A potential larval recruitment pathway originating from a Florida marine protected area

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ABSTRACT

Studies that track the dispersal of eggs and larvae from a point source are important to the emerging field of marine protected area (MPA) science. Two thousand ballasted drifter vials were released over a mutton snapper (*Lutjanus analis*) spawning aggregation in the Dry Tortugas, Florida, over two consecutive years (1999, 2000). The site, called Riley's Hump, is located within an MPA. The drifter vials were used as a means to model the potential dispersal and distribution of recruits originating from this site. Eleven percent of the vials were recovered each year by beachcombers. Results for each year indicated that Riley's Hump might be a source of mutton snapper recruits for a broad expanse of the Florida Keys and southeast Florida. Riley's Hump may therefore be functioning as an important fisheries reserve.

Key words: connectivity, Florida, larval, MPA, recruitment, snapper

INTRODUCTION

Marine resource managers are increasingly turning to the implementation of marine protected areas (MPAs) as a means of managing fisheries. In the United States, large systems of MPAs have recently been established in both Florida and California. It is argued that the increase in fish size and density within protected areas will result in increased reproductive potential and the movement of fish out of the reserve. The nature of marine fish and invertebrate reproduction lends itself to spillover if the reserve is sited such that ocean currents move larvae out of the protected area and allow for settling in nearby regions. Although a growing body of literature has demonstrated fishery benefits due to the creation of an MPA, these benefits are attributed to the spillover of adult fish (reviewed by Gell and Roberts, 2002). However, spillover based on the export of larvae from a reserve and subsequent recruitment of juveniles in adjacent areas has been very difficult to demonstrate because of the difficulty in determining the source of recruits (Palumbi, 2001). It is vitally important to establish an understanding of larval connectivity between MPA sites and adjacent regions (Roberts, 1997; Jones *et al.*, 1999; Cowen *et al.*, 2000; Crowder *et al.*, 2000) because it is possible that an MPA may be located in a larval sink that does not also act as a source. The emerging science of otolith (Swearer *et al.*, 1999) and exoskeleton (DiBacco and Chadwick, 2001) microchemistry holds promise for determining larval sources, but presently is only useful in environments with a strong gradient of trace metals (Largier, 2003). Although satellite-tracked drifters are a good means of tracking ocean currents, only two previous studies (Colin, 1992; Dahlgren *et al.*, 2001) have used this technique to follow a water mass that originated over spawning fishes.

Spawning aggregation sites of important species of reef fish (reviewed by Domeier and Colin, 1997) are obvious locations for the establishment of MPAs, as the predictable behavior makes the stock vulnerable to overfishing and the huge release of gametes may be an important point source of recruits. The Dry Tortugas Ecological Reserve South (see Fig. 1), a relatively new MPA established within the south Florida reef tract, presents a unique opportunity to study connectivity. The physical oceanography of the region has been extensively studied (e.g. Lee *et al.*, 1995; Fratantoni *et al.*, 1998; Lee and Williams, 1999) and a site within the reserve is a known spawning aggregation site for an important snapper species, *Lutjanus analis* (Domeier and Colin, 1997; Domeier *et al.*, 1997).

Lutjanus analis is a medium-sized species of snapper, commonly called mutton snapper, with considerable economic importance to both the commercial and recreational fishing industries in south Florida. Mutton snapper form large spawning aggregations at very precise locations and times of the year throughout its range (Claro, 1981; Domeier *et al.*,

