modeled drifters moved around the reef and field observation reflected instrument data.

Though wind speed and direction were not measured, estimations of the wind speed and direction were registered at the beginning of deployment for May 16 to 20, 25 and 27. These observations support the notion that there is a relationship between the wind direction and the path taken by the drifters. Generally, wind speed and direction have not been considered in propagule dispersal because dewatering, prolonged exposure of eggs to air, causes desiccation and renders eggs, embryos and even larvae non-viable (Holland 1987, Stocco and Beer 1972). Eggs caught in the air/water interphase area vulnerable to desiccation, because of this deeper water layers (>2 m) are typically considered in dispersion studies. For future studies, measuring wind speed and direction simultaneously with currents at the time and location of spawning is strongly suggested. If the motion of the top layers of the water column is partially driven by wind, and the fertilized eggs of Cubera snapper are drifting within these superficial water parcels, the eggs that stay submerged and survive predation will be drifting with this water masses until they reach settlement areas, places were larvae remain after completing larval development, where they will adopt adult characteristics and behavior after having their pelagic larval phase.

The fact that eggs drift towards the reef after spawning, reflect the impact of dispersal and mean current flow at Gladden Spit in the passive propagules (eggs and pre-flexion larvae). Most importantly, drifters are not just moving inshore, but likely through the barrier reef and into the enclosed barrier reef lagoon as shown by the track of the overnight drift. If eggs are in fact drifting to the lagoon, larvae will likely get trapped in inside it in shallower inshore waters, rather than being transported over great distances by large-scale oceanic currents (100 to 1000 km). This finding indicates that several factors determine egg transport in the area, and that long distance offshore advection is not the only transport mechanism available as prior studies have suggested (Williams et al. 1984, Paris & Cowen 2004, Karnauskas et al. 2011). Though the appropriately designed models are reliable, the scale and the resolution of the data used to generate them dictates their results. If they are not based on field-collected data at scales relevant to the processes occurring at the time and location of spawning their finding do not represent biological processes they seek to explain (Heyman et al. 2008). Few studies for Gladden Spit report findings the sub-kilometer scale observations used in the experiment described here (Ezer et al. 2011).

This study represents a simple and easily replicable method to track ocean currents at spawning aggregation sites in resource limited situations. More sophisticated instruments may provide more reliable data. However, they are rarely available across the Caribbean where massive spawning aggregations as well as other intricate ecological processes occur. They present a viable alternative for monitoring egg dispersal from reef fish spawning aggregations. Not requiring high-tech materials, training or service these drifters can be effectively handled by diverse users (Colin et al. 2003, Heyman et al. 2004, Pet J.S. et al. 2006).

Though the methodology should be subjected to revision and modification, techniques used herein could become a guide as to how to build and employ low-cost surface drifters for fish spawning aggregation monitoring. Comparing measurements of the speed and direction of currents recorded with surface drifters and those recorded by the ACP, we feel cautiously confident that drifters are an accurate measure of surface currents. The overnight experiment showed that the Astro dog collar permits the autonomous deployment of the drifters. When the observer was placed at a fixed location at sea, it was possible to tract the movement of the drifters to a distance up to 7 km with few signal interruptions (between 24 h 28 May and 1 h 29 May). Since demonstrating that the drifters can be found after spending the night adrift, longer drifts could be conducted without compromising the safety of the researchers or the equipment. It is recommended that such drifts will be conducted during the peak of the spawning season to determine the path of eggs during the first 12 to 24 h after spawning.

Divergence: dispersion rate at the spawning aggregation site

Data collected with surface drifters in this study showed that the area of the water parcels increased with time, and that dispersion at Gladden Spit obeys to a square-power dependence. However, these observations are of limited duration and applicability (See Appendix A: Table A6, Figs. A11). Like wise, dispersal measured as a function as egg density was demonstrated by decreasing egg counts as time increased but more data would be required to appropriately addressed this hypothesis (See Appendix A: Table A8; Fig. A13).

Drifters moved away from the location of spawning and from each other as each time passed, allowing the quantification of the degree of spreading around the spawning area. In most cases the area of water parcels increased with every time step and the measure of the area change was quantified as divergence. The area rate of change (ARC), a measurement of horizontal divergence, indicates the rate at which areas were changing ever time step.

In general, the longer the drifters stayed in the water the more factors (e.g. wind speed and direction, water density, tides, bathymetry, and Coriolis effect) influenced the size of the area drawn by them. There was low variability in the triangular areas within the first hour after deployment, but that variability increased with every time step (See Appendix A: Fig. A11). Because this longer time scale variability is not the focus of this study, none of these variables will be addressed, but it is recommended that they will be accounted for in future studies.

During some sampling days with positive ARC values, the triangle's area increased at different rates over the same time period (~15 min). Though the duration of the drifts was not the same every day, and variability increased as time passed (See Appendix A: Fig. A11), these results provide evidence that divergence at the time and location of spawning occur as a square dependence relation. Area increased as a function of time, when time doubled area increased by 4 times. This might be evidence for the effect of wind on divergence observed and in the future it should be quantified, as spreading tends to increase at the wind-driven surface layer (Williams et al. 1984).

To track dispersion at the time of spawning and directly link these data to egg density, we suggest deploying a set of +3 drifters equipped with Astro dog collars <1 min after spawning is first observed. This simultaneous quantification of the ARC, and egg density would allow evaluating the effectiveness of surface drifters to track the dispersal pathway of eggs from their spawning site.

Though vorticity, the measure of the orientation change of the water parcels (Molinari & Kirwan 1975), was not examined and there seems to be little rotation in the positioning of the drogues throughout deployment. For future studies quantifying the rotation of the individual drifters would provide information about the way in which water parcels behave and how they might be influencing egg dispersal. Water parcel rotation can be quantified determining vorticity, the measure of the orientation change without area or shape change of a parcel. This kinematic property is related to external functions of circulation such as wind and bathymetry, and can be evaluated from sets of more than 3 drifters using the formulation in Molinari and Kirwan (1975), and calculating the horizontal components of velocity relative to center of mass of a cluster of drifters (Kirwan 1988).

Moreover, using 4 or more drogues is recommended, this will allow better estimates of the changes in rates and orientation of dispersion of water parcels. Using more than 4 drogues also increases the statistical confidence in the values of divergence and vorticity Molinari and Kirwan (1975). By default, when using only 3 drifters, the only possible shape that can be delineate is a triangle, and changes in the shape and orientations of the water parcels cannot be quantified.

Egg density: egg abundance through space over time

Based on the 3 viable replicate days of the experiment, egg densities generally decreased with time as gamete clouds drifted away from the time and location of spawning (See Appendix A: Fig. A13). There was not sufficient replication to conclusively address the hypothesis, however, egg densities decreased as the cloud disperses and initial egg densities increased through the spawning season (See Appendix A: Table A8 Fig. A13). This is consistent with reports by Heyman et al. (2005), as the spawning period progresses adults come closer to the water surface to release their gametes.

Direct egg counts for the area were conducted by Heyman et al. (2005), during the peak spawning period for May 2000 and June 2001. During this study, sampling happened in consecutive evenings each year and a total of 14 samples were gathered, though it is not specified how many samples were collected each year. They reported that the mean egg density, immediately after spawning, within the top meter of the spawning cloud was 1450±240 eggs m^{-3}. Heyman et al. (2005), used a single net with a slightly smaller mouth diameter (25 cm), with a bigger mesh size (0.5 mm) than the one used in the current study. Heyman et al. (2005) towed the net at 1 m depth, and during this experiment it was dragged just below the surface (~30 cm deep). The difference in the mesh size is negligible as the egg's diameter is greater in any case but the tow depth has and impact on the number of eggs present in the water at the time of the experiment. A greater egg density is expected closer to the surface immediately after spawning, as it takes at least 8 min for the gamete cloud to disperse (Heyman et al. 2005). Because the mean between both nets from the bongo was used to determine egg density, and Heyman et al. (2005) egg counts correspond to instants immediately after spawning, their results were compared against the first tow of each sampling day from this experiment. Egg densities reported here (See Appendix A: Table A8), are higher in most cases than those obtained by Heyman et al. (2005). The difference in the methodology employed could account for these differences, or changes in population abundances during the past decade. However, further research would be necessary assess both explanations. Nonetheless, the fact their data was collected over two different spawning seasons, and different months and with different sampling efforts makes it impossible to make a direct reliable comparison.

Visual analysis of the paths followed by the set of drifters deployed before sunset and the single drifter placed at the estimated center of the spawning cloud showed that water parcels flow in the same general direction before sunset and while spawning events are taking place (See Appendix A: Fig. A14). The diminishing eggs densities calculated from egg counts from tows taken widthwise as the cloud dispersed, indicate that the spawning cloud disperses as times passes. Nonetheless, to accurately estimate how much of this reduction is due to dispersion, predation and egg mortality should also be quantified. The fact that the drifters closely followed the dispersal pathway of the cloud shows that these low-cost drifters are a good alternative to track the fate of gametes immediately after spawning.

Egg samples are fundamental to test dispersal from the spawning aggregation site however, implementation was difficult, and plankton tows across the spawning cloud were only achieved on 3 days of the experiment (See Appendix A: Figs. A14, A15, A16). The large variability between sampling days and tows, as well as the difficult implementation suggest that the egg sampling technique must be carefully revised.

