Multidirectional movements of sportfish species between an estuarine no-take zone and surrounding waters of the Indian River Lagoon, Florida

Derek M. Tremain
Christopher W. Harnden
Douglas H. Adams
Florida Fish and Wildlife Conservation Commission
Florida Marine Research Institute
1220 Prospect Avenue, Suite 285
Melbourne, Florida 32901
Email: Derek.Tremain@fwc.state.fl.us

Abstract—We examined movement patterns of sportfish that were tagged in the northern Indian River Lagoon, Florida, between 1990 and 1999 to assess the degree of fish exchange between an estuarine no-take zone (NTZ) and surrounding waters. The tagged fish were from seven species: red drum (*Sciaenops ocellatus*); black drum (*Pogonias cromis*); sheepshead (*Archosargus probatocephalus*); common snook (*Centropomus undecimalis*); spotted seatrout (*Cynoscion nebulosus*); bull shark (*Carcharhinus leucas*); and crevalle jack (*Caranx hippos*). A total of 403 tagged fish were recaptured during the study period, including 65 individuals that emigrated from the NTZ and 16 individuals that immigrated into the NTZ from surrounding waters of the lagoon. Migration distances between the original tagging location and the sites where emigrating fish were recaptured were from 0 to 150 km, and these migration distances appeared to be influenced by the proximity of the NTZ to spawning areas or other habitats that are important to specific life-history stages of individual species. Fish that immigrated into the NTZ moved distances ranging from approximately 10 to 75 km. Recapture rates for sportfish species that migrated across the NTZ boundary suggested that more individuals may move into the protected habitats than move out. These data demonstrated that although this estuarine no-take reserve can protect species from fishing, it may also serve to extract exploitable individuals from surrounding fisheries; therefore, if the no-take reserve does function to replenish surrounding fisheries, then increased egg production and larval export may be more important mechanisms of replenishment than the spillover of excess adults from the reserve into fishable areas.

Manuscript submitted 12 May 2003
to Scientific Editor's Office.

Manuscript approved for publication
20 January 2004 by the Scientific Editor.

Fish. Bull 102:533–544 (2004).

Fishery reserves or no-take sanctuaries, defined as areas where all fishing activities are prohibited, are increasingly proposed as an additional measure to traditional fishery management practices for protecting fish populations from overexploitation (PDT, 1990; Bohnsack and Ault, 1996). The American Fisheries Society recently issued a policy statement on the protection of marine fish stocks at risk of extinction and supported the development of large marine reserves to protect and rebuild vulnerable populations (Musick et al., 2000). Although reserves have been established primarily in reef or coastal marine habitats, the potential to apply similar management strategies in estuarine systems may also be possible (Johnson et al., 1999; Roberts et al., 2001).

Reserves in estuarine areas may help protect exploitable fishery species. Increases in species' sizes and densities within these reserves may also enhance adjacent fisheries by two separate mechanisms. Johnson et al. (1999) found that an existing estuarine no-take sanctuary on Florida's central east coast protected populations of larger, spawning-age sportfish species. As a result, they suggested that protection of populations in no-take sanctuaries could also lead to the replenishment of surrounding fisheries through increased egg production, larval export, and juvenile recruitment. Additionally, mark-recapture data have demonstrated that large juvenile and adult fishes emigrate from estuarine protected areas to surrounding waters (Bryant et al., 1989; Funicelli et al., 1989; Johnson et al., 1999; Roberts et al., 2001; Stevens and Sulak, 2001) and these data have been used to suggest that spillover of excess adult fish from estuarine reserve areas can directly supplement nearby fisheries. Roberts et al. (2001) concluded that the abundance of International Game Fish Association based on line-class-record catches in the vicinity of the estuarine no-take sanctuary on Florida's east coast resulted indirectly from protection and spillover of large adults to outlying waters.

It has also been suggested that reserves protect areas of undisturbed habitat (PDT, 1990), either by design or through cessation of destructive practices, and reserves are commonly established in areas of pristine, productive, or otherwise important habitats required by the species being protected (e.g., Russ, 1985). Furthermore, studies have shown that protecting fishery species can indirectly change the overall community structure (Cole and Keuskamp, 1998) and, under certain circumstances, can increase primary and secondary productivity (Sala and Zabala, 1996; Babcock et al., 1999). The influence of habitat quality on fish movements in relation to protected areas has not been investigated; however, reserve habitats that offer potential advantages in the form of improved habitat quality (Chapman and Kramer, 1999)

or increased food and habitat availability could be expected to attract, or at least retain, individuals that immigrate to the reserves from surrounding unprotected habitats. Reserve areas that attract and retain exploitable individuals from surrounding habitats at higher rates than they replenish the surrounding habitats could be considered to be sinks in terms of their ability to directly supplement adjacent fisheries through spillover of exploitable-size individuals. Fish emigration from reserve habitats and the replenishment of nearby fisheries is a commonly predicted benefit of harvest reserves (see reviews in Roberts and Polunin, 1991, and Rowley, 1994). However, there are currently no studies that simultaneously examine emigration and immigration in relation to estuarine reserves or that document the extent to which reserve areas may also function to withdraw individuals from surrounding fisheries. Without an assessment of net exchange, the interpretation of reserve benefits with respect to replenishment cannot be properly evaluated.