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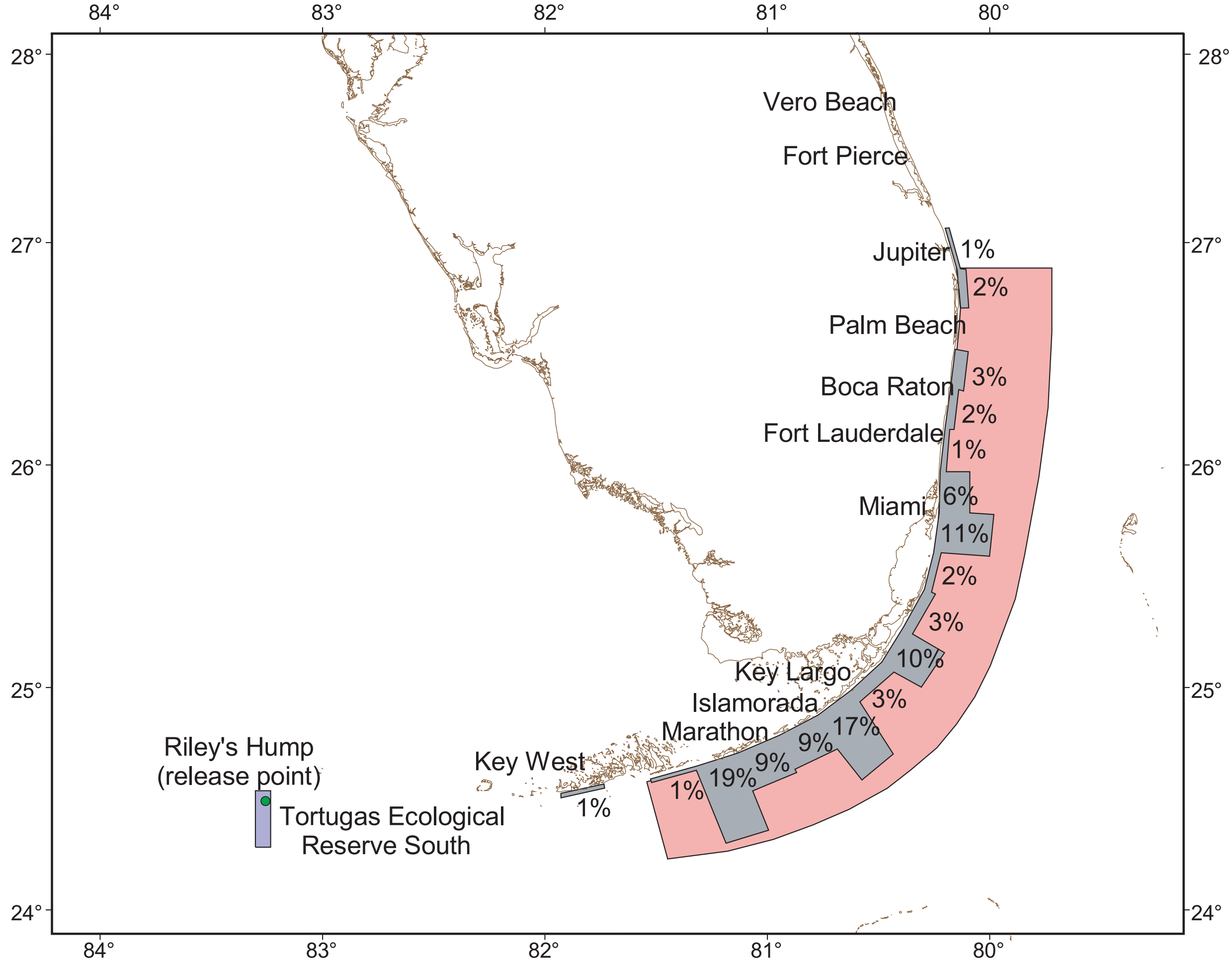
Figure 1. 1999 drifter vial recoveries. This figure illustrates the geographic range of drifter vial recoveries and the percentage of recoveries per 20 km stretch of coastline. The red zone denotes the range of drifters recovered in the first 45 days. Two outliers recovered to the north are not included in the figure. The spawning aggregation/drifter release site is shown within the Dry Tortugas Ecological Reserve South (blue).



1997; Gárcia-Cagide *et al.*, 2001). Riley's Hump, a site within the Dry Tortugas Ecological Reserve South, attracts a spawning aggregation of mutton snapper in Florida during the full moon periods of the late spring and early summer. The month of May usually has the highest concentrations of snapper, but a very early or late full moon can shift the peak month to April or June, respectively. The aggregation lasts about a week, with its peak being 3–5 days following the full moon (M. Stanfill, commercial fisherman, Key West, Florida, pers. comm.).