V. SUMMARY AND CONCLUSIONS

Summary

Tropical marine conservation depends on understanding the life history of commercially exploited species, particularly during their early life stages. Many ecologically and commercially important reef fish species form spawning aggregations, groups of fish of the same species that migrate long distances for the sole purpose of reproducing. Better understanding of this reproductive strategy and of the oceanographic features that determine its occurrence will contribute to the development of ecologically driven management strategies.

This study aimed to examine the influence of surface currents on gametes released at a spawning aggregation of Cubera snapper *Lutjanus cyanopterus* at Gladden Spit, Belize. It was hypothesized that surface currents flowed offshore at the time and location of spawning, that freshly released eggs dispersed at a constant rate from the time and location of spawning, and that egg density within the spawning cloud decreased over time as it dispersed with the predominant currents.

The results of the present study do not support the hypothesis that surface currents at Gladden Spit flow offshore during Cubera snapper spawning. Surface drifters traveled largely westward towards the reef, indicating a predominantly inshore flow. Because water flow within the superficial layers of the water column is greatly driven by wind, it is necessary to measure wind speed and direction simultaneously with current measurements at the time and location of spawning, to account for this wind driven variability. If fertilized eggs of Cubera snapper are drifting within these superficial water masses, eggs that stay submerged and survive predation will be drifting with these water parcels until they reach settlement areas, the places where they will inhabit as adults. Surface drifters moved inshore, through the barrier reef and into the barrier reef lagoon. If eggs are transported in the same manner, larvae will likely get trapped in shallower inshore waters, rather than being transported over great distances by oceanic currents, or retained off the reef by seasonal eddies.

Divergence of the water parcels, as a function of area change over time is explained by a square-power dependence. No consistent pattern was observable in the area rate of change (ARC), indicating that the area of the water parcels and thus the area of the spawning cloud most likely changes depending on numerous environmental conditions including currents, winds, and tides.

Initial egg densities increased throughout the spawning season, with higher egg counts registered for the final days of the season; however, egg densities for each sampling day decreased over time.

The pelagic phase of reef fishes has major biogeographic, evolutionary and ecological implications for reef fish populations. A complete understanding of this crucial stage will only come from empirical data derived from scale appropriate studies. This experiment focused in a sub-kilometer scale, a scale relevant to the processes occurring during spawning. This preliminary attempt shows that more site-specific data is required to understand the transport mechanics determining egg dispersal.

Conclusions

Extensive field data do not support the hypothesis that surface currents at Gladden Spit flow offshore during the peak of the spawning season for Cubera snapper, in fact surface currents flow inshore during the peak of the spawning season.

Comparison between the mean speed and traveling direction recorded with low-cost surface drifters against the measurements recorded with an ACP, 26 m and 27 m above the bottom, support these findings as the traveling direction and magnitude of registered with the drifters, in most cases, coincides with those registered by the ACP.

Divergence of the water parcels, estimated as the change in the area size is explained by a square-power dependence, but further more replicate intense research is needed. No consistent pattern is observable in the area rate of change (ARC).

Egg density generally decreased over time, though there was not sufficient replication to conclusively state that egg density within the spawning cloud decreases over time as it disperses with the predominant surface currents.

The tracks followed by the set of drifters deployed before sunset and the single drifter placed at the estimated center of the gamete cloud showed that water parcels flow in the same general direction. Therefore, these low-cost drifters can closely follow the dispersal pathway of freshly released gametes. And the techniques used during this study could become a guide as to how to build and employ low-cost surface drifters to monitor fish spawning aggregations.

Understanding how abiotic factors influence the occurrence of multispecies spawning aggregations will lead to better conservation and management strategies in Belize and across the Western Caribbean.

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APPENDIX A

TABLES AND FIGURES

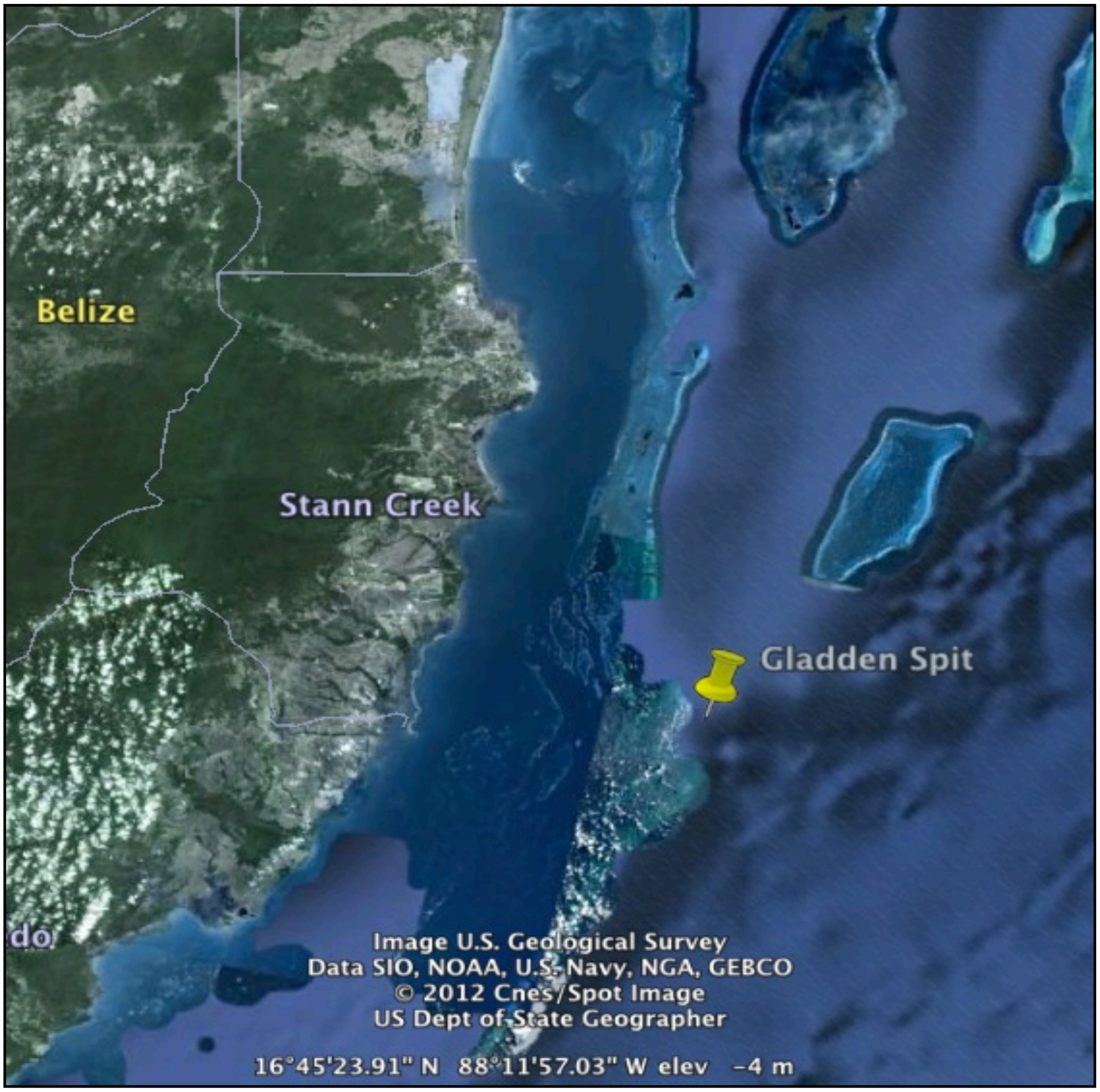


Fig. A1. Map showing the position of Gladden Spit (16°35′N, 88°00′W), a reef promontory 46 km away from continental Belize and directly adjacent to the 1000 m isobath. Map shows the area between Lat 16° N and 18° N and Lon 86° W and 88° W

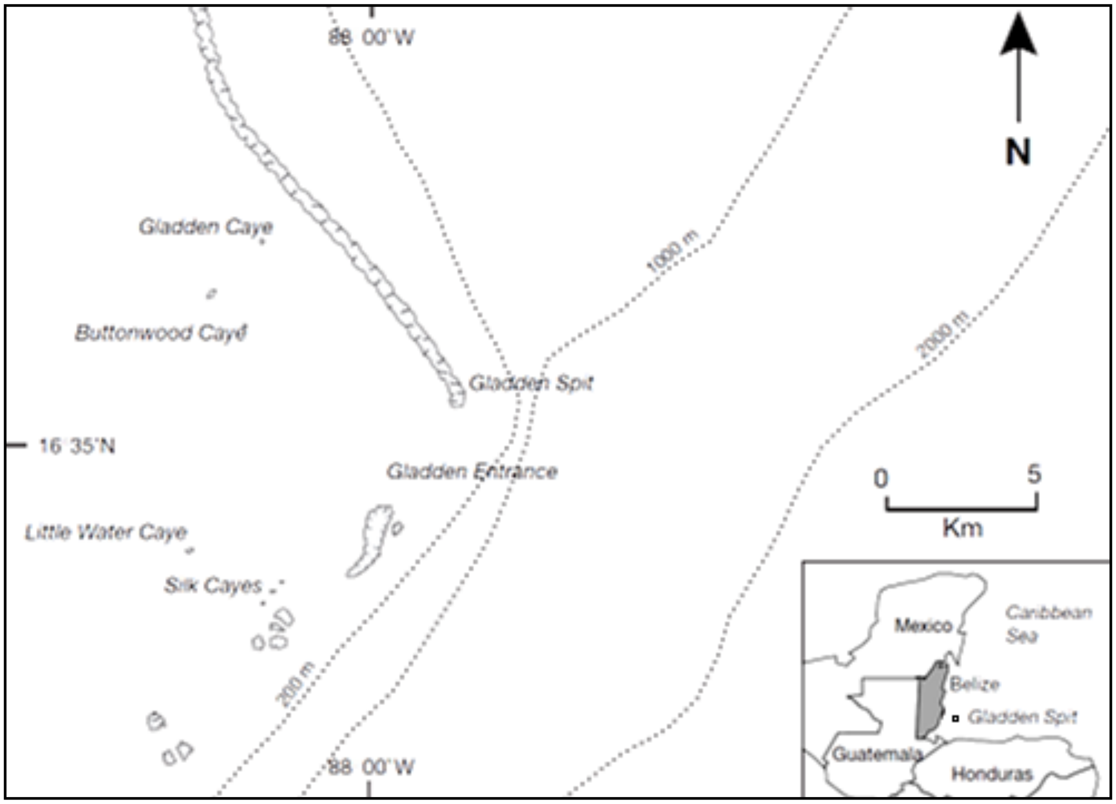


Fig. A2. Location of Gladden Spit (16°35′N, 88°00′W) at the Belize Barrier Reef (BBR). Modified from Heyman et al. (2008) and Heyman et al. (2001)

