Planktonic linkages among marine protected areas on the south Florida and southeast United States continental shelves

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Abstract: One proposed benefit of marine protected areas (MPAs) is increased larval export, potentially increasing recruitment in unprotected areas. Because most marine species have planktonic larvae, information regarding planktonic transport is needed to evaluate the benefit of larval export. We used satellite-tracked drifters to define planktonic transport routes and rates from three MPAs along the south Florida and southeast United States (US) continental shelves. Drifter tracks indicated both long-distance transport and local retention. A probability model was developed based on drifter releases. The region was broken into zones; zone-specific residence times and movements between zones were defined from the drifter tracks. Transport out of the region in association with the Loop Current – Florida Current – Gulf Stream was the most frequently observed outcome, yet retention was high in the lower Florida Keys and on the Georgia shelf. From the model results, long-distance planktonic transport and local retention are the endpoints of a continuum rather than a dichotomy. Further, the outcome of planktonic transport is spatially heterogeneous with some regions exhibiting more retention and others exhibiting more export. The spatial aspects of planktonic transport described here should be considered in designing MPAs with fishery management objectives in the south Florida and southeast US shelf ecosystems.

Résumé : Un des bénéfices attendus des zones de protection marines (« MPAs ») est l'accroissement de l'exportation de larves, ce qui augmente potentiellement le recrutement dans les zones non protégées. Puisque la plupart des espèces marines ont des larves planctoniques, il faut connaître les déplacements du plancton pour pouvoir évaluer le bénéfice de l'exportation de larves. Nous avons utilisé des balises dérivantes suivies par satellite afin de déterminer les voies et les taux de transport planctoniques à partir de trois MPAs situées le long des plate-formes continentales du sud de la Floride et du sud-est des É.-U. Les tracés des balises représentent à la fois le transport à grande distance et la rétention locale. Nous avons mis au point un modèle basé sur les libérations des balises. Nous avons divisé la région en zones et déterminé les temps spécifiques de séjour dans les zones et les déplacements entre les zones d'après les tracés des balises. Le résultat le plus fréquemment observé est un transport vers l'extérieur en rapport avec le courant Loop, le courant de Floride et le Gulf Stream, mais il y a aussi une forte rétention dans les Keys de Floride inférieurs et la plate-forme de Géorgie. D'après les résultats du modèle, le transport planctonique de grande distance et la rétention locale sont plus les points extrêmes d'un continuum que les points opposés d'une dichotomie. De plus, le résultat du transport planctonique est hétérogène dans l'espace, certaines régions connaissant plus de rétention et d'autres plus d'exportation. Les aspects spatiaux du transport planctonique que nous décrivons devraient être pris en considération dans l'établissement de MPAs pour la gestion des pêches dans les écosystèmes de la plate-forme continentale dans le sud de la Floride et le sud-est des É.-U.

[Traduit par la Rédaction]

Introduction

Larvae of marine fish and invertebrates are collected far from known spawning locations, indicating long-distance transport (Scheltema 1971, 1986; Leis 1985). These observations are supported by calculations made with average current speed and direction indicating long-distance transport of passive planktonic particles (McGowan and Richards 1989; Roberts 1997). Additionally, many marine populations are genetically homogenous over large spatial scales, which is

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taken as evidence for planktonic exchange among distant locations (Mitton et al. 1989; Bowen and Avise 1990; Shulman and Bermingham 1995).

Long-distance planktonic transport is considered an important element in the management of marine populations (Doherty and Williams 1988; Fogarty et al. 1991; Caley et al. 1996). The scale of many marine populations is hypothesized to be quite large, in part owing to the concept that planktonic larval transport effectively mixes individuals over large distances (see Sinclair 1988). Consequently, the scale of managed units (stocks) is also large; for example, the 73 species in the snapper–grouper complex of the South Atlantic Bight Fishery Management Council are managed as single stocks from the Florida Keys to North Carolina (NOAA 2005), a linear distance of ~1500 km.

The concept of long-distance planktonic transport also has been incorporated into theories of marine protected area (MPA) design and function. MPAs can be designed with different objectives: protect biodiversity, protect specific habitats, act as a buffer against stock collapse or extinction, and contribute to fishery management (National Research Council (NRC) 2001). MPAs designed with fishery management objectives are expected to provide local fishery benefits through the spillover of juvenile and adults (Roberts et al. 2001; Russ et al. 2004). Larger-scale benefits are predicted through increased input to the larval pool, which hypothetically increases recruitment to the population as a whole, again through the thorough mixing of planktonic individuals (Roberts 1995, 1997; Gaines et al. 2003).

Although the concept of long-distance planktonic transport is embedded in views of marine populations, many recent studies indicate local retention of planktonic stages. In some physical systems (e.g., estuaries), there are well-defined biophysical mechanisms that result in local retention (e.g., selective tidal-stream transport; Cronin and Forward 1986; Rowe and Epifanio 1994). Larval behavior may also interact with circulation in the open ocean to promote local retention (Cowen et al. 2000; Paris and Cowen 2004; Hare and Govoni 2005). Biophysical models of larval transport have revealed that local retention may dominate over long-distance transport in some areas (James et al. 2002; Cowen et al. 2003; Paris et al. 2005). Additionally, recent genetic studies have found differences among locations in species with pelagic larvae, thereby indicating limited mixing of individuals among locations (Taylor and Hellberg 2003). Finally, some of the best evidence for local retention comes from larval tagging studies, which use chemical marks on otoliths; these studies have found self-recruitment rates of 5%–60% (Jones et al. 1999, 2005; Almany et al. 2007). With evidence for both long-distance planktonic transport and local planktonic retention, the critical need is to quantify actual planktonic transport and incorporate this knowledge into spatially explicit management strategies (see Hare 2005; Cowen et al. 2006).

Our purpose was to quantify planktonic transport pathways along the continental shelves of south Florida and the southeast United States (US). We used satellite-tracked drifters released at three MPAs to examine site-specific routes and rates of planktonic transport. We then used these drifter tracks and other drifter tracks from the region to develop a model that quantified the probability of planktonic transport among different areas of the south Florida and southeast US shelves. Drifters have been used previously to study planktonic transport routes and rates in the region (Lee et al. 1994; Domeier 2004; Edwards et al. 2006), but this is one of the first attempts to build a region-wide probabilistic model of larval transport (see Zakardjian et al. 2003).

Material and methods

Study area

The marine regions bordering the southeastern US (Texas to North Carolina) can be divided into three systems: the Gulf of Mexico, south Florida, and the southeast US continental shelves. The Gulf of Mexico extends from the Yucatan Peninsula to southern Florida. South Florida extends from the Florida Keys to West Palm Beach, Florida, and is distinguished by near continuous coral reefs on a very narrow continental shelf. The southeast US continental shelf extends from West Palm Beach, Florida, to Cape Hatteras, North Carolina. Our study examines planktonic transport processes in the south Florida and southeast US continental shelf regions (see Fig. 1a).

These three marine systems are connected by the western Atlantic Ocean boundary current, which includes the Loop Current, Florida Current, and Gulf Stream (Boicourt et al. 1998). The Loop Current flows northward through the Yucatan Straits into the Gulf of Mexico and then turns 180° to flow south and then 90° to flow east into the Florida Straits. The Florida Current continues to flow east along the Florida Keys reef tract and then turns to the northeast and north around southeastern Florida following the shelf break. The Gulf Stream continues to follow the shelf break along the southeast US continental shelf and detaches from the shelf at Cape Hatteras. Velocities in this western boundary current can exceed 2 m·s^{-1}. Given the length scale of the system (westernmost Florida Keys to Cape Hatteras = ~1500 km) and these maximal velocities, planktonic transport can theoretically occur along the entire length in less than 10 days (McGowan and Richards 1989).

Although the Loop Current – Florida Current – Gulf Stream causes downstream transport of plankton from the Gulf of Mexico to Florida and the Carolinas (Ortner et al. 1995; Tester and Steidinger 1997), the current speed and direction at any place along the shelf break is quite variable owing to the occurrence of cyclonic eddies on the inshore side of the current. Along the Florida Keys reef track, large cyclonic eddies form in association with the turning of the Loop Current into the Florida Straits (Lee et al. 1991). Meanders in the Gulf Stream along the southeast US shelf also generate cyclonic frontal eddies that propagate downstream with the current (Bane and Dewar 1988; Lee et al. 1991). Cyclonic eddies have been implicated in the retention of planktonic larvae in the vicinity of the Florida Keys (Paris et al. 1997; Sponaugle et al. 2005), but their importance to larval transport along the southeast US shelf is largely unknown (see Govoni and Hare 2001). Thus, even though the Loop Current – Florida Current – Gulf Stream can be thought of as a conveyor belt transporting plankton downstream, there are features of the system that can provide retention.

Fig. 1. (*a*) Map of the North American eastern coast; the study region is indicated by the box. Approximate path of the Loop Current – Florida Current – Gulf Stream is shown as a shaded dotted line. (*b*) Map of marine protected areas on the south Florida and southeast US continental shelves. MPA designation based on definition used by the US government (Federal Register 2000).
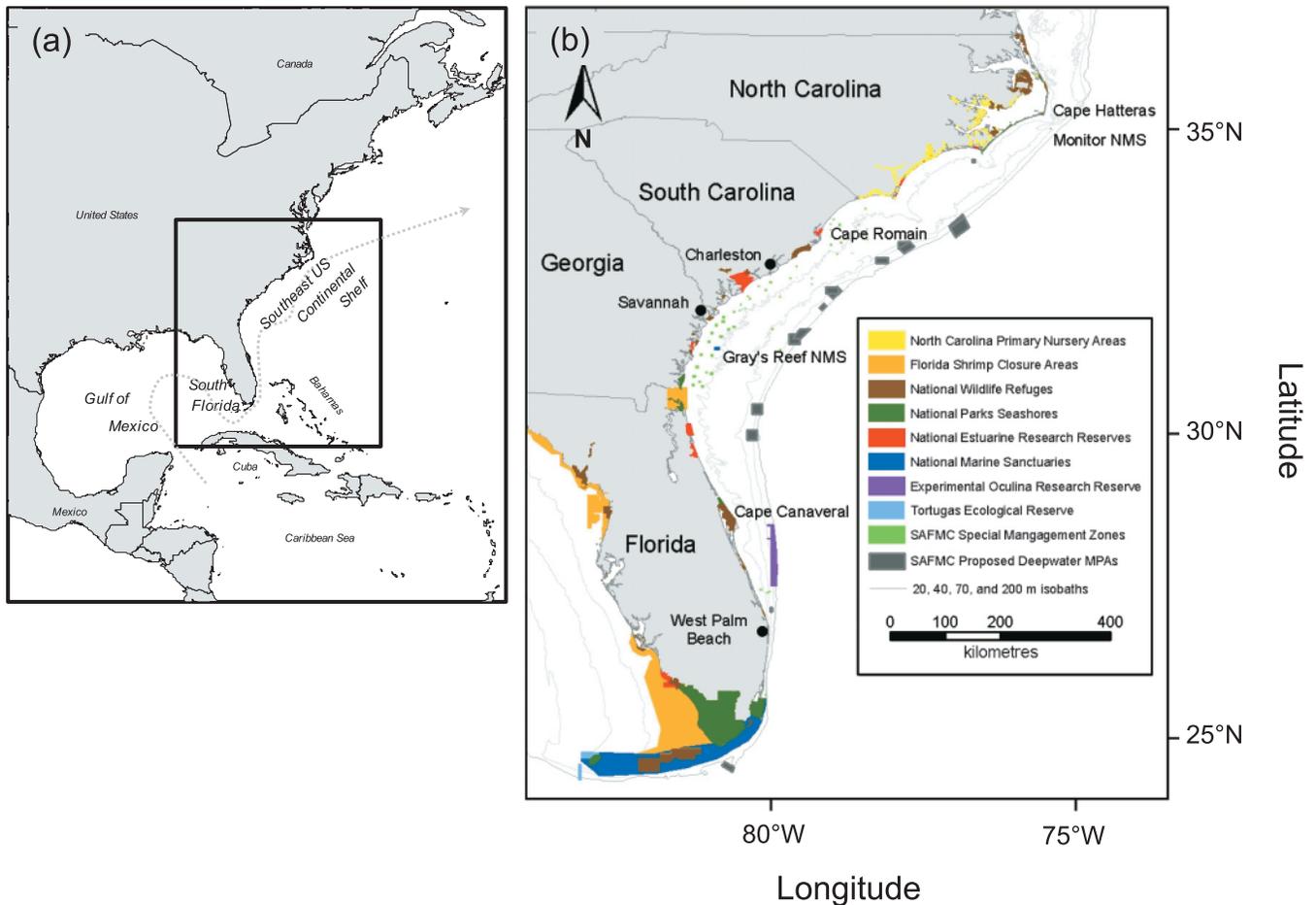
There are a number of MPAs in the south Florida and southeast US shelf systems (Fig. 1*b*). South Florida has a large amount of area protected (but to varying degrees) with the Florida Bay National Park, Biscayne Bay National Park, and the Florida Keys National Marine Sanctuary (NMS). At the westernmost end of the Florida Keys NMS is the Tortugas Ecological Reserve, a large (~520 km²) no-take marine reserve established in 2001 with the objective of protecting diverse marine life and lush coral reefs in the Dry Tortugas area. The reserve is split into two sections: Tortugas North, which protects coral reef habitat on the Tortugas Bank, and Tortugas South, which protects Riley's Hump, an important snapper and grouper spawning aggregation site.