Mutton snapper are believed to spawn at dusk or shortly after (Domeier and Colin, 1997; Domeier *et al.*, 1997) at which time planktonic eggs and sperm are released into the water column. Fertile eggs float to the surface and hatch in approximately 24 h (at 28°C, M. L. Domeier, pers. obs.). Captive-reared mutton snapper began feeding within 48 h, underwent flexion 11–12 days after hatching and settled approximately 28 days after hatching at 15–18 mm (Clarke *et al.*, 1997). Otoliths removed from newly settled juveniles produced time-to-settlement estimates between 27 and 37 days (mode 31 days) (Lindeman *et al.*, 2001). The collection of small juveniles (15–50 mm) over high salinity grass beds along the coast of south Florida and Cuba (Lindeman *et al.*, 2000; Lindeman, Env. Def., Miami, pers. comm.) has implicated this shallow water environment as nursery habitat. These seagrass beds can be found in the nearshore regions of the Florida Keys, Florida Bay, Biscayne Bay and the intra-coastal waterway that extends up the east coast of Florida (Eiseman and McMillan, 1980; Fourqurean *et al.*, 2002).

Although no estimates of the number of mutton snapper at Riley's Hump have been made, an indication of the magnitude of the aggregation comes from the fishery. The aggregation was discovered by a commercial hand liner in 1979. Over the next few years the fishery became dominated by long liners landing between 10 and 21 metric tons per boat per trip; by 1986 fish trapping predominated with typical trip landings of 11.5 metric tons, representing perhaps 4000 fish (P. Gladding, commercial fisherman, Key West, Florida, pers. comm.). The total number of trips is not known, but the aggregation probably consisted of tens of thousands of snapper. Unfortunately, landings statistics are not kept in a manner that allow tracking catches from this region alone (Key West is lumped with all of Monroe County). In 1992 Riley's Hump was closed to all fishing during the months of May and June, and in July 2001 it was incorporated into the Dry Tortugas Ecological Reserve South (see Fig. 1), which provides year round protection from any form of fishing activity.

The close proximity of Florida's reef system to the rapidly northward moving Florida Current gives rise to the possibility that larvae originating in Florida may be swept away and lost to unsuitable conditions to the north (Lewis, 1951; Austin, 1972; Bohnsack and Ault, 1996); although these ideas were not supported with empirical evidence. Certainly this does happen to some degree, accounting for the seasonal settlement of tropical fauna as far north as Cape Cod, Massachusetts (Robins *et al.*, 1986), but these recruits perish with the onset of winter. More recently, data have been collected that suggest larvae produced in south Florida may be locally retained by gyres, counter currents and Ekman drift (Lee *et al.*, 1992, 1994; Limouzy-Paris *et al.*, 1997; Porch, 1998; Lee and Williams, 1999). Evidence to support these theories of larval retention have come from current meters, ARGOS-tracked drifter buoys, larval collections and mathematical models. The satellite-tracked drifters have come the closest to directly measuring possible larval recruitment pathways over a time frame equivalent to the 4–6-week planktonic duration of a typical reef fish larva (Thresher, 1984; Tucker, 1998; Grantham *et al.*, 2003). Unfortunately, a single ARGOS drifter cannot adequately describe the dispersal potential of a large number of larvae originating at a single point. The present study was designed to address this particular weakness by deploying, on two occasions, nearly 1000 small drifters at a single point in time and space. The relevance of the study was enhanced by deploying the small drifters over a mutton snapper spawning aggregation that is located within an MPA.

METHODS

Description of site

Riley's Hump, located adjacent to the seven islands known as the Dry Tortugas, Florida [137 km west of Key West, Florida (83°7′W, 24°30′N)], is at the far western edge of the island chain and reef tract referred to as the Florida Keys. Riley's Hump is an irregularly shaped reef with a longer axis in the north to south direction. Several SCUBA dives were made at Riley's Hump to characterize the site. Bottom depths range from 40 to 80 m, with the deepest water lying to the southwest. The four 'corners' of the site tend to be the highest spots, with the northeast corner being the shallowest at 23.5 m. Large living coral colonies were mostly absent, with the exception being the southwest corner, where very large isolated coral heads were found. The southwest corner is traditionally the region where the highest concentrations of mutton snapper aggregate to spawn (P. Gladding, pers. comm.).