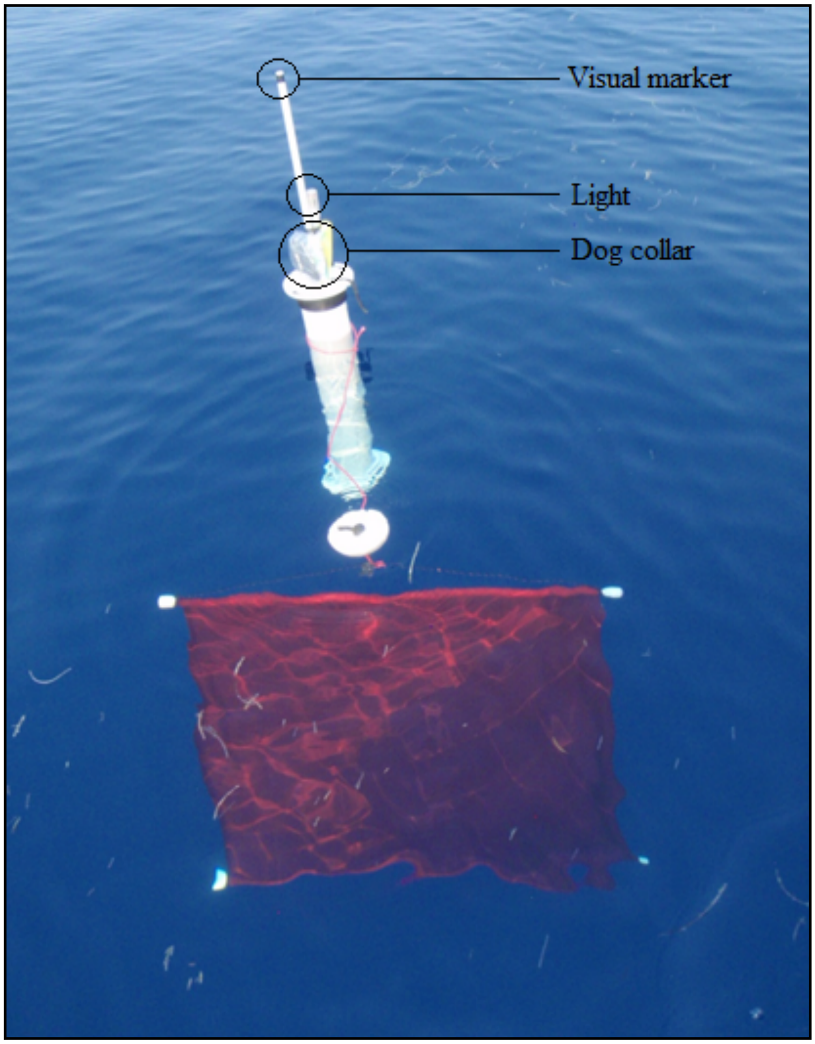


Fig. A3. Drogue deployed in the water, the weighted PVC at the bottom guarantee that the cloth vane was extended during deployment, therefore drifting predominantly by the action of the surface currents. The PVC buoy granted buoyance and stability to the drifter. The dog collar registered the location of the drifter and together with the LED light facilitated retrieval. Unique visual markers facilitated drifter identification and data orderly data collection

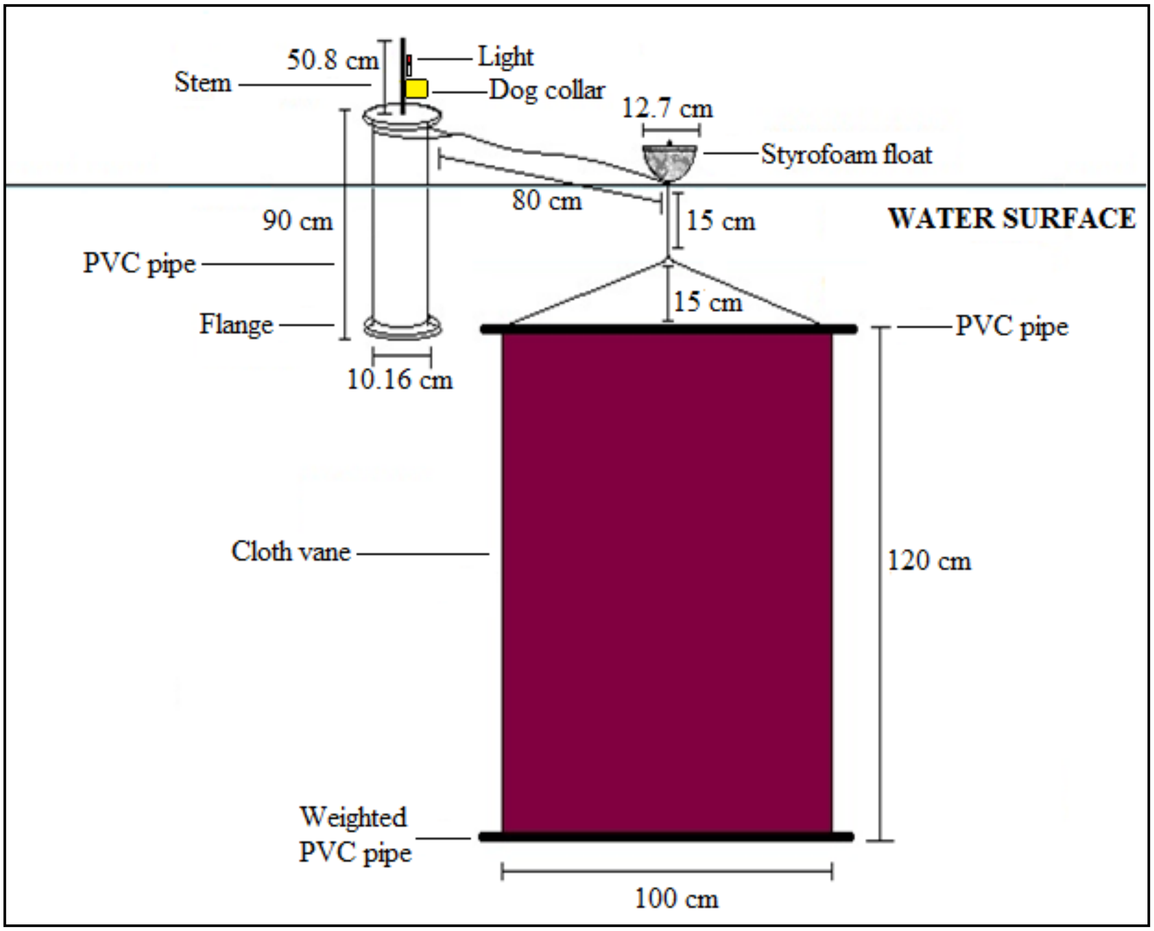


Fig. A4. Drogued surface drifter design, modified from Heyman et al. (2004) and Houser (Unpublished data). The drifters consist on a drogue made from a single 1x1.20 m cloth vane (40% polyester, 60% cotton) fastened on both ends to 1.27 cm diameter PVC tubes capped at both ends. The buoy was constructed using 15.2 cm (6 in) diameter PVC sewer pipe cut into 1 m lengths and capped at both ends with standard commode flanges. All parts and dimensions are shown, picture not to scale

Table A1. Summary of the 2-week *in situ* experiment, early afternoon (n=8), sunset (n=11) and overnight (n=1) deployments were conducted. Drift duration varied due to environmental conditions, start and end times for each track were recorded. When spawning was observed plankton tows were conducted

Date	Early afternoon			Sunset			Spawning	Tows
	Start	End	Duration (min)	Start	End	Duration (min)		
16-May	14:26	16:48	142	17:05	18:36	91	Not observed	-
17-May	15:45	19:08	203	17:00	19:30	210	Not observed	-
18-May	13:07	16:44	217	17:15	19:45	210	Observed	Conducted
19-May	-	-	-	17:14	18:08	58	Observed	Conducted
20-May	16:10	17:20	70	17:15	18:15	60	Observed	Conducted
21-May	-	-	-	17:08	18:00	52	Observed	Conducted
22-May	-	-	-	16:54	17:55	61	Observed	Conducted
23-May	15:06	16:46	97	17:01	18:53	112	Observed	Conducted
24-May	-	-	-	17:10	18:42	92	Observed	Conducted
25-May	16:23	17:29	66	17:06	18:28	82	Not observed	-
27-May	16:08	17:26	78	17:04	18:14	70	Not observed	-
28-May	-	-	-	17:06	9:04 (+1d)	962	Not observed	-