Much less area is protected along the southeast US continental shelf relative to the south Florida system (Fig. 1*b*). The Experimental Oculina Research Reserve was established in 1994 to protect deepwater coral habitat and grouper spawning aggregations. The Reserve includes 322 km² stretched along the east Florida shelf break. The region is closed to bottom fishing, but pelagic fishing is allowed. Gray's Reef National Marine Sanctuary is a small MPA (~58 km²) located 32 km off the coast of Sapelo Island, Georgia. The Sanctuary is near the boundary between inner- and mid-shelf zones, with depth at the site sloping from

12 m to 20 m. Bottom trawling is prohibited but hook-and-line fishing is allowed.

Drifter releases and tracking

A total of 56 satellite-tracked drifters were released in the three MPAs: Tortugas South Ecological Reserve (Tortugas South ER), Experimental Oculina Research Reserve (Oculina RR), and Gray's Reef National Marine Sanctuary (Gray's Reef NMS) (Fig. 1*b*; Table 1). All drifters were the WOCE SVP design, which includes a surface float attached to a holey sock drogue (Sybrandy and Niiler 1990). Drogues were centered at 15 m for the Oculina RR and Tortugas South ER releases and at 10 m for the Gray's Reef NMS releases. Drogue lengths were between 3.5 and 6.6 m depending on drogue depth and drifter manufacturer. Twenty-one drifters were released in the Tortugas South ER over Riley's Hump; drifters were released in a triangular pattern approximately 2.5 km apart. Only 17 tracks were analyzed because of transmission failures and premature retrievals. Twenty drifters were released in the Oculina RR; on a given date, four drifters were released in a rectangular pattern with a north–south dimension of 24 km and an east–west dimension of 8 km. Nineteen tracks were analyzed because of a premature retrieval. Fifteen drifters were released at Gray's Reef NMS; on a given date, drifters were released in a trian-

Table 1. Summary of drifter releases made in three marine protected areas along the south Florida and southeast US shelves: Tortugas Ecological Reserve (Tortugas ER), Experimental Oculina Research Reserve (Oculina RR), and Gray's Reef National Marine Sanctuary (Gray's Reef NMS).

Release site	Release date	No. of drifters released	No. of drifter tracks analyzed	Drogue depth (m)
Gray's Reef NMS	26 April 2000	3	2*	10
Gray's Reef NMS	21 June 2000	3	2†	10
Gray's Reef NMS	3 October 2000	3	3	10
Gray's Reef NMS	30 January 2001	3	3	10
Gray's Reef NMS	22 March 2001	3	3	10
Tortugas ER	24 June 2000	3	2†	15
Tortugas ER	17 July 2000	3	3	15
Tortugas ER	24 July 2000	3	2†	15
Tortugas ER	31 July 2000	3	3	15
Tortugas ER	8 July 2001	3	2†	15
Tortugas ER	16 July 2001	3	2†	15
Tortugas ER	20 July 2001	3	3	15
Oculina RR	15 February 2002	4	4	15
Oculina RR	12 March 2002	4	4	15
Oculina RR	20 April 2002	4	3†	15
Oculina RR	22 July 2002	4	4	15
Oculina RR	19 August 2002	4	4	15

*Two drifters were tangled after release and treated as one drifter for the analyses presented here.
†Drifter was either retrieved prematurely or stopped transmitting <10 days after release.

Table 2. Larval durations of members of the South Atlantic Fisheries Management Council (SAFMC) snapper–grouper complex (summarized from Lindeman et al. 2000).

Family (or subfamily)	Common name	Approximate larval duration (days)	No. of species in SAFMC snapper–grouper complex
Epinepheline	Groupers	45	21
Lutjanidae	Snappers	30	14
Haemulidae	Grunts	15	10
Sparidae	Porgies	25	9
Labridae	Wrasses	25	2

gular pattern approximately 2.5 km apart near the center of the Sanctuary. Two drifters collided with each other and remained together for an extended period of time; these two drifters were treated as one. Another drifter was retrieved prematurely, so only 13 tracks were analyzed from Gray's Reef NMS releases. Thus, of the 56 drifters released, 49 were included in the analyses.

Drifter location was tracked via Service ARGOS with approximately four fixes per day. Location data from all drifters were quality checked and linearly interpolated to produce tracks at 6-h time intervals. Tracks were truncated when drifters crossed inshore of the 20 m isobath for the drifters drogued at 15 m and at the 15 m isobath for drifters drogued at 10 m.

Data analysis

Three analyses were conducted to provide a general view of planktonic larval transport from the three release locations. First, a simple spaghetti plot was created to provide a general overview of planktonic transport routes along southern Florida and the southeastern US coast. Second, specific transport routes were identified and drifter tracks were clas-

sified to these specific routes to provide an estimate of the likelihood of larvae being transported over the various routes. Finally, drifter locations were examined at 15, 30, 45, and 60 days after release. These times correspond to the planktonic duration of many important fishery species in the region (Table 2), and this analysis provides insights into the time scales of the various transport routes.

Planktonic transport model

Overview

A probability model was developed to provide a more quantitative view of larval transport along the south Florida and southeast US continental shelves. The model was, in essence, a box model with the spatial structure based on along-shelf and cross-shelf zones. A probability function of the residence times of drifters in each box was estimated from drifter tracks. The probability of movement from one box to all neighboring boxes also was calculated from drifter tracks. The zone-specific functions of residence times and movements to neighboring boxes were then used to construct a probability model of planktonic transport in the study area.

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Fig. 2. Along-shelf and cross-shelf zones used in the probability model of larval transport along the south Florida and southeast US shelves.
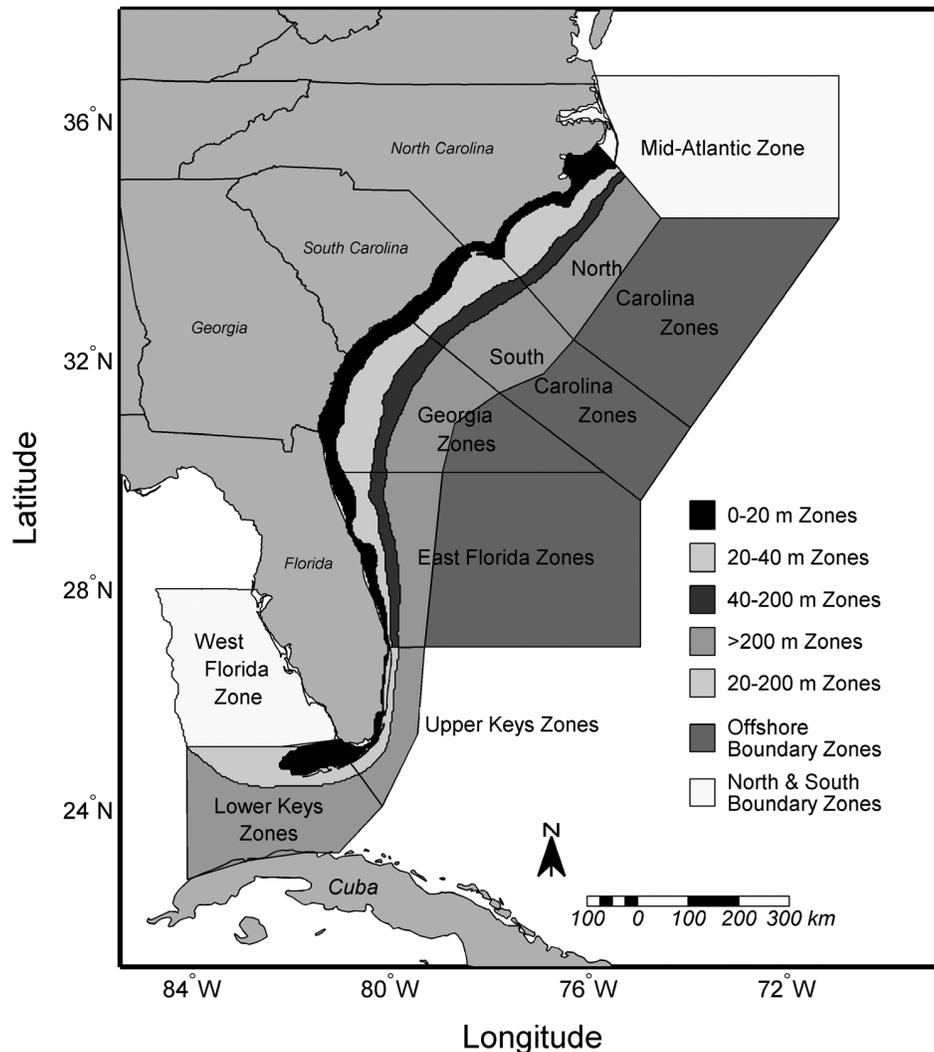
Particles were released in various zones of the model and moved in accordance with the residence-time probability distributions and movement probability distributions. Analyses were conducted of the movement of particles through the spatial domain, including examination of the location of particles from a given release zone over time and the number of particles present in a zone that were released in that zone (a measure of retention).