Description of drifter vials

For two consecutive years (1999 and 2000) 1000 scintillation vials (20 mL capacity; 28 × 61 mm) were individually ballasted with 14.8 g of steel pellets. A label was placed in each vial indicating that the vial was part of a mutton snapper larval transport study, and contact information was given. The word 'REWARD' was boldly printed on the label as an incentive for the discovering party to participate in the study (the nature of the reward was not specified). A foam-lined polyethylene cap was tightly screwed onto the vial prior to deployment. The ballasted vial was extremely low profile, with only about 3 mm of cap showing above the waterline. The intent was to produce a drifter that had minimal surface area exposed to the wind, so the vials would be more likely to remain within the surface water that originated at Riley's Hump during the time of snapper spawning.

Deployment

The drifter vials were deployed at the estimated time and location of spawning; one hour after sunset on the full moon over the southwest corner of Riley's Hump. This occurred on May 30, 1999 and May 18, 2000. In 1999, seven vials were broken for a total of 993 deployed; three were broken and 997 deployed in 2000.

Recovery

Recovery information was taken over the phone and by email. Individuals who found vials were asked to provide a precise location, time and date of recovery. After 30 days information was also recorded about the condition of the vial; bio-fouling of the vial would indicate that it had been adrift for a prolonged period and recently came ashore, while a clean vial would indicate the vial came ashore soon after deployment. The Florida coast was broken into 20 km segments and recoveries were summed and plotted within each segment as a bar graph representing the relative percentage of recoveries for each segment of coastline.

RESULTS

A total of 113 vials (11%) were recovered between 14 and 193 days post-deployment in 1999. Twenty-four percent of the recoveries were made between 14 and 25 days post-deployment and the majority of recoveries (60%) were made in the first 50 days. All recoveries in 1999 were made between Key West and Palm Coast, Florida (730 km north of Key West), with the majority found between Marathon Key and Miami (Fig. 1). The earliest vials (days 14–20) were recovered in the middle Keys with areas to the north receiving vials later. Only two vials were found on the Florida Bay side of the Keys. Only one vial was recovered with fouling organisms growing on it.

A total of 114 vials (11%) were recovered between 19 and 141 days post-deployment in 2000. The majority of recoveries (58%) were made between 19 and 25 days post-deployment and 78% were recovered in the first 50 days. Recoveries in 2000 were made between Big Pine Key and Vero Beach, Florida with the majority found between Miami and Palm Beach (Fig. 2). The earliest vials (day 19) were recovered between Miami and Ft. Lauderdale with the first vial reported from the Florida Keys 5 days later. No vials were recovered in Florida Bay and no vials were recovered with fouling organisms. One most unusual recovery was made from the stomach of a 3-kg dolphin (*Coryphaena hippurus*) caught by a recreational angler 2 km offshore of the Boca Raton inlet. The fish was caught 21 days post-release.

In an effort to better understand the timing of bottle dispersal as it relates to the duration of the planktonic larval phase of mutton snapper, the geographic limits of bottle recoveries for the first 45 days post-deployment were plotted for each year (Figs 1 and 2; zone shown in red). The zone of recoveries for this data subset is essentially the same as the overall data set, with the exception of a very few outliers.