Table A2. Total drift time, total distance traveled, mean drift speed and angle of travel (bearing) for all sunset drift tracks. A set 3 of drifters was deployed daily 1 h before sunset (~18:15 local time). The location of the 3 drifters was recorded at ~15 min intervals. [α]This angle does not accurately represent the direction followed by the set 3 of drifters due to a sudden change in direction throughout deployment

Date	Duration (min)	Distance (m)	Speed (cm s^{-1})	Angle of travel (°)
16-May	91	666	12	305
17-May	210	2,260	5	002[α]
18-May	210	2,253	25	242
19-May	58	609	19	249
20-May	60	612	17	282
21-May	52	654	20	208
22-May	61	638	18	217
23-May	112	460	7	301
24-May	92	601	10	226
25-May	82	753	15	217
27-May	70	828	15	197
28-May	962	7,032	12	254

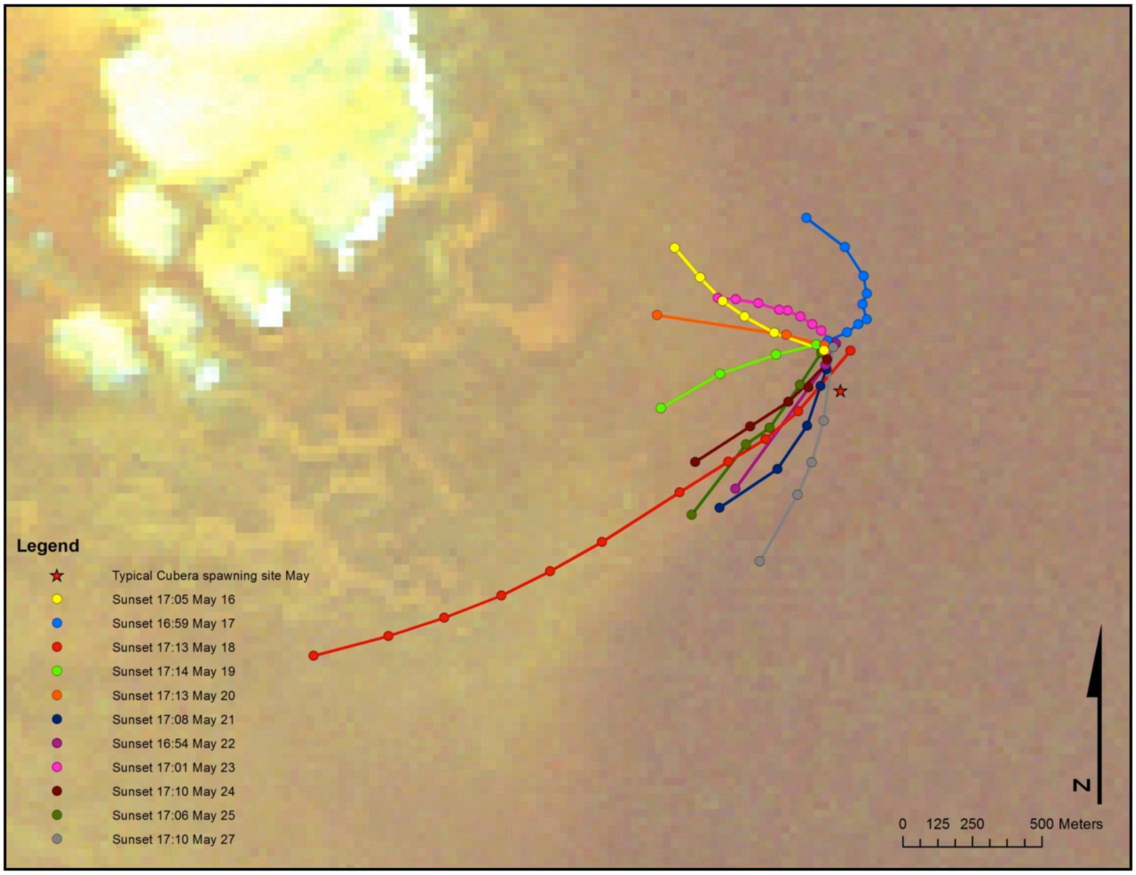


Fig. A5. Drift tracks for sunset deployments. Circles represent the centroid for the triangular area drawn by each set of drifters. The location of the 3 drifters was recorded at ~15 min intervals. Map shows a close up of Lat 16° N and Lon 88° W

Table A3. Total drift time, distance traveled, mean drift speed and angle of travel (bearing) for early afternoon deployments. The location of the drifters was recorded at ~15 min intervals

Date	Duration (min)	Distance (m)	Speed (cm s-1)	Angle of travel (°)
16-May	142	1,293	15	286
17-May	203	950	8	70
18-May	217	1,512	12	165
20-May	70	676	16	290
23-May	97	690	12	318
25-May	66	679	17	226
27-May	78	830	18	205