The model was developed in five steps: (*i*) the study region was divided into along-shelf and cross-shelf zones (i.e., boxes); (*ii*) the position of each drifter at each time was assigned to a zone; (*iii*) zone-specific residence times were calculated and zone-specific movements were tallied for each drifter; (*iv*) probability functions were estimated for residence time and movement for each zone; and (*v*) particles were moved through model domain using probability functions of residence time and movement. These steps are outlined below and more detail is given in Supplemental Appendix S1 (available from the NRC Depository of Unpublished Data).[4]

Division of study region into zones

The study region was divided into zones based on previously defined along-shelf and cross-shelf patterns in circulation (Atkinson and Menzel 1985; Pietrafesa et al. 1985; Lee et al. 1991, 1994). Six along-shelf zones were defined: North Carolina, South Carolina, Georgia, East Florida, Upper Keys, and Lower Keys (Fig. 2). A maximum of five cross-shelf zones were defined for each along-shelf zone: 0–20 m, 20–40 m, 40–200 m, >200 m, and an offshore boundary zone. In addition, zones were designated upstream (West Florida) and downstream (Mid-Atlantic) of the study region; these two zones had no across-shelf structure. Owing to the narrowness of the continental shelf in the Lower and Upper

Keys region, two continental shelf zones were combined into one: 20–200 m. Further, owing the narrowness of the Florida Straits, with Cuba and the Bahamas to the south and east, the offshore boundary zones were excluded for the Lower and Upper Keys. The boundaries of the along-shelf and cross-shelf zones (Fig. 2) then were converted into polygons.

Assignment of drifter positions to zones

The position of each drifter at every 6-h interval was assigned to a zone using the *inpoly* function of MatLab (The MathWorks Inc., Natick, Massachusetts, www.mathworks.com). The 49 drifters releases analyzed in this study were included (Table 1). Drifters tracks from two additional sources also were included (see Supplemental Appendix S1)[4]. In all, the tracks of 105 drifters were included in the development of the model.

Calculation of residence time and tally of movements

Once the zone assignments were made, the instances of movement between zones were identified. Based on the zone assignments and the instances of movement between zones, the residence time of each drifter in each zone was determined. In addition, when a drifter left a zone, the zone it moved into was determined. This resulted in a list of zones, residence times within these zones, and movement to new zones.

Residence-time and movement probability functions

The list of residence times for each zone was used to calculate a residence-time distribution based on the gamma distribution. The gamma distribution closely approximates the normal distribution with the advantage that it has density only for positive real numbers (i.e., residence times cannot be negative). In addition, for each zone, the frequencies of movement to every other zone were calculated from the tally of movements. Frequencies were expressed from 0 to 1 and, thus, represent the probability of movement from each zone to every other zone (see Supplemental Table S1.1).[4]

Model calculation

Ten thousand particles were started in zones encompassing the shelf and slope of the region. Releases were made in the following zones: 20–40 m, 40–200 m, and >200 m in North Carolina, South Carolina, Georgia, and east Florida and 20–200 m and >200 m in Upper Keys and Lower Keys. Each particle then randomly moved through the model domain based on the probability distribution of residence times and the probability of movement from a zone to every other zone. If a particle moved into a <20 m zone, it stayed there. Similarly, if a particle moved into the Mid-Atlantic zone or the West Florida shelf zone, it remained there. Particles were tracked for 60 days, and the results were used to quantify several aspects of larval transport in the system, including the number of particles transported northward in Gulf Stream flows, the number of particles remaining on the south Florida and southeast US shelves, the number of particles remaining in or returning to their release zones, and the specific movement of particles released in zones containing the three focal MPAs of this study.

Results

Analysis of drifter tracks

General circulation patterns

Most of the drifters were transported downstream in association with the Loop Current – Florida Current – Gulf Stream (i.e., eastward along Florida Keys, northwards along east Florida, and northeastward along Georgia, South Carolina, and North Carolina; Fig. 3). Many of the drifters eventually moved past Cape Hatteras and out of the southeast US continental shelf system. Embedded in this general pattern, however, were several specific aspects of the circulation that are important to planktonic transport in the south Florida and southeast US shelf systems. (*i*) Some drifters released at the Tortugas South ER moved up the west Florida shelf. (*ii*) Large and small cyclonic eddies were evident in the region of the Tortugas and Florida Keys. (*iii*) A retention area on the Georgia shelf was observed. (*iv*) A region of onshore transport both south and north of the Georgia shelf was evident with drifters moving out of Gulf Stream associated flows.

Identification of transport routes

Four transport routes were identified for drifters released at the Tortugas South ER (Fig. 4a). (*i*) Some drifters remained in the vicinity of the Florida Keys reef track, often exhibiting cyclonic motions to the west and south of the Florida Keys. (*ii*) Some drifters moved northwards along the west Florida shelf. (*iii*) Three drifters moved downstream in the Florida Current but exited onto the east Florida shelf. (*iv*) Three drifters were caught in the Florida Current and continued northward past Cape Hatteras in the Gulf Stream.

Four transports routes also were evident for drifters released at the Oculina RR (Fig. 4b). (*i*) About half of the drifters moved rapidly along the shelf break in Gulf Stream associated flows and moved out of the southeast US shelf system. The remaining drifters moved north in Gulf Stream associated flows, but then exited onto the (*ii*) north Florida – Georgia shelf, (*iii*) the South Carolina shelf, and (*iv*) the North Carolina shelf.

Drifters released at Gray's Reef NMS exhibited three transport routes (Fig. 4c). (*i*) A majority of the drifters slowly moved offshore, yet remained on the Georgia shelf. The remaining drifters moved along the shelf to (*ii*) the northeast and (*iii*) the southwest.

Time scale of transport routes

Examining drifter locations at specific time intervals indicated that the various transport routes identified above operated at time scales relevant to planktonic larval transport (Fig. 5). More than half of the drifters released at the Tortugas ER remained in the area at 15 and 30 days, but the percentage dropped to ~20% and ~15% at 45 and 60 days, respectively. The percentage of Tortugas ER drifters occurring on the west Florida shelf increased over time from ~20% at 15 and 30 days to ~45% at 45 and 60 days. The percentage of drifters occurring on the east Florida shelf ranged from about 15% at 15 and 60 days to 20% at 30 and 45 days. These data indicate that larvae spawned at the Tortugas South ER can be transported to the west and east

Fig. 3. Spaghetti plot of drifters released at Tortugas South Ecological Reserve (Tortugas South ER), Experimental Oculina Research Reserve (Oculina RR), and Gray's Reef National Marine Sanctuary (Gray's Reef NMS). Drifter release locations are indicated by stars.
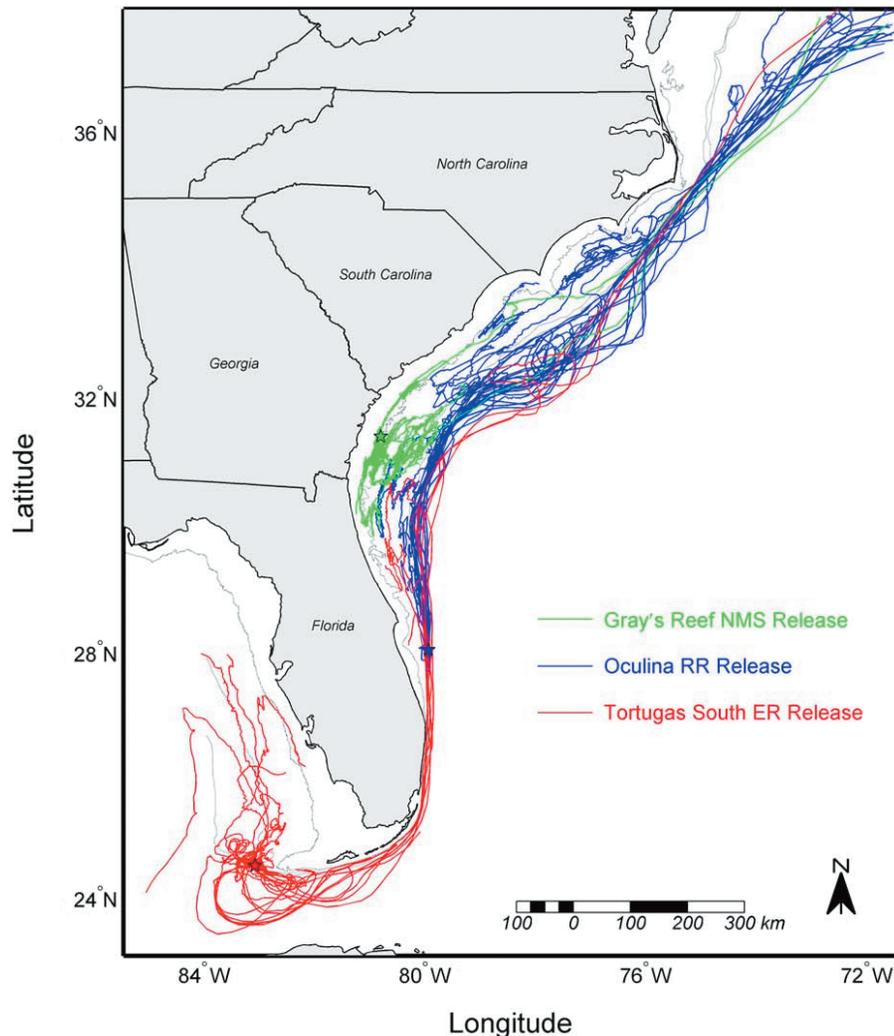
Florida shelves and be retained in the vicinity of the Florida Keys at the time scales of planktonic larval durations.

Many of the drifters released at Oculina RR were rapidly transported north of Cape Hatteras: ~20% of the drifters were north of Cape Hatteras at 15 days, ~40% at 30 days, and ~80% at 45 and 60 days. These data indicate that many of the larvae spawned at Oculina RR are likely lost from the southeast US shelf to the north. However, ~30% of the drifters remained on the southeast US shelf at 15 days. The percentage increased to 50% at 30 days, resulting from the movement of drifters from the Gulf Stream onto the Georgia, South Carolina, and North Carolina shelves. At 45 and 60 days, 20% and 15%, respectively, of the drifters remained on the southeast US shelf. Thus, for larvae spawned at Oculina RR, significant retention on the shelf is likely, albeit to the north of the Oculina RR.

Most of the drifters released at Gray's Reef NMS were retained on the Georgia shelf, and some remained in the area for as long as 60 days. Some transport to the north was evident at 30- and 45-day time intervals and loss to north of Cape Hatteras was evident at 60 days. These data indicate

that many of the larvae spawned at Gray's Reef NMS are likely retained on the Georgia continental shelf.

Transport model

The probability model clearly showed that the Loop Current – Florida Current – Gulf Stream influenced particle transport in the region (Fig. 6). The percentage of total particles in the Mid-Atlantic zone was 25%, 48%, 59%, and 65% at 15, 30, 45, and 60 days, respectively. The >200 m South and North Carolina zones also contained large numbers of particles over time as particles moved downstream en route to the Mid-Atlantic zone.