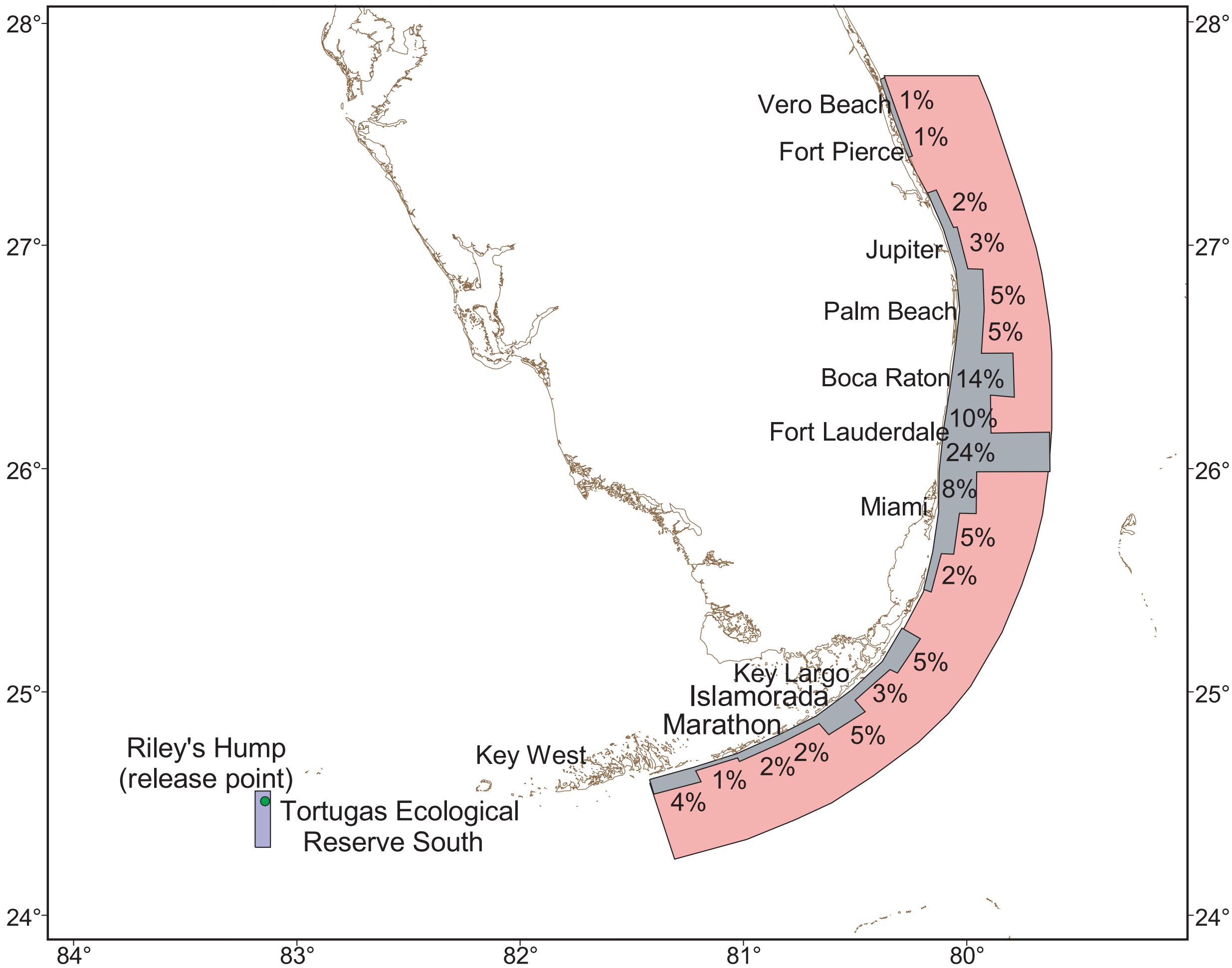
DISCUSSION

The 'low-tech' nature of this experiment made it extremely cost-effective, but unavoidable uncertainties must be taken into consideration. It is impossible to identify the precise track the vials took before washing ashore and it is also difficult to estimate the precise time/date the vial washed ashore. Vials that were found at resorts and public beaches provide the best opportunity to pinpoint the time of arrival as these beaches are well traveled and many are cleaned daily. In fact, several vials were recovered by ground keepers of beach resorts. Many vials were returned from remote and mangrove-lined coastlines, but certainly there was a delay between the time they washed ashore and were discovered. In each year there were initial waves of bottle returns likely associated with actual timing of bottles coming ashore, followed by a constant low level of returns from remote regions and pulses of returns from high traffic areas immediately following very high tides or storms. These pulses indicate that bottles were being pulled from relatively inaccessible shoreline and redeposited on nearby areas where they were more likely to be found.