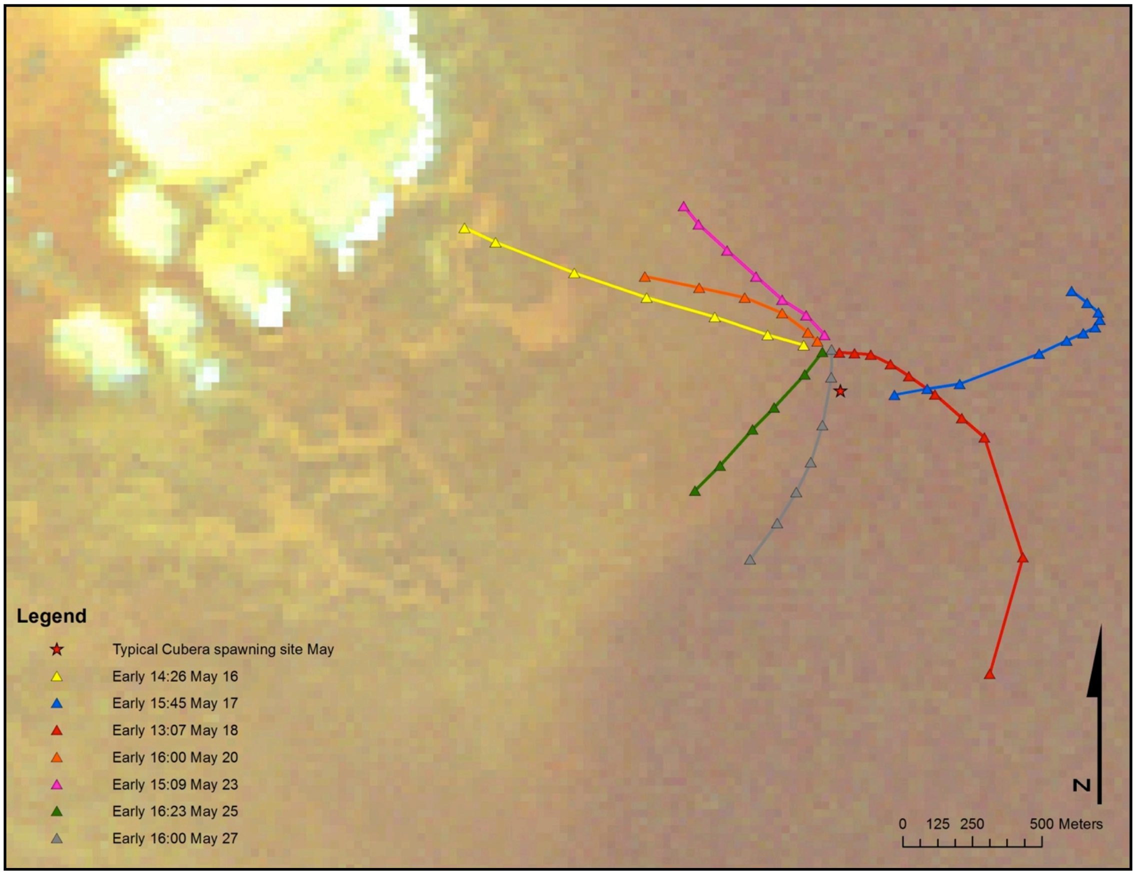


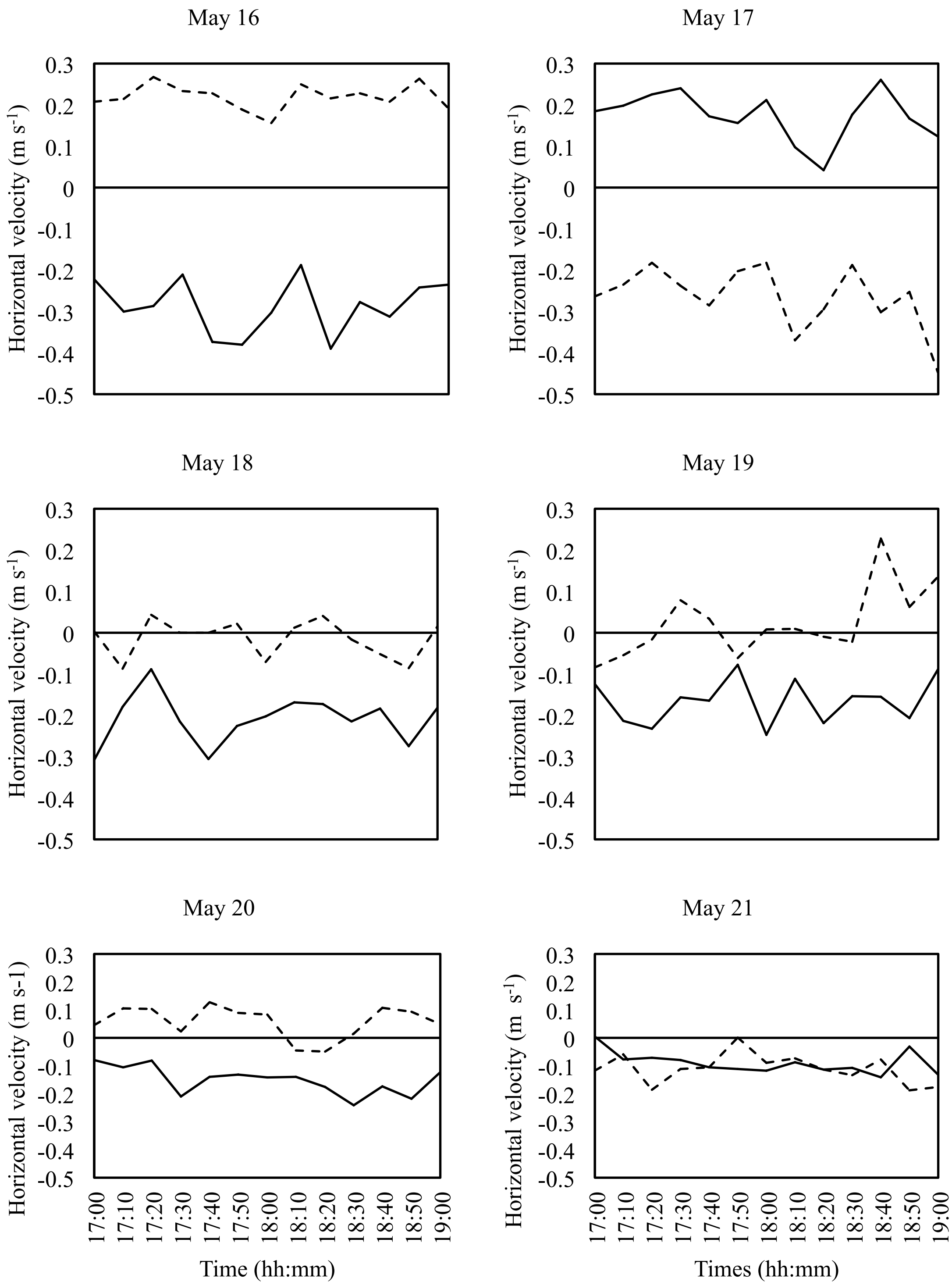
Fig. A6. Drift tracks for early afternoon deployments. Triangles represent the centroid for each set of 3 surface drifters. The location of the drifters was recorded at ~15 min intervals. Map shows a close up of Lat 16° N and Lon 88° W

Table A4. Comparison between the magnitude and the direction of early afternoon and sunset drifts carried out during the same day. **Bold $^{\alpha}$:** Angle does not represent the distance of travel, the path of the drifter's changed quickly throughout deployment. Values from the Pearson product-moment correlation coefficient (r) represent the relation between the drifter's speed and direction for sunset and early afternoon deployments

Date	Bearing (°)		Speed (m s^{-1})		Direction	
	Early	Sunset	Early	Sunset	Early	Sunset
16-May	286	305	0.1518	0.1220	NW	NW
17-May	70	**002**$^{\alpha}$	0.0780	0.1794	NE	NE
18-May	165	242	0.1161	0.1788	SE	SW
20-May	290	282	0.1610	0.1700	NW	NW
23-May	318	301	0.1186	0.0685	NW	NW
25-May	226	217	0.1715	0.1530	SW	SW
	r = 0.91		r= -0.10			

Table A5. Speed and the direction of surface currents measured with surface drifts and ACP (bins 27, 26 and 25) below water surface during the same day. Values from the Pearson product-moment correlation coefficient (r) represent the relation between the drifter's speed and direction versus the ACP's speed and direction for all bins. In most cases r indicates a moderate or strong correlation

Date	Drifters		ACP (bin 27)		ACP (bin 26)		ACP (bin 25)	
	Speed (m s-1)	Direction (°)	Speed (m s-1)	Direction (°)	Speed (m s-1)	Direction (°)	Speed (m s-1)	Direction (°)
16-May	0.12	305	0.36	307	0.17	288	0.10	337
18-May	0.18	242	0.21	184	0.20	244	0.12	241
19-May	0.18	249	0.19	188	0.10	264	0.07	179
20-May	0.17	282	0.17	291	0.13	260	0.12	261
21-May	0.21	208	0.15	231	0.20	160	0.17	214
22-May	0.17	217	0.16	218	0.22	249	0.14	179
23-May	0.07	301	0.17	300	0.13	221	0.02	150
24-May	0.11	226	0.1	198	0.10	212	0.02	134
25-May	0.15	217	0.15	217	0.13	235	0.12	176
27-May	0.20	197	0.19	254	0.27	256	0.28	167
			r= -0.09	r = 0.67	r = 0.54	r = 0.42	r = 0.76	r = 0.51


May 16
May 17
May 18
May 19
May 20
May 21
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
-0.5
Horizontal velocity (m s-1)
17:00
17:10
17:20
17:30
17:40
17:50
18:00
18:10
18:20
18:30
18:40
18:50
19:00
Time (hh:mm)
Times (hh:mm)

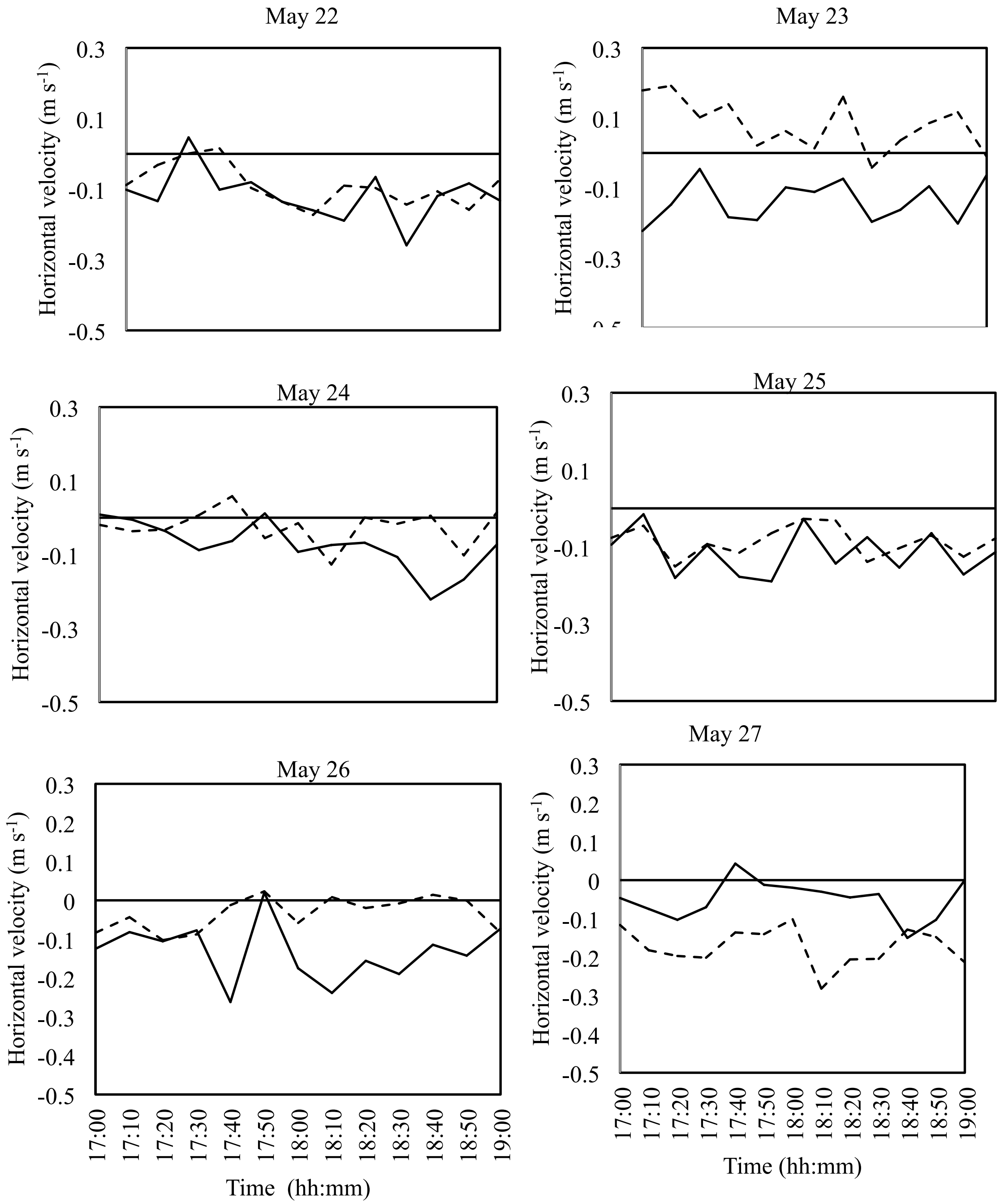


Fig. A7. Eastward *u* (—) and northward *v* (---) components of the horizontal velocity 2 - 3 m below the water surface. Data were collected at the spawning aggregation site from 16 - 27 May around sunset between 17 h and 19 h. Positive values represent E and N, and negative values represent W and S