Despite this obvious downstream transport, there was evidence for the retention of particles within the south Florida and southeast US shelf systems. Although most zones lost particles over time, the 20–40 m Georgia zone accumulated particles, and it was not until after day 25 that there were fewer particles than were released in the zone (Fig. 6). Also, the inshore zones (<20 m zones from the Lower Keys to North Carolina zones) accumulated particles over time, particularly in the inshore Georgia and east Florida zones. Parti-

Fig. 4. Examples of transport routes for drifters released at (*a*) Tortugas South Ecological Reserve, (*b*) Experimental Oculina Research Reserve, and (*c*) Gray's Reef National Marine Sanctuary. Each drifter track shown is representative of several similar drifter tracks. Drifter release locations are indicated by stars. Drifter positions every 5 days are shown as black dots overlain on drifter tracks.
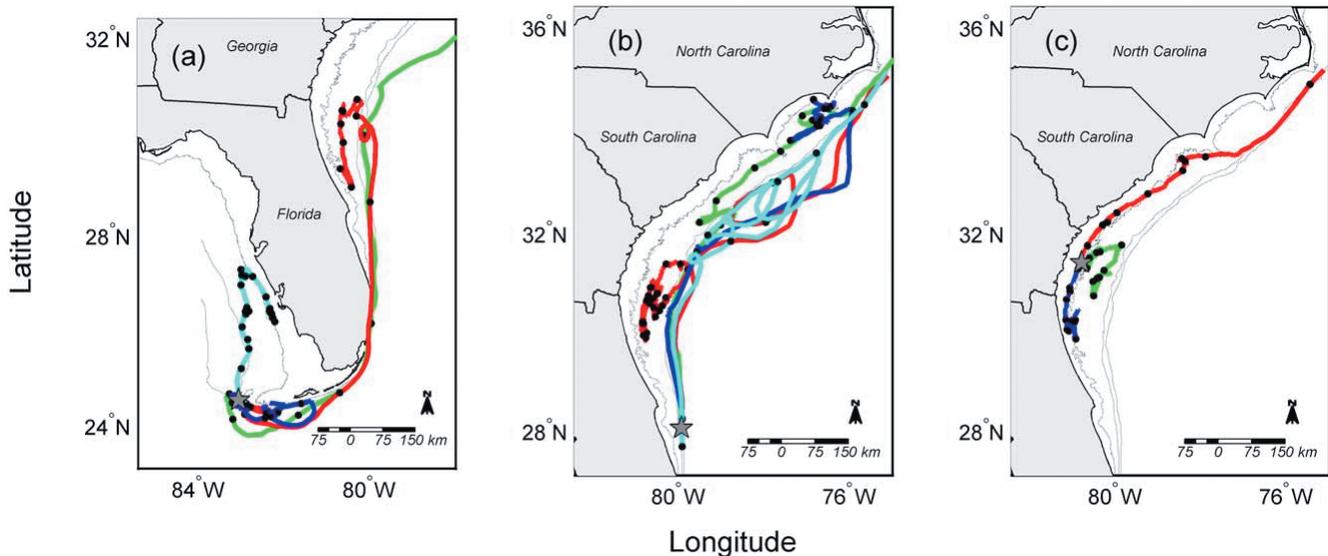
cles could not leave these zones once they entered, but their arrival indicates a consistent supply to inshore areas.

The number of particles on the shelf from each release area also provided evidence for retention (Fig. 7). "On the shelf" is defined as particles moving into or remaining in shelf zones (<20 m, 20–40 m, and 40–200 m) from the Lower Keys to North Carolina. There is a clear inshore–offshore gradient, with more particles released inshore remaining or returning to the shelf over time compared with particles released offshore. There are also along-shelf differences, with more particles from the Lower Keys, east Florida, and Georgia than from the Upper Keys, South Carolina, and North Carolina zones remaining on the shelf.

The number of particles remaining in (or returning to) their release zone provides further evidence for retention and potential self-recruitment (Fig. 8). The 20–40 m zones of North Carolina, South Carolina, and Georgia exhibited higher self-returning, with the Georgia zone exhibiting the highest self-retention. The Lower Keys zone also exhibited relatively high self-returning rates (Fig. 8).

The fate of released particles from zones containing Tortugas South ER, Oculina RR, and Gray's Reef NMS and the source of arriving particles for these zones are provided in Supplemental Figs. S2.1–S2.3.[4] All three MPAs likely supply larvae to adequate settlement habitats; this result was also suggested in the analysis of individual drifter tracks (see above). Thus, from the perspective of larval export, the Tortugas ER is well positioned to support populations in south Florida, on the west Florida shelf, and along the southeast US shelf. Oculina RR and Gray's Reef NMS are positioned to support populations along the southeast US shelf.

Discussion

Implications for MPAs in the south Florida and southeast US regions

For a benefit from larval export to be realized, MPAs need to protect spawning areas that successfully supply larvae to appropriate settlement habitats. Under these criteria, MPA design requires information of the life history of specific species, the location of spawning, the pathways of larval transport from each spawning location, and the spatial and temporal distribution of settlement habitats (Hockey and Branch 1997). As the design criteria for MPAs include more species, the distribution of spawning habitats, larval transport pathways, and settlement habitats begin to encompass the entire continental shelf system (Hockey and Branch 1997; Lindeman et al. 2000). The results of this study could be interpreted within the context of specific species and include details such as spawning locations and juvenile habitat distribution. However, given the number of fishery species present on the southeast US shelf (73 species in the snapper–grouper fishery management unit alone), such an undertaking is well beyond the scope of this study.

The analysis of drifter tracks indicate that the Tortugas ER, Oculina RR, and Gray's Reef NMS likely export larvae to broad areas throughout the region and that the Tortugas ER and Gray's Reef NMS may also be self-recruiting to a degree. Thus, these MPAs could contribute to fishery management through larval export to unprotected areas. Most studies indicate that 20%–50% of a species' habitat needs to be protected (i.e., no-take marine reserve) for MPAs to meet fishery management objectives (DeMartini 1993; Parrish 1999; NRC 2001). The combined area of the Tortugas ER is ~500 km^2 and much of the south Florida shelf is part of the Florida Keys National Marine Sanctuary (9600 km^2), which includes more than 20 no-take zones. However, the total percent area of no-take zones on the south Florida shelf is on the order of 5%, providing only some benefit for fisheries management (Dahlgren and Sobel 2000). MPAs and no-take areas along the southeast US shelf encompass much less area. Gray's Reef NMS is 54 km^2, whereas the inner Georgia shelf is ~15 000 km^2. Oculina RR and recent additions encompass about 1300 km^2, whereas the outer east Florida shelf is ~15 000 km^2. There are other MPAs in the region, with varying degrees of protection, but the amount currently

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Fig. 5. Drifter locations (*a*) 15, (*b*) 30, (*c*) 45, and (*d*) 60 days after release at Tortugas South Ecological Reserve (Tortugas South ER), Experimental Oculina Research Reserve (Oculina RR), and Gray's Reef National Marine Sanctuary (Gray's Reef NMS). Drifter release locations are indicated by stars.
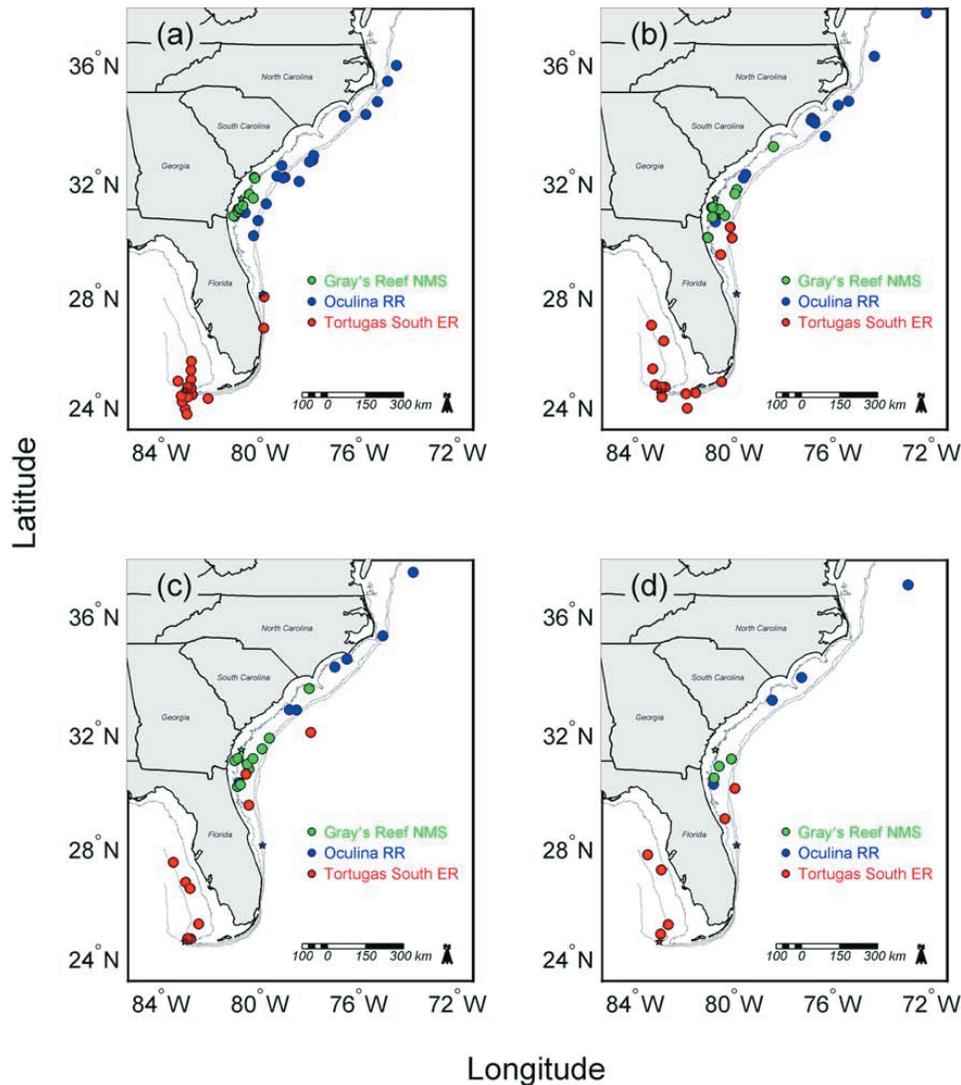
protected in no-take reserves is much less than that generally recommended for fisheries management objectives. Although well positioned, these smaller MPAs are likely to have only marginal influence on the dynamics of exploited fish populations across the regions. That said, these areas do protect reef habitat from destructive fishing practices and spawning aggregation sites (Gilmore and Jones 1992; Koenig et al. 2000; Burton et al. 2005), which are also important objectives of MPAs.

Larval transport processes

The drifter tracks and probability model identified several important larval transport processes in the south Florida and southeast US shelf systems. The role of cyclonic eddies in affecting retention and onshore larval transport in the Florida Keys region has been documented in prior studies (Lee et al. 1994; Paris et al. 1997; Sponaugle et al. 2005). The drifter tracks analyzed here provide further support for the importance of these cyclonic eddies in larval transport.