Interpreting the relative frequency of vial recoveries for different areas is complicated by the fact that recovery effort cannot be the same for the entire coastline. Extensive stretches of undeveloped mangrove coast would not have as much recovery effort as public beaches and resorts. The Florida Keys, Florida Bay and Biscayne Bay all have large tracts of mangrove coast, but from Miami northward the coastline is primarily developed. Certainly regions that are less accessible are under-represented, but public beaches and resorts are likely good relative indicators of bottle recruitment throughout the range of the experiment. Fortunately, even the Florida Keys and Biscayne Bay have resorts, marinas and public beaches scattered throughout, albeit separated by stretches of mangrove.

Although there are problems in analyzing and comparing these data, certain aspects of the results lend credibility to the study. For instance, each year saw an identical bottle return rate of 11%, suggesting similar recovery effort between years. Assuming that the recovery effort for each of the 2 yr was similar, the two figures make an interesting comparison. Although the total dispersal range is similar between the 2 yr, the regions of concentrated bottle returns was different: 1999 bottle returns were concentrated in the

Figure 2. 2000 drifter vial recoveries. This figure illustrates the geographic range of drifter vial recoveries and the percentage of recoveries per 20 km stretch of coastline. The red zone denotes the range of drifters recovered in the first 45 days. One outlier recovered to the north is not included in this figure. The spawning aggregation/drifter release site is shown within the Dry Tortugas Ecological Reserve South (blue).



middle to upper Florida Keys while 2000 returns were concentrated in the Ft. Lauderdale area. The fact that the upper and middle Keys had the bulk of recoveries in 1999, despite the greater percentage of mangrove coast, suggests this as a real difference and not an artifact of sampling. The somewhat slower rate of return in 1999 can also be explained by the fact that the bulk of the vials came ashore in mangrove areas (where they will take longer to find).

There exists the possibility that bottles that were not found right away could wash back into the ocean and be transported to another location, thereby introducing error into the results. The pulses of bottle recoveries after very high tides and storms indicates that bottles were in fact being redistributed, but it does not seem that they moved very far before grounding again and being found. This is suggested by the fact that the geographic limit of bottle returns for the first 45 days of the experiment was nearly identical to the total ranges of bottle recoveries in each year (Figs 1 and 2). In addition, only a single bottle was found with biofouling organisms growing on it, also suggesting bottles did not spend prolonged periods at sea.

Certainly larval fishes exhibit behaviors that are impossible for a drifter vial to duplicate. Vertical and horizontal movements could significantly affect the overall dispersal of larvae. These movements are not well understood and it is impossible to predict the magnitude of the sum of all vertical and horizontal vectors, but theoretically, larval fish movements can serve to enhance the individual's chances of remaining near suitable settlement habitat. Work done in the

Florida Keys has found lutjanid larvae to occur most frequently in the top 25 m (Cha *et al.*, 1994), suggesting that surface flow may in fact be the most important factor that determines their transport.

It has been suggested that the formation and movement of a quasi-stationary gyre in the vicinity of the Dry Tortugas entrains larvae originating from nearby reefs and returns them to suitable habitat to settle (Lee *et al.*, 1992, 1994, 1995). The gyre, called a Tortugas eddy, evolves from a cyclonic frontal eddy which forms along the boundary of the Loop Current. Tortugas eddies are elliptical with alongshore diameters reaching 180 km and cross-shore diameters reaching 100 km (Lee *et al.*, 1995). A Tortugas eddy typically remains stationary for a period of 50–140 days, until it is replaced by a new Loop Current frontal eddy which becomes a new Tortugas eddy (Lee *et al.*, 1995; Fratantoni *et al.*, 1998). The old eddy moves downstream at a rate of about 5 km day^{-1}, until it is dispersed by the constriction of the Florida Straits (Lee *et al.*, 1995).