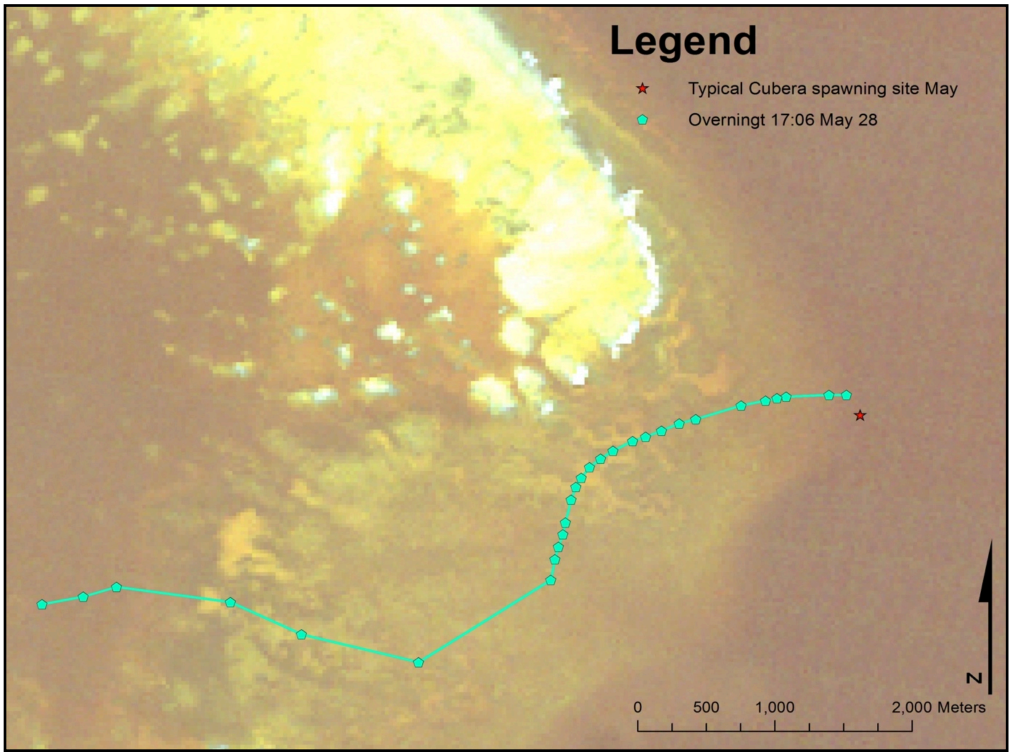


Fig. A8. Track for the overnight drift (28 - 29 May). Pentagons represent the centroid for each set of 3 surface drifters. The location of the drifters was recorded at ~1 h intervals except when there was no communication between the transmitters and the receptor. Map shows a close up of Lat 16° N and Lon 88° W

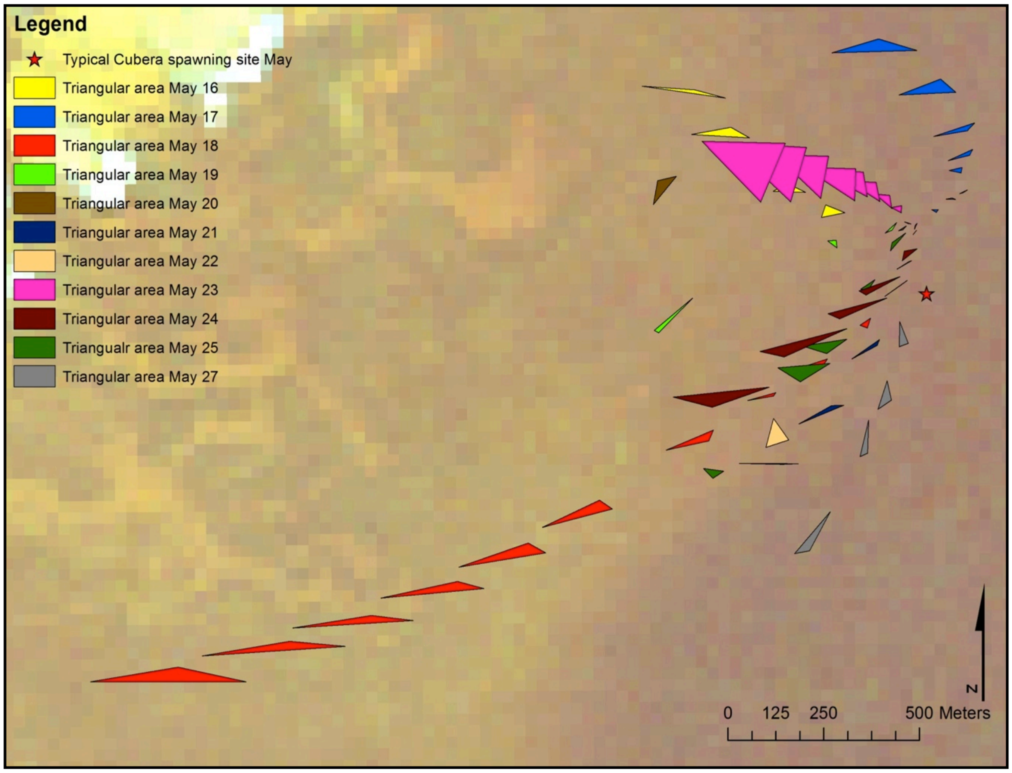


Fig. A9. Triangular areas formed by each set of 3 drifters during sunset deployments. Coordinates were recorded 15 min. Triangular areas were drawn using editing tools in ArcMap 10. Map shows a close up of Lat 16° N and Lon 88° W

Table A6. Triangular areas formed by each set of 3 drifters. Coordinates were collected approximately every 15 min with a hand held GPS. Total areas were calculated using the geometric calculator from ArcMap 10

	Area (m^2)										
Date	A_{t1}	A_{t2}	A_{t3}	A_{t4}	A_{t5}	A_{t6}	A_{t7}	A_{t8}	A_{t9}	A_{t10}	A_{t11}
16-May	0	-	874	829	1028	1745	1031	-	-	-	-
17-May	12	59	39	19	214	344	669	2553	3442	-	-
18-May	249	424	241	1345	2727	3504	3163	2906	3950	7273	385
19-May	123	193	598	688	-	-	-	-	-	-	-
20-May	36	-	-	-	1364	-	-	-	-	-	-
21-May	27	4	343	647	103	-	-	-	-	-	-
22-May	0	-	-	-	1906	-	-	-	-	-	-
23-May	19	253	593	1691	3499	5310	7252	13699	15732	-	-
24-May	372	822	1470	3195	4318	-	-	-	-	-	-
25-May	298	255	1539	2633	548	-	-	-	-	-	-
27-May	4	697	944	774	688	-	-	-	-	-	-

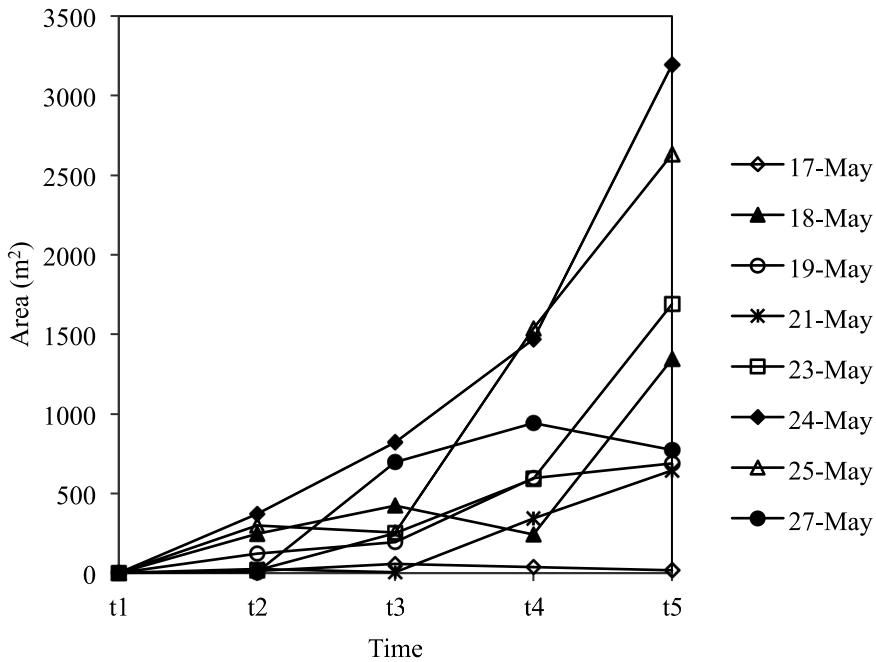


Fig. A10. Divergence. Area change over time for the first 5 recording times after initial deployment (~60 min long). Time is presented as time steps