The drifter tracks also show that even after drifters are entrained in Gulf Stream associated flows, they can be detrained and move onto the southeast US shelf. Similar patterns of entrainment and detrainment have been documented in the Gulf Stream system north of Cape Hatteras (Ashjian 1993; Hare et al. 2002). The consequence is that downstream transport speeds for individual drifters rarely match the average current speeds reported for the Gulf Stream (1.5 m·s^{-1}; McGowan and Richards 1989) over periods of time exceeding 5–10 days; by extension, estimates of transport distances based on average current speeds (see McGowan and Richards 1989; Roberts 1997) likely overestimate actual planktonic transport distances.

The drifter tracks also identify the Georgia shelf as a retention area. Some of the drifters released in the 20–40 m Georgia shelf zone remained for up to 60 days, and the probability model showed retention–return rates of 7% at 60 days. These retention times are similar to the estimates of Atkinson et al. (1978) based on flushing rates from freshwater runoff

Fig. 6. Number of particles present in different zones following release calculated from the probability model. Data for the along-shelf zones are included in different panels; data for the cross-shelf zones are defined by different lines in each panel. A schematic of the distribution of particles at day 30 is also shown; along-shelf zones are denoted by lines and cross-shelf zones are from the closest to the coast (<20 m zone) to furthest from the coast (>200 m or the offshore boundary). See Fig. 2 for map of zones.
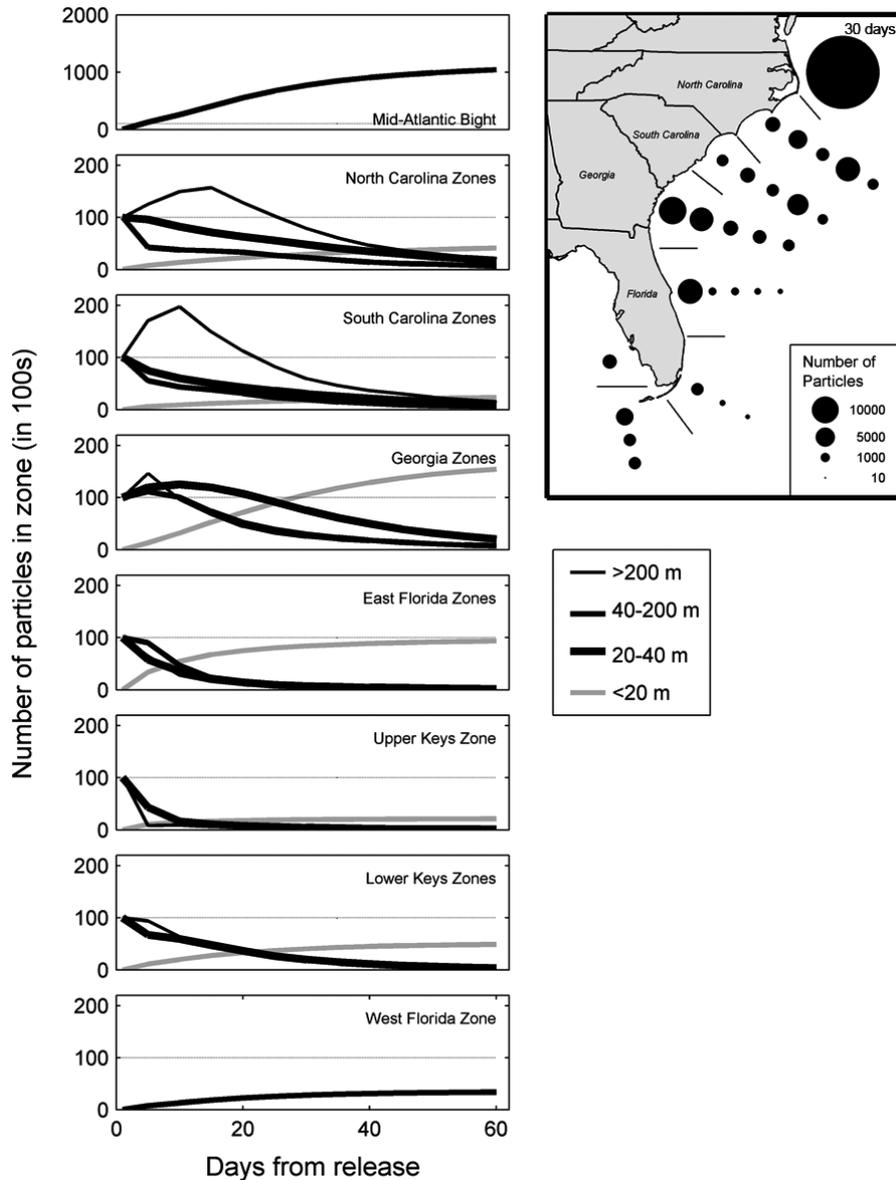

(81 days), as well as Gulf Stream meander frequency and entrainment volume estimates (60–90 days). The agreement between these disparate approaches provides strong evidence for the hypothesis that the Georgia shelf is a retention zone on time scales of most larval durations (15–60 days). The inner shelves (20–40 m) of the South and North Carolina zones also exhibited relatively high retention, but less than the 20–40 m Georgia zone. Further, the Georgia 20–40 m zone experienced less loss from the shelf overall compared with the North and South Carolina 20–40 m zones.

Review of approach

The probability model developed here was based on observational data and assumes constant probabilities of residence time and movement between zones. This assumption

is certainly not correct (see Edwards et al. 2006, 2007). Drifters were released in every month of the year, so seasonal variability is incorporated into the probability distributions, but more drifters were released during the summer (Supplemental Fig. S1.2).[4] Another limitation is that the probability model is based on a limited number of releases (105), whereas the model used a large number of particles (10 000 in each zone). However, the drifter releases resulted in more than 500 observations of residence time and movements between zones, and in most cases, the gamma distribution fit the residence-time observations very well (see Supplemental Fig. S1.4).[4] An alternative, widely used approach for quantifying larval transport is three-dimensional circulation models coupled with Lagrangian particle tracking algorithms (Werner et al. 2001). Individ-

Fig. 7. Number of particles released within a zone remaining on the shelf following release. "On the shelf" is defined as in the <20 m, 20–40 m, and 40–200 m zones from the Lower Keys to North Carolina. Data for the along-shelf zones are included in different panels; data for the cross-shelf zones are defined by different lines. A schematic of the distribution of particles at day 30 is also shown; along-shelf zones are denoted by lines and cross-shelf zones are from the closest to the coast (< 20 m zone) to furthest from the coast (>200 m or the offshore boundary). See Fig. 2 for map of zones.
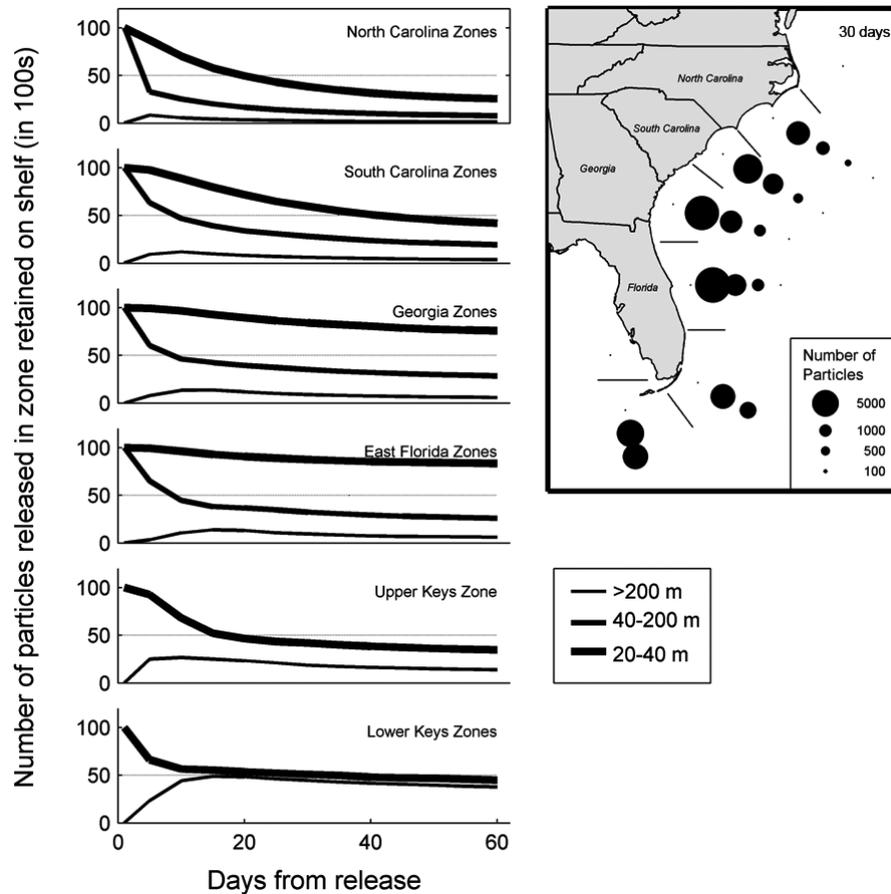
ual drifter tracks are often used to assess the accuracy of circulation models (e.g., Paris et al. 2005; Edwards et al. 2006), so in many instances, the two approaches can be developed simultaneously, with results from the circulation model aggregated spatially to match the resolution of an observation-based probability model (see Zakardjian et al. 2003). Concurrence between the two approaches provides validation of each and supports the application of circulation models at finer spatial scales.

The lack of larval behavior in the probability model deserves special attention. A number of studies have indicated that larval fish can modify their horizontal transport by occupying different vertical levels in the water column (Cowen et al. 1993; Hare et al. 1999; Paris and Cowen 2004). Hare and Govoni (2005) concluded that larvae in surface waters of the southeast US shelf were more likely to be exported to the Gulf Stream; larvae deeper in the water column were more likely to be transported onshore or remain on the shelf (see also Werner et al. 1999). The model developed here was based on surface drifters, so the results favor export, not retention. In addition, evidence that larvae are able to swim horizontally and orient this behavior is growing (Leis 2006). Thus, the amount of retention estimated by the probability

model is likely an underestimate of the actual amount of larval retention in the system.

Future directions

The drifter tracks and probability models indicate that both long-distance transport and local retention occur in the south Florida and southeast US shelf systems. Thus, these two outcomes of planktonic transport represent part of a continuum, not a dichotomy. Further, the distribution of outcomes is not spatially homogenous; there are areas that promote retention and areas that promote long-distance transport. Thus, for management applications, it is difficult to generalize: system, region, and site-specific characterizations of actual planktonic transport will be required. There are also a broad variety of life history patterns exhibited by marine species and these species-specific attributes will need to be incorporated into management frameworks.