The longevity of a typical Tortugas eddy is greater than the planktonic larval period of mutton snapper (approximately 30 days), although a typical single circuit is on the order of 7–10 days (Dr Tom Lee, University of Miami, FL, pers. com.). Mutton snapper larvae that become entrained in the Tortugas eddy would require a mechanism for exiting the gyre in order to successfully recruit back to the nearshore regions of south Florida. Three ARGOS drifters have been successfully tracked over Riley's Hump during the time of mutton snapper spawning (full moon May of 1991 and 1999; full moon June 1991) (Lee *et al.*, 1994; Dahlgren *et al.*, 2001). Although one of the drifters briefly traced the outside of the gyre (Dahlgren *et al.*, 2001), none became entrained in the gyre and all were transported north along the reef tract. Lee *et al.* (1994) did not report whether the 1991 drifters traveled north into the Gulf Stream or grounded in south Florida, but Dahlgren *et al.* (2001) reported that the 1999 drifter entered Biscayne Bay. The timing of deployment of this 1999 drifter coincided with the deployment of the drifter vials from the present study, and the termination of the ARGOS-tracked drifter was in the center of the distribution area for the vials.

Lee *et al.* (1994) concluded that larval transport at the time of their May and June, 1991, drifter releases was controlled by a combination of gyre circulation and wind-driven Ekman transport. The combination of wind-driven Ekman transport and the Tortugas Eddy may both be necessary for successful larval entrainment and transport to shallow water seagrass beds (nursery grounds). In the absence of wind, the larvae could be caught in the eddy for too long a period of time; in the absence of an eddy, the Florida Current flows close to the reef at velocities exceeding 100 cm s^{-1}, enough to send the larvae well north of any suitable settlement habitat. It has also been suggested that larvae within the Florida Current may recruit back to the reef via sub-mesoscale spin-off eddies from the Florida Current (Limouzy-Paris *et al.*, 1997). This may be the process by which the drifter vials exited the Florida Current for this study.

An advantage to the method used here over single ARGOS drifter deployments is that the large number of vials allows for an estimation of the overall dispersal pattern of the snapper larvae. Most importantly, the timing and location of drifter vial returns overlaps with the known larval duration of mutton snapper and known nursery habitat for this species (Lindeman *et al.*, 2000).

Records exist for eight other ARGOS drifters that passed near Riley's Hump during different times of the year (RSMAS Website, 2002). Interestingly, only one of these tracks would have been suitable for successful mutton snapper recruitment (track 21008, March 1999); the other seven either became entrained in the Tortugas Eddy, were lost to the Gulf Stream or lost into the Gulf of Mexico. These provide evidence of month to month variability in potential recruitment pathways, whereas the satellite drifters and drifter vial data from this study (May/June) show a much lesser degree of variation between different years. Further research that explores the consistency of potential recruitment patterns originating from Riley's Hump throughout the year could lend valuable insight into the significance of the timing of spawning.

Transport of larvae across frontal boundaries has been deemed important for the successful recruitment of late stage fish larvae from the oceanic habitat to the juvenile nursery habitat (Moser and Smith, 1993). This of course requires that early stage larvae were transported across the same frontal boundaries in the opposite direction, thus placing them in the oceanic environ to begin with. It is possible that the majority of successful recruits are those that are not initially transported across the frontal boundary that separates the nearshore waters from those of the Florida Current.

This study demonstrated an inexpensive technique for estimating the potential dispersal end points of larvae from a point of origin. The results suggest that it is possible for eggs and larvae at Riley's Hump to remain in Florida and be returned to suitable settlement habitat in a period of time similar to the average larval duration for reef fishes. It is equally important to note that for both years of this study the recovery area was remote from the origin, suggesting that this MPA could be functioning as a fisheries reserve by acting as a source of mutton snapper recruits for much of south Florida. Is the population of mutton snapper that form spawning aggregations at Riley's Hump self-recruiting? The answer to this question depends upon the scale under consideration and the movement pattern of adult and juvenile mutton snapper. Nursery habitat does not exist in the immediate vicinity of Riley's Hump, so self-recruitment is not possible at a very fine scale. The Fort Jefferson National Park facility is only 24 km east of Riley's Hump; seagrass beds can be found in this area and beaches are visited by the public, yet no bottles were recovered from this location. In fact, the closest region of significant vial recoveries for either year of the study, the middle Keys, is located over 200 km to the east. This still does not preclude Riley's Hump from benefiting from self-recruitment if adults eventually find their way back to Riley's Hump to spawn. Future work on the population structure and adult movement patterns of Florida mutton snapper would greatly benefit this discussion.

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