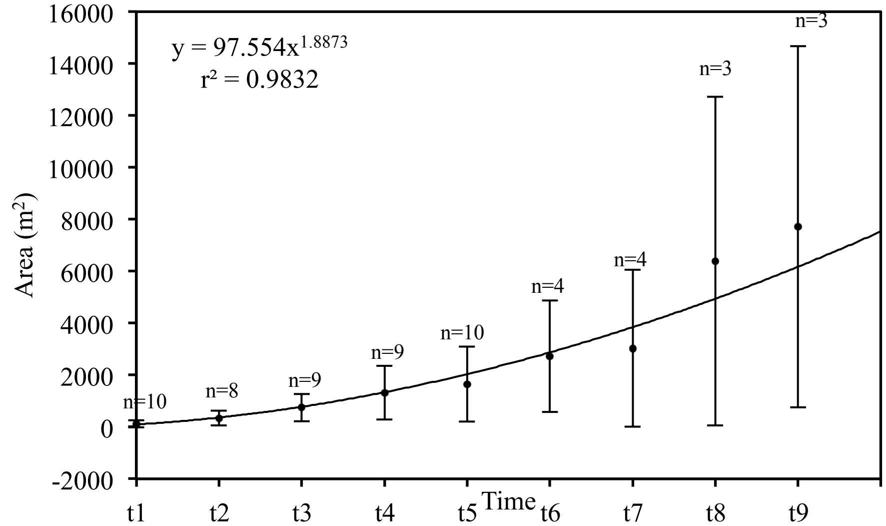


Fig. A11. Areas over time for the first time steps per day for all sampling days in which enough data points were collected to draw triangles (~120 min long). Time is presented as time steps

Table A7. Area Rate of Change (ARC) as a estimation of divergence, only days when trinagular areas formed for the first 5 time steps where formed were considered

Date	Area rate of change (ARC)			
	A_{t2}- A_{t1}	A_{t3}- A_{t2}	A_{t4}- A_{t3}	A_{t5}- A_{t4}
17-May	4,230	-1,516	-1,800	17,550
18-May	13,237	-20,269	113,587	117,076
19-May	7,738	32,357	6,207	912
21-May	-5,525	34,869	27,360	-48,960
23-May	28,104	54,400	131,760	200,271
24-May	32,371	84,829	108,000	57,754
25-May	-4,770	92,448	196,920	-76,985
27-May	52,553	29,640	-20,400	4,763

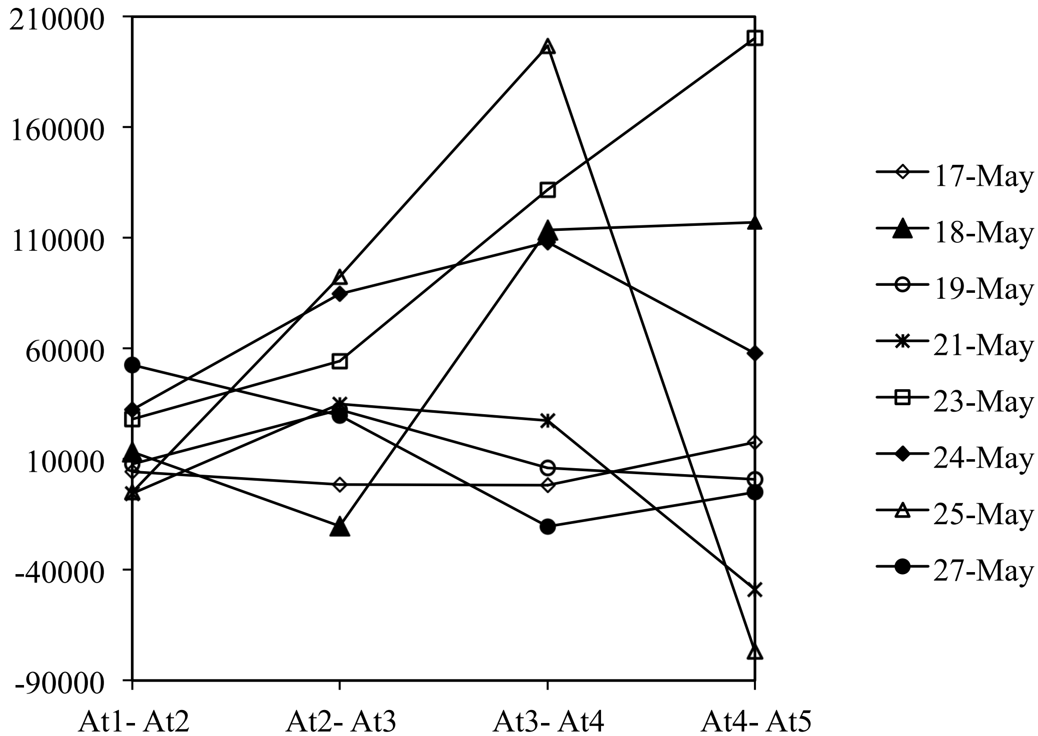


Fig. A12. Area rate of change for the first time steps per day for all sampling days in which enough data points were collected to draw triangles. All time steps with more than one measurement were considered. The number of samples is indicated above every error

Table A8. Egg densities of the entire gamete cloud >1 min after spawning as determine by egg abundance per volume filtered for the first tow (T1) of each sampling day. No egg samples were collected for T1 for May 18 and 19. During May 20 the cod end of both nets was completely full thus the sample was deem uncountable and the total number of eggs was estimated based on the volume one egg of Cubera snapper and the volume of the cod end. The total number of eggs in each replicate was used to calculate the mean count of eggs per sample. Mean egg density indicates the mean number of eggs in each tow

Date	Replicates (eggs)		Mean	S.D.	Tow volume	Egg density
	R1	R2			(m^3)	(eggs m^{-3})
18-May	-	-	-	-	3.7	-
19-May	-	-	-	-	11.5	-
20-May	Uncountable				4.6	**63000***
21-May	156,050	164,500	160,275	5,975	1.8	86,221
22-May	121,700	120,050	120,875	1,167	3.5	34,470
23-May	165,500	128,300	146,900	26,304	3.6	41,332
24-May	123,950	112,350	118,150	8,202	2.8	41,571
25-May	79,300	75,700	77,500	2,546	3.8	20,441

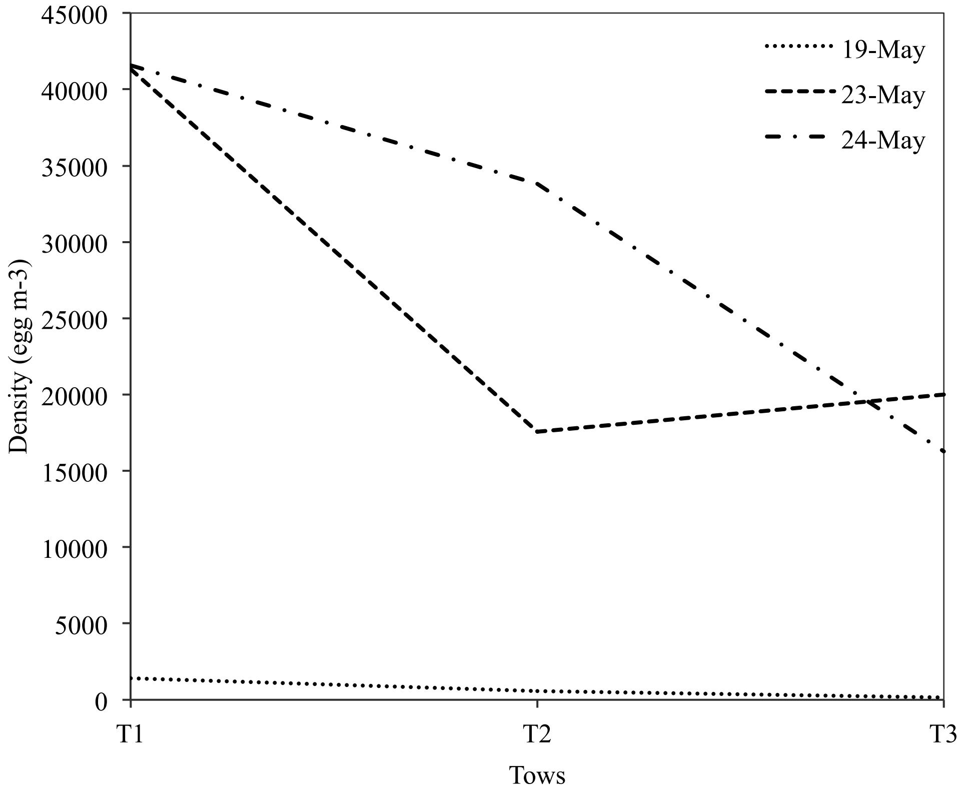


Fig. A13. Egg densities per plankton tow during May 19, 23 and 24, the best data available to evaluate divergence and egg dispersal. For each day, the samples collected was transferred to a labeled sampling bottle and fixed with 20 ml of 100% ethanol. Each bottle was fill with seawater to complete a total volume of 1000 ml. Then 4 replicate 5-ml aliquots were taken and all eggs present were counted using an AmScope 10x-20x-30x Student Binocular Stereo Microscope and a CST/Berger 30-100 4-digit mechanical counter