To understand the actual impact of planktonic transport processes on marine populations, estimates of exchange between spawning locations need to be incorporated into spatially explicit, stage-specific population models (see Fogarty 1998; Yakubu and Fogarty 2006). For most marine fish species, these models need to include exchange during juvenile

Fig. 8. Number of particles released within a zone remaining or returning to that zone following release. Data for the along-shelf zones are included in different panels; data for the cross-shelf zones are defined by different lines. A schematic of the distribution of particles at day 30 is also shown; along-shelf zones are denoted by lines and cross-shelf zones are from the closest to the coast (<20 m zone) to furthest from the coast (>200 m or the offshore boundary). See Fig. 2 for map of zones.
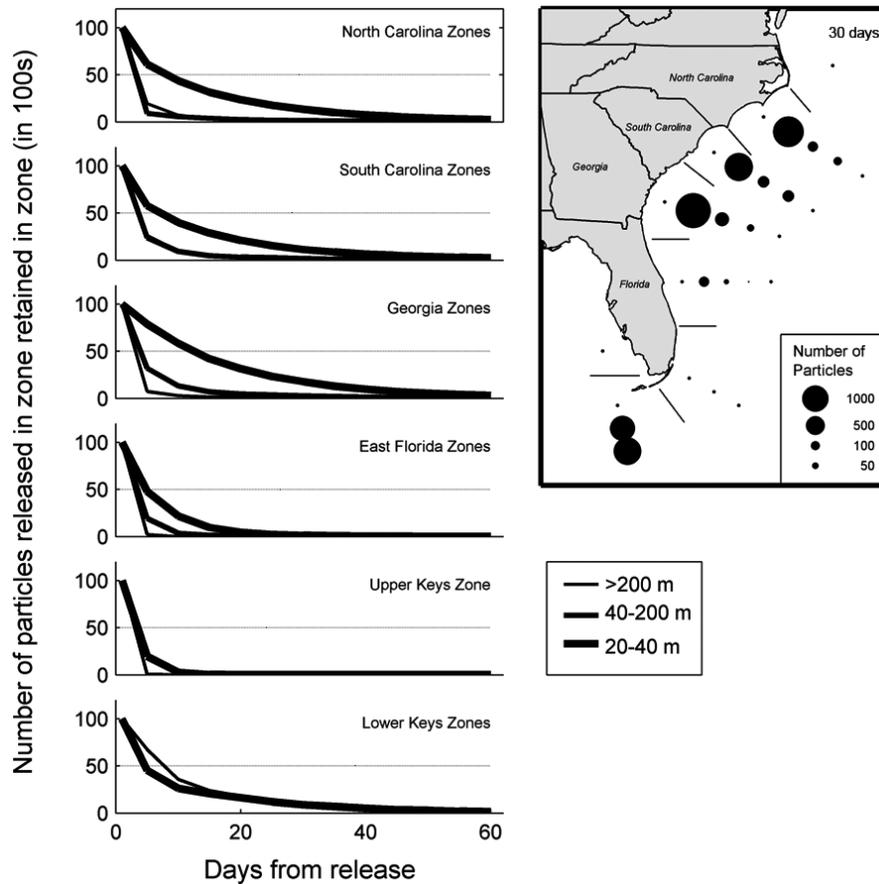
and adult stages, as well as during the planktonic stages (see Hare 2005). This coupling of planktonic transport models and population dynamic models based on real systems will allow the specific design and assessment of spatially explicit management strategies.

Acknowledgements

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Supplementary Material

Hare, J.A. and H. J. Walsh. 2007. Planktonic linkages among Marine Protected Areas on the south Florida and southeast United States continental shelf. Canadian Journal of Fisheries and Aquatic Sciences 64: 1234-1247

Supplementary Material 1 – Details of probability transport model

Division of study region into zones

      The probability model was in essence a box model based on observational data and the first step in developing the model was to define the box structure. The study region was divided into zones based on the general physical oceanography of the region. The along-shelf zones were based largely on patterns in eddy formation and decay resulting from motions of the Loop Current-Florida Current-Gulf Stream; a dominant feature of regional circulation (see Boicourt et al. 1998). The Lower Keys zone is an area of eddy formation and the Upper Keys zone is an area of eddy decay (Lee et al. 1994). Along the southeast coast, the East Florida zone and South Carolina zones are areas of eddy formation and the Georgia and North Carolina zones are areas of eddy decay (Lee et al. 1991).

      The cross-shelf zone structure was based on patterns in physical oceanographic forcing mechanisms. Circulation on the inner-shelf (<20 m) is influenced mainly by tidal forcing and freshwater input. Mid-shelf (20-40 m) flow is predominantly affected by wind and tidal forcing. Outer-shelf circulation (40-200 m) is largely determined by forcing from the western boundary current (Atkinson and Menzel 1985; Pietrafesa et al. 1985, Lee et al. 1991).

      Since the drogue center depths and drogue lengths varied, the depth of the inner most zone varied to ensure that dragging on the bottom did not influence the results of the model. For drifters that were drogued at 10m or less, 0-16.3 m and 16.3-40 m polygons were used allowing for 3 m clearance between maximum drogue depth and the bottom (10 m drogue center plus half of 6.6 m - the maximum drogue length). Similarly for drifters drogued at 15 m, 0-21.3 m and 21.3-40 m polygons were used, again allowing for 3 m clearance between maximum drogue depth and the bottom. For simplicity, the 0-16.3 m and 0-21.3 m zones are termed 0-20 m, the 16.3-40 m and 21.3-40 m zones are termed 20-40 m, and the 16.3-200 m and 21.3-200 m are termed 20-200 m.

Assignment of drifter positions to zones

      Prior to assigning drifter position to zones, drifters from two other sources were combined with the drifters released in MPAs as part of this study. First, tracks of 44 drifters released in the region as part of the Global Drifter Program (GDP) were included (see Figure S1.1); 6 hr interpolated data were downloaded from the GDP website (http://www.aoml.noaa.gov/envids/gld/). The area of inclusion for GDP drifters is shown as a polygon in Figure S1.1. Second, tracks of 12 drifters released on the North Carolina shelf and described in Hare et al. (2002) were included. Locations for these drifters were also interpolated at 6 hr interval. In sum, 105
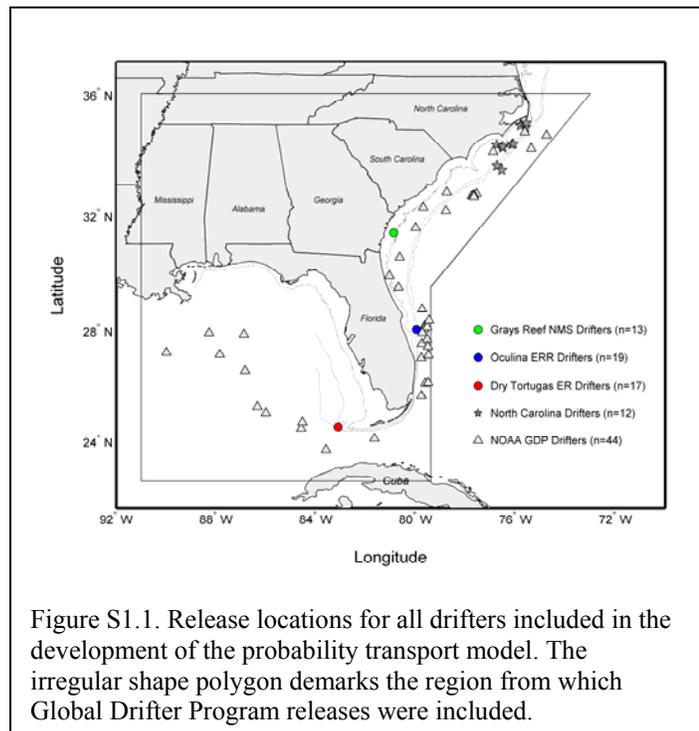
Figure S1.1. Release locations for all drifters included in the development of the probability transport model. The irregular shape polygon demarks the region from which Global Drifter Program releases were included.

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drifter tracks were used in the development of the probability model.

Drifters were released in every month of the year (Figure S1.2), so the probability model incorporates seasonal variability in circulation patterns. However, more drifters were released in July, largely owing to the releases in the Tortugas South ER and as a result, the model will be biased toward describing larval transport in the summer and fall.

Calculation of residence time and tally of movements

Residence time and movement probabilities were calculated for each drifter. Residence time was the amount of time that a drifter was in a given zone. Movement was the movement from Zone A to Zone B. Movement always occurred between adjacent zones. Two or more residence times for a zone could be estimated from one drifter track if the drifter was in the zone at two different times (see example below). Similarly two or more movements of a drifter from a zone could be recorded, again if the drifter moved from the zone on two or more separate occasions.

Wobbles of a drifter between zones were not included in the calculation of residence time and movement. Wobbling was defined as a drifter moving from Zone A to Zone B, and back to Zone A in ≤2 days. Wobbles were removed by assuming that the drifter remained in the original zone (Zone A). Two days was chosen since the Lagrangian time scales, which were calculated for many of the drifter tracks following Pal et al. (1998), were approximately 2 days (Hare, unpublished data). These wobbles usually occurred when a drifter was skirting the boundary of a polygon and vacillating into the adjacent polygon.

An example of the residence time and movement calculations is provided in Figure S1.3. A drifter was released in East Florida 40-200 m zone as part of the Oculina RR releases. While in the East Florida 40-200 m zone there were two <0.5 d wobbles into the East Florida 20-40 m zone. These were removed from the estimate of residence time in the East Florida 40-200 m zone. After 8.25 days, the drifter moved into the Georgia > 200 m zone (Seq 1-2). After 0.5 days in the Georgia > 200 m zone, the drifter moved into the Georgia 40-200 m (Seq 2-3) where it remained for 2.5 d before returning the Georgia > 200 m (Seq 3-4). Since the time in the Georgia 40-200 m exceeded 2 days, this movement was not considered a wobble and was included in the calculation of residence time and movement.
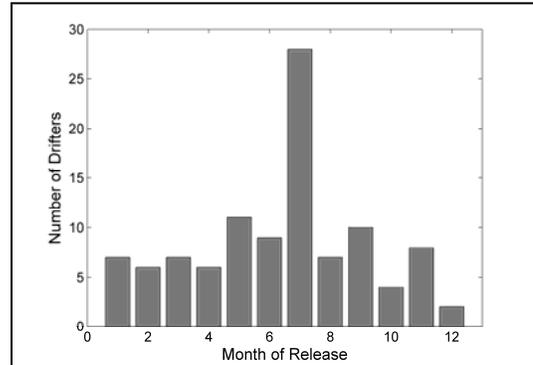
Figure S1.2. The monthly distribution of release times for drifters used in the model.
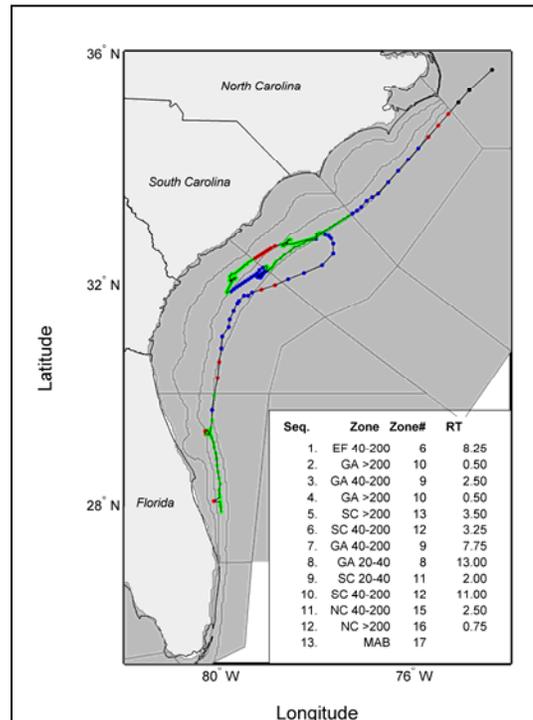
Figure S1.3. Example of a drifter track through the model domain. Positions are at 6 hour intervals. The color of the positions indicate the model zone that the drifter is in. A summary of zones and residence times is provided in the lower left corner.

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The drifter then spent 0.5 d in the Georgia > 200 m zone before moving to the South Carolina > 200 m zone (Seq 4-5). The drifter then continued to move through the model domain and residence time and movement data were extracted from the drifter track. It is important to note that a drifter can leave a zone more than once – for example the South Carolina 40-200 m zone in Figure S1.3. In this example, two residence times were obtained because the drifter occupied this zone twice. Similarly, two movements to other zones (1 to GA 40-200 and 1 to NC 40-200) were compiled in the tally of this drifter's movements.

Residence time and movement probability functions

A probability distribution of residence for each zone was calculated based on the gamma distribution and using all the residence times observed in each zone. Histograms of residence times are shown in Figure S1.4 as are the resulting gamma distributions.

Movement of each drifter from each zone was also tallied and used to calculate the probability of movement from one zone to any other zone in the domain. Movement was only observed among adjoining zones. The matrix of movement probabilities is provided in Table S1.1.
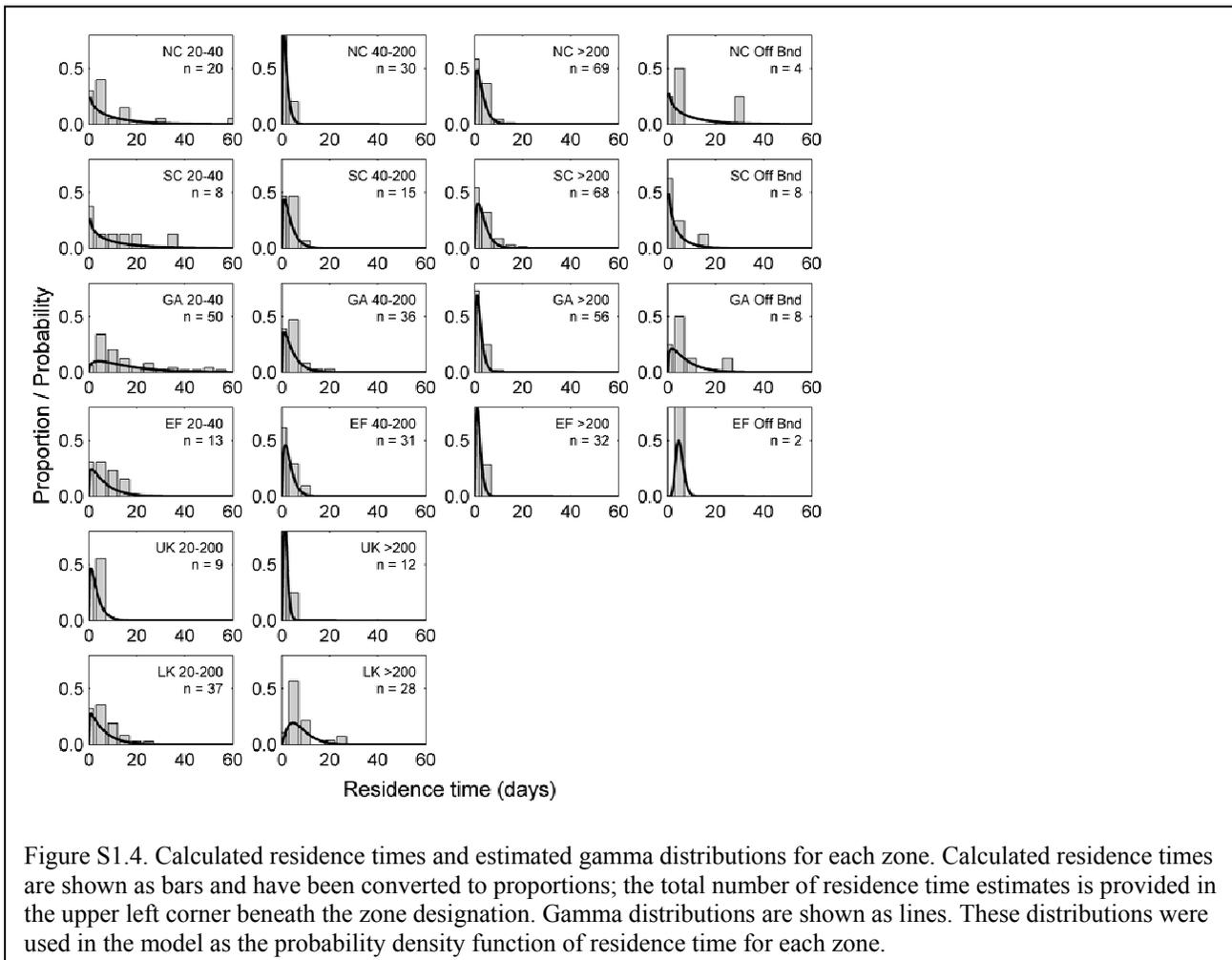
Figure S1.4. Calculated residence times and estimated gamma distributions for each zone. Calculated residence times are shown as bars and have been converted to proportions; the total number of residence time estimates is provided in the upper left corner beneath the zone designation. Gamma distributions are shown as lines. These distributions were used in the model as the probability density function of residence time for each zone.

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Table S1.1 Frequencies of movement from each zone to every other zone. Rows represent the current zone, columns represent the zone to be moved to, and numbers represent the probability of moving to zone designated in the column when movement occurs. For example, if a particle is in the Upper Keys 20-200 m zone, once the residence time of the particle in the zone is reached, there is a 11% chance of moving to the Upper Keys < 20 m zone and a 89% chance of moving to the East Florida 40-200 m zone. The diagonal is shown in red; the probability of moving from a zone to that zone. The probability of movement from a zone to itself is 0 for active zones in the model. The probability of movement from a zone to itself is 1 for <20 m zones, the Mid-Atlantic zone, and the West Florida Shelf zone; once particles enter these zones, they cannot leave (see text). Probabilities > 0 are shown in bold.

| Zone	Zone Number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	20	21	22	23	24	25	26	27	28	29	30
LK 20-200	1	0	**0.49**	**0.19**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0.14**	**0.19**	0	0	0	0	0
LK >200	2	**0.71**	0	0	**0.29**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
UK 20-200	3	0	0	0	0	0	**0.89**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0.11**	0	0	0	0
UK >200	4	0	0	**0.25**	0	0	0	**0.75**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
EF 20-40	5	0	0	0	0	0	**0.15**	0	**0.23**	0	0	0	0	0	0	0	0	0	**0.62**	0	0	0	0	0	0	0	0	0	0
EF 40-200	6	0	0	0	0	**0.10**	0	**0.35**	0	**0.55**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
EF >200	7	0	0	0	0	0	0	0	0	0	**1.00**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GA 20-40	8	0	0	0	0	**0.09**	0	0	0	**0.30**	0	**0.06**	0	0	0	0	0	0	0	**0.55**	0	0	0	0	0	0	0	0	0
GA 40-200	9	0	0	0	0	0	**0.06**	0	**0.29**	0	**0.57**	0	**0.09**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GA >200	10	0	0	0	0	0	0	0	0	**0.07**	0	0	0	**0.89**	0	0	0	0	0	0	0	0	0	0	0	0	0	**0.04**	0
SC 20-40	11	0	0	0	0	0	0	0	**0.13**	0	0	0	**0.38**	0	**0.38**	0	0	0	0	0	**0.13**	0	0	0	0	0	0	0	0
SC 40-200	12	0	0	0	0	0	0	0	0	**0.27**	0	**0.20**	0	**0.40**	0	**0.13**	0	0	0	0	0	0	0	0	0	0	0	0	0
SC >200	13	0	0	0	0	0	0	0	0	0	**0.03**	0	**0.10**	0	0	0	**0.81**	0	0	0	0	0	0	0	0	0	0	**0.06**	0
NC 20-40	14	0	0	0	0	0	0	0	0	0	0	**0.05**	0	0	0	**0.75**	0	**0.05**	0	0	0	**0.15**	0	0	0	0	0	0	0
NC 40-200	15	0	0	0	0	0	0	0	0	0	0	0	**0.07**	0	**0.23**	0	**0.43**	**0.27**	0	0	0	0	0	0	0	0	0	0	0
NC >200	16	0	0	0	0	0	0	0	0	0	0	0	0	**0.03**	0	**0.14**	0	**0.77**	0	0	0	0	0	0	0	0	0	0	**0.06**
MAB	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1.00**	0	0	0	0	0	0	0	0	0	0	0
EF <20	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1.00**	0	0	0	0	0	0	0	0	0	0
GA <20	21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1.00**	0	0	0	0	0	0	0	0	0
SC <20	22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1.00**	0	0	0	0	0	0	0	0
NC <20	23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1.00**	0	0	0	0	0	0	0
WFS	24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1.00**	0	0	0	0	0	0
LK <20	25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1.00**	0	0	0	0	0
UK <20	26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1.00**	0	0	0	0
EF Off Bnd	27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1.00**	0	0
GA Off Bnd	28	0	0	0	0	0	0	0	0	0	**0.38**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0.25**	0	**0.38**	0
SC Off Bnd	29	0	0	0	0	0	0	0	0	0	0	0	0	**0.50**	0	0	0	0	0	0	0	0	0	0	0	0	**0.50**	0	0
NC Off Bnd	30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0.75**	0	0	0	0	0	0	0	0	0	0	**0.25**	0

Model calculation

  The model uses the zone specific probability distributions of residence time (Figure S1.4) and movements (Table S1.1) to move particles through the model domain. An example is given in Figure S1.5. In this example, a particle is released in the Lower Keys > 200 m zone. At its release, the residence time of the particle (r_{p1}) in the zone is calculated using a random number generator and the cumulative probability distribution for the zone specific residence time (Figure S1.5 Step 1A). The particle then remains in the zone, until r_{p1} is reached. Once r_{p1} is reached, the particle leaves the zone; the new zone is determined using a random number generator and the cumulative probability distribution of movement for the current zone (Figure S1.5 Step 1B). In this example, the particle remains in the Lower Keys > 200 m zone for 6 d and then moves to the Upper Keys > 200 m zone. The residence time and movement calculations are then repeated (Figure S1.5 Step 2A and 2B). In this example, the particle remains in the Upper Keys > 200 m zone for 4 days and then moves to the East Florida > 200 m zone. Upon entering the new zone, a new residence time is calculated and this process is repeated until day 60. This procedure was then repeated for 10,000 particles released in each of the 16 release zones.

  If particles entered the <20 m zones, the West Florida Shelf zone or the Mid-Atlantic Zone, they stayed in that zone for the remainder of the model run. Since the drifters were drogued at 10 m and 15 m, residence time and movement probabilities were not calculated for the <20 m zones, to avoid any bias from drifters dragging on the bottom. Thus, if a particle entered any of these <20 m zones, they remained. If particles entered the Mid-Atlantic zone, they remained, since none of the drifters that entered the Mid-Atlantic zone moved back into the North Carolina zones. Drifters did move from the West Florida to the Lower Keys zone, but the average residence time in the West Florida zone was 56 days; to simplify the model, once particles entered the West Florida zone they did not leave.