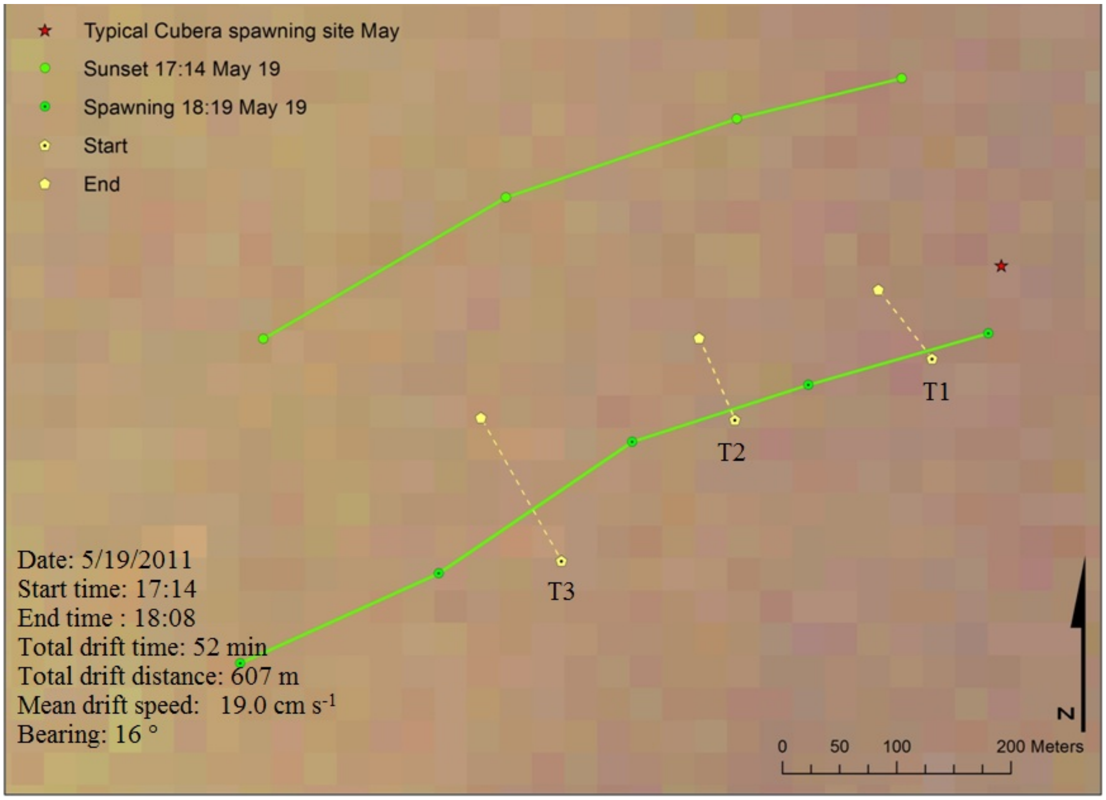


Fig. A14. Drift tracks for the set of 3 drifters and the drifter placed at the center of the spawning cloud. Upper line depicts the path followed by the 3 drifters starting 1 h before sunset. Bottom track represents the path followed by a single drifter deployed immediately after spawning was first observed. Dashed lines show the 3 plankton tows conducted at ~5 min intervals across the cloud as it dispersed. Map shows a close up of Lat 16° N and Lon 88° W

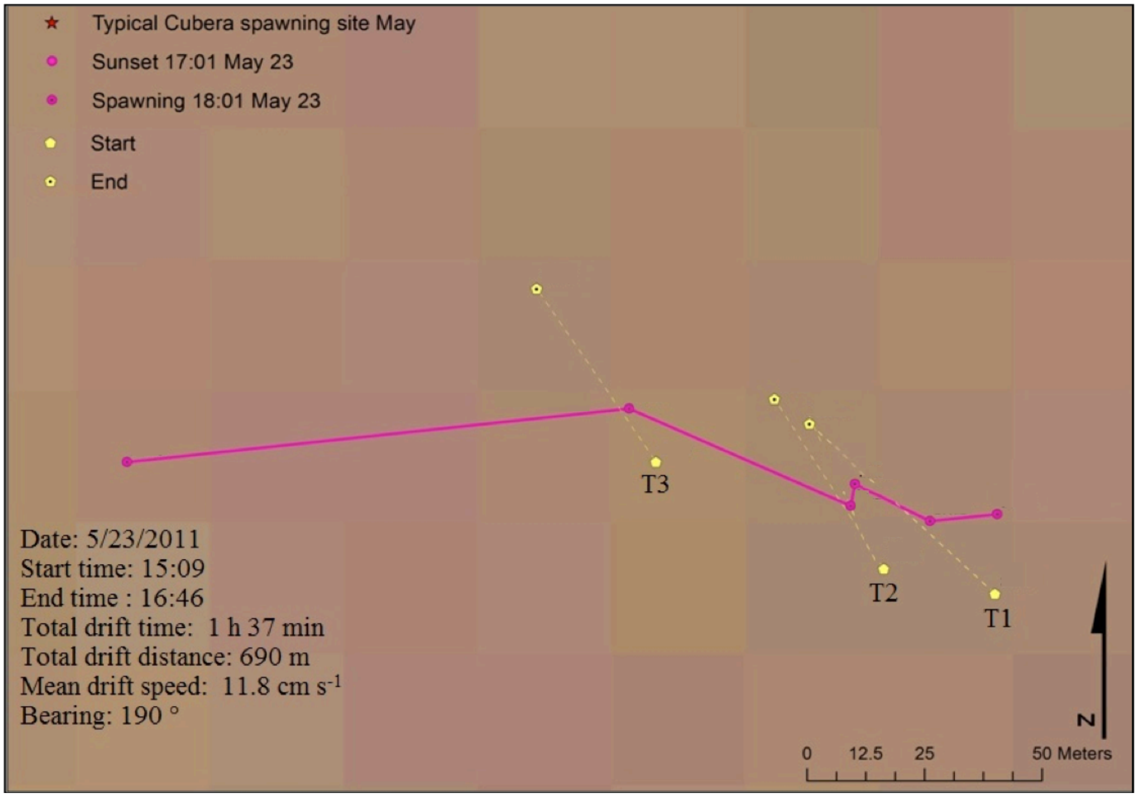


Fig. A15. Drift tracks for the drifter placed at the center of the spawning cloud. The track represents the path followed by a single drifter deployed immediately after spawning was first observed. Dashed lines show the 3 plankton tows conducted at ~5 min intervals across the cloud as it dispersed. Map shows a close up of Lat 16° N and Lon 88° W

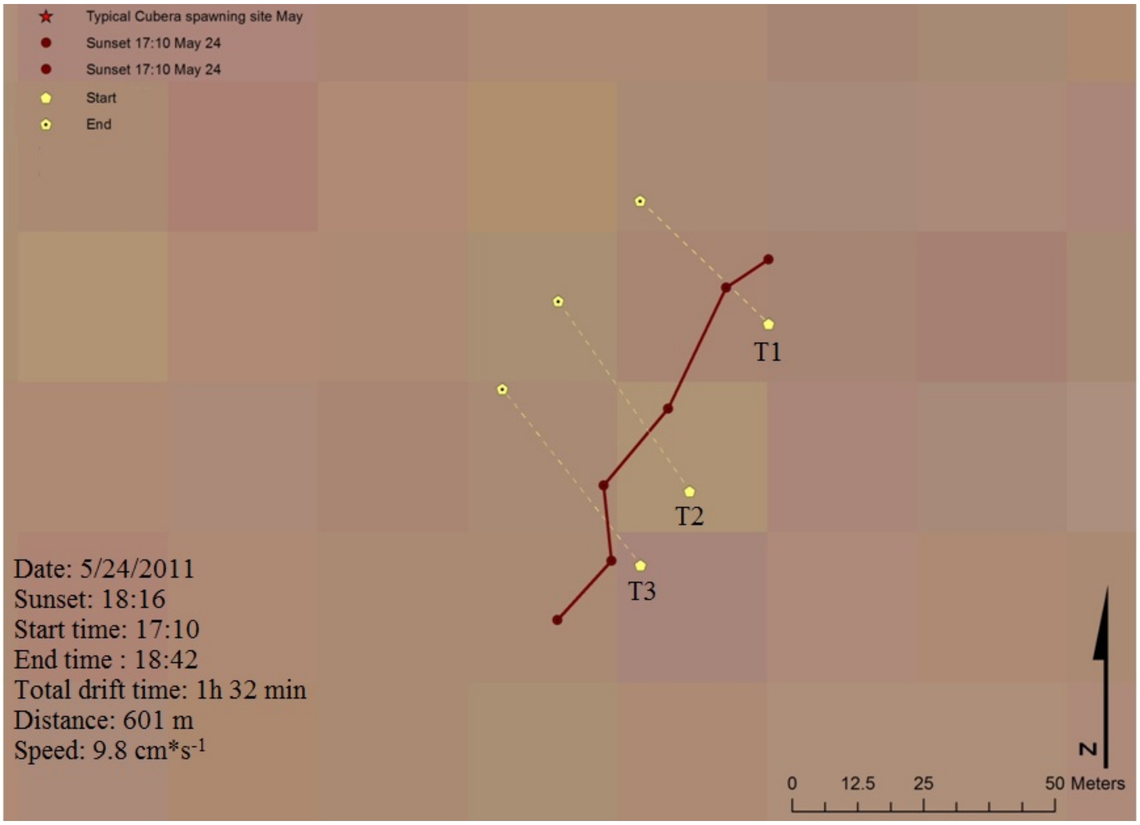


Fig. A16. Drift tracks for the drifter placed at the center of the spawning cloud. The track represents the path followed by a single drifter deployed immediately after spawning was first observed. Dashed lines show the 3 plankton tows conducted at ~5 min intervals across the cloud as it dispersed. Map shows a close up of Lat 16° N and Lon 88° W