Figure S1.5. An example of the model calculation for the first two steps of one particle (see accompanying text).

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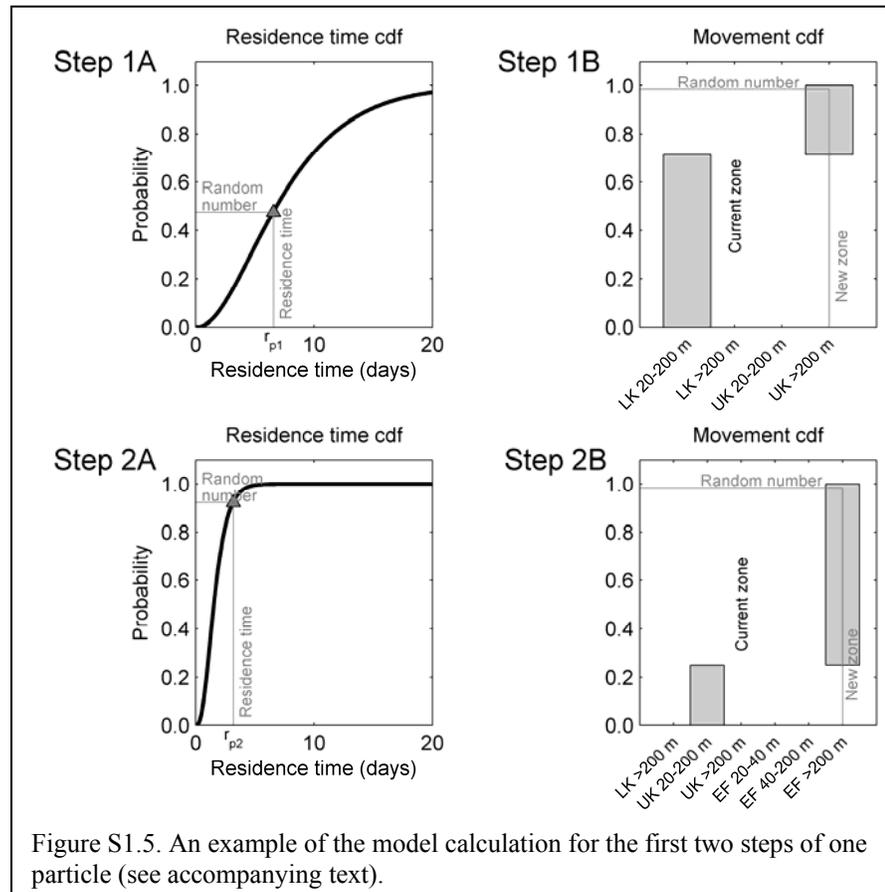
Supplementary Material 2 – Model results for three MPAs: Tortugas South Ecological Reserve, Experimental Oculina Research Reserve, and Gray's Reef National Marine Sanctuary

Introduction

The probability model allows for the fate of particles released in all release zones to be determined and allows for the source of all particles arriving to a zone to be determined. The fate of particles provides insight into where larvae from a particular location go and the source of particles provides insights into where larvae have come from.

Three MPAs were the focus of this study: Tortugas Ecological Reserve in the 20-200 m Lower Keys zone, Experimental Oculina Research Reserve in the 40-200 m East Florida zone, and Gray's Reef National Marine Sanctuary in the 20-40 m Georgia zone. The fate and source of particles for these zones are presented here.

Lower Keys 20-200 m zone

Particles released in the 20-200 m Lower Keys zone move 'downstream' initially into the Upper Keys and East Florida zones and then into the Georgia, South Carolina, and North Carolina zones (Figure S2.1). Onshore transport is evident in the East Florida and Georgia zone at 30-60 d and the North Carolina zone at 45-60 d. Accumulation of particles north of Cape Hatteras occurs at 30-60 d. Even with broad supply to other areas, retention of particles in the Lower Key zones is evident throughout the 60 d. Particles released in this zone also moved to the west Florida shelf; into the area identified as the 'forbidden zone' by Yang et al. (1999).

The source regions of the 20-200 m Lower Key zone are restricted and include the Lower Keys only, suggesting that Tortugas ER is highly dependent on self recruitment. This conclusion is tempered by Yang et al. (1999); they indicated substantial movement of drifters from the northern west Florida shelf to the Lower Keys and east. It is possible that the 'forbidden zone' receives particles from the Lower Keys, while areas to the north of the 'forbidden zone' supply particles to the Florida Keys and downstream. Thus, the source regions for the Lower Keys likely include areas on the west Florida shelf, which is outside of the domain studied here. These 'boundary' conditions could be examined with a larger spatial domain that includes the entire Gulf of Mexico.

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(a) Fate of particles released in Lower Keys 20-200 m Zone
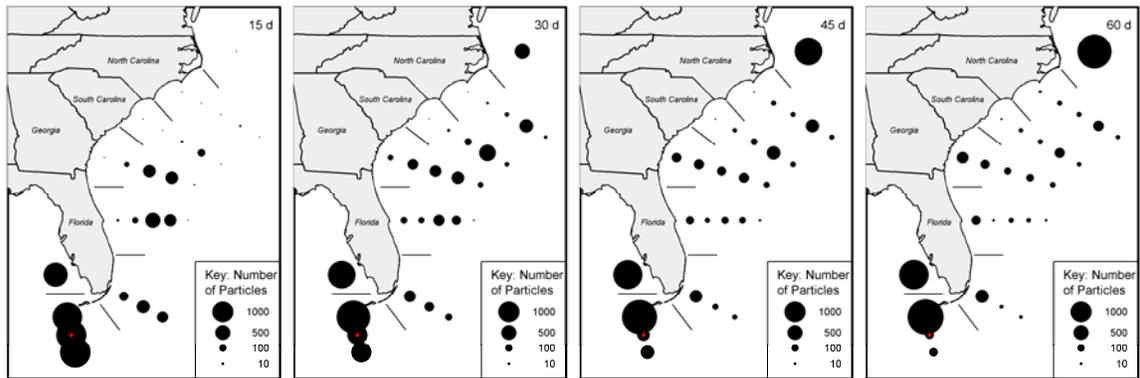
(b) Source of particles arriving in Lower Keys 20-200 m Zone
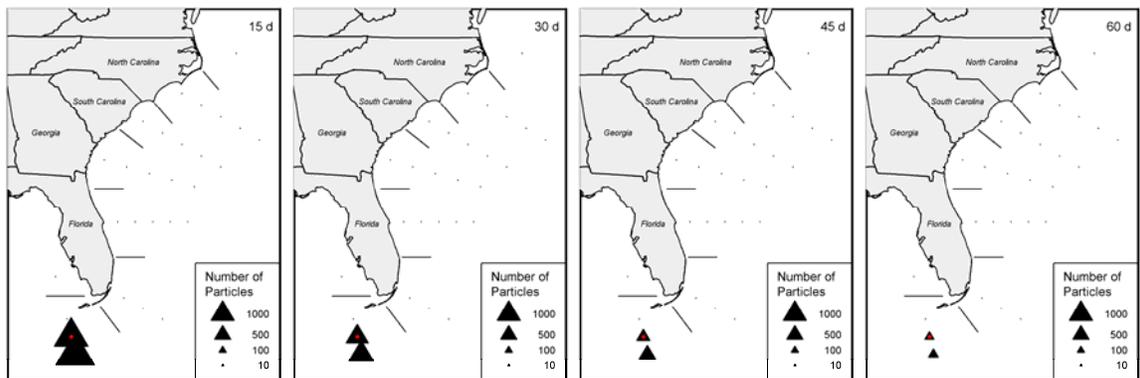
Figure S2.1. A) A schematic of the fate of particles released in the 20-200 m Lower Keys zone, which contains the Tortugas Ecological Reserve, at 15, 30, 45, and 60 d. The release zone is indicated by a red square. Along shelf zones are denoted by lines and cross-shelf zones are from the closest to the coast (<20 m zone) to furthest from the coast (> 200 m). B) A schematic of the source of particles arriving in the 20-200 m Lower Keys zone, which contains the Tortugas Ecological Reserve, at 15, 30, 45, and 60 d. The receiving zone is indicated by a red square. Along shelf zones are denoted by lines and cross-shelf zones are from the closest to the coast (<20 m zone) to furthest from the coast (> 200 m).

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East Florida 40-200 m zone

Particles released in the 40-200 m East Florida zone move 'downstream' and onshore (Figure S2.2). By 45 days, particles were supplied to inshore zones (< 20 m) from East Florida to North Carolina. Accumulation of particles north of Cape Hatteras occurs rapidly with a substantial number of particles north of Cape Hatteras by 30 d. No zone-specific retention is evident, but retention 'on the shelf' is about 26% at 60 d (see Fig 7).

The source regions of the 40-200 m East Florida zone are restricted and variable through time. At 15 d, source regions include the Lower Keys to South Carolina. This general distribution of source locations is similar over time, but the number of particles supplied decreases through time. These results indicate that Oculina RR is likely dependent on other areas for recruitment of sessile organisms.

Figure S2.2. A) A schematic of the fate of particles released in the 40-200 m East Florida zone, which contains the Experimental Oculina Research Reserve, at 15, 30, 45, and 60 d. The release zone is indicated by a red square. Along shelf zones are denoted by lines and cross-shelf zones are from the closest to the coast (<20 m zone) to furthest from the coast (> 200 m).B) A schematic of the source of particles arriving 40-200 m East Florida zone, which contains the Experimental Oculina Research Reserve, at 15, 30, 45, and 60 d. The receiving zone is indicated by a red square. Along shelf zones are denoted by lines and cross-shelf zones are from the closest to the coast (<20 m zone) to furthest from the coast (> 200 m).

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Georgia 20-40 m zone

Particles released in the 20-40 m Georgia zone remain in the zone and move 'downstream' and onshore (Figure S2.3). Zone-specific retention is high (Fig. 7) as is the supply of particles to the inshore (<20 m) Georgia zone. A small amount of movement to the East Florida zones is also evident. Accumulation of particles north of Cape Hatteras occurs slowly.

The source regions of the 20-40 m Georgia zone are broadly distributed. Since it is an area of retention, particles that move into the zone have a high probability of remaining there. At 45 d, sources regions include zones from the Lower Keys to North Carolina. These results indicate that Gray's Reef NMS is well situated to supply larvae and receive larvae from a broad range of areas.

Figure S2.3. A) A schematic of the fate of particles released in the 20-40 m Georgia zone, which contains the Gray's Reef National Marine Sanctuary, at 15, 30, 45, and 60 d. The release zone is indicated by a red square. Along shelf zones are denoted by lines and cross-shelf zones are from the closest to the coast (<20 m zone) to furthest from the coast (> 200 m). B) A schematic of the source of particles arriving in the 20-40 m Georgia zone, which contains the Gray's Reef National Marine Sanctuary, at 15, 30, 45, and 60 d. The receiving zone is indicated by a red square. Along shelf zones are denoted by lines and cross-shelf zones are from the closest to the coast (<20 m zone) to furthest from the coast (> 200 m).

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