The National Aeronautics and Space Administration (NASA) closed a portion of the Indian River Lagoon at the Merritt Island National Wildlife Refuge (MINWR) on Florida's east coast for security purposes in 1962. A direct result of this closure was the effective creation of an estuarine no-take zone that remains to the present time. The proximity of this no-take zone to productive estuarine fisheries provided an opportunity to examine sportfish movements in the area with mark-recapture methods. Johnson et al. (1999) first documented sportfish migrations out of this no-take sanctuary, and in a related study, Stevens and Sulak (2001) provided more complete descriptions of movement patterns of individual species; each of these studies provided evidence that the restricted habitats protected fish populations and that adult sportfish egressed into surrounding waters open to fishing. However, because all tagged fish originated from within restricted habitats, in neither of these studies was it possible to consider the potential for the movements of fish into protected areas from surrounding waters. Therefore, we (sponsored by the Florida Fish and Wildlife Conservation Commission-Florida Marine Research Institute [hereafter referred to as FMRI] Fisheries-Independent Monitoring Program) tagged fish species throughout the northern Indian River Lagoon system, including both the MINWR no-take zone and the surrounding lagoon waters, from 1990 to 1999. We investigated the relationship between sportfish egress and ingress in relation to the MINWR no-take zone and offer a quantitative foundation for the discussion of net fish movements into or away from protected estuarine habitats.

Materials and methods

Study area

The Indian River Lagoon (IRL) is a shallow barrier island estuarine system spanning 253 km along the central east coast of Florida between Ponce de Leon Inlet in Volusia County and Jupiter Inlet in Palm Beach County. The lagoon is composed of three relatively isolated basins: Mosquito Lagoon, the Indian River proper, and the Banana River (Fig. 1). These three basins maintain hydrological connections with each other through narrow man-made channels at Haulover Canal and the Merritt Island Barge Canal (shown on Fig. 2) and through a natural channel at the southern end of the Banana River. Hydrodynamic exchange and fish passage between the lagoon and the Atlantic Ocean occur primarily through five inlets, which are concentrated in the southern half of the system. The hydraulic lock system located at Port Canaveral provides only an intermittent opportunity for exchange between the IRL and Atlantic Ocean. Gilmore et al. (1981) and Mulligan and Snelson (1983) have provided detailed descriptions of the lagoon and its habitats.

The no-take zone (NTZ) created by NASA and MINWR is located at the northern terminus of the Banana River basin of the lagoon. An earthen causeway defines the southern boundary of this no-access security area and contains only two openings that permit fish to migrate to and from adjacent waters. Much of the natural shoreline and saltmarsh habitats in the lagoon have been altered for mosquito control purposes. However, actual shoreline habitats surrounding MINWR—including the NTZ, the northern Banana River basin, the northern Indian River basin, and Mosquito Lagoon—remain relatively undeveloped in comparison to the urban shoreline development in the southern IRL. Detailed descriptions of the habitat composition within the NTZ and surrounding study area were provided by Johnson et al. (1999).

Data collection

Fish were tagged as part of several related FMRI projects (stratified-random, fixed-station, and directed sampling designs) in the northern IRL between 1990 and 1999 (FMRI[1]). In most cases, tagging was conducted opportunistically on healthy fish following capture in multipanel monofilament gill nets, nylon trammel nets, nylon haul seines, or on hook and line. In other cases, projects were designed specifically to assess tag-recapture information (Murphy et al., 1998). Because of the focus of our sampling programs in this area, the majority of our tagging efforts occurred north of Sebastian Inlet within the Indian and Banana River basins of the lagoon. A small percentage of tags were placed in fish captured south of Sebastian Inlet or in Mosquito Lagoon. Overall, our sampling collections in the NTZ

[1] FMRI (Florida Fish and Wildlife Conservation Commission). 1999. Florida Marine Research Institute, Fisheries-independent monitoring program, 1999 annual data summary report. In-house Report, Florida Fish and Wildlife Conservation Commission, Florida Marine Research Institute, 100 Eighth Ave. S.E., St. Petersburg, Florida, 33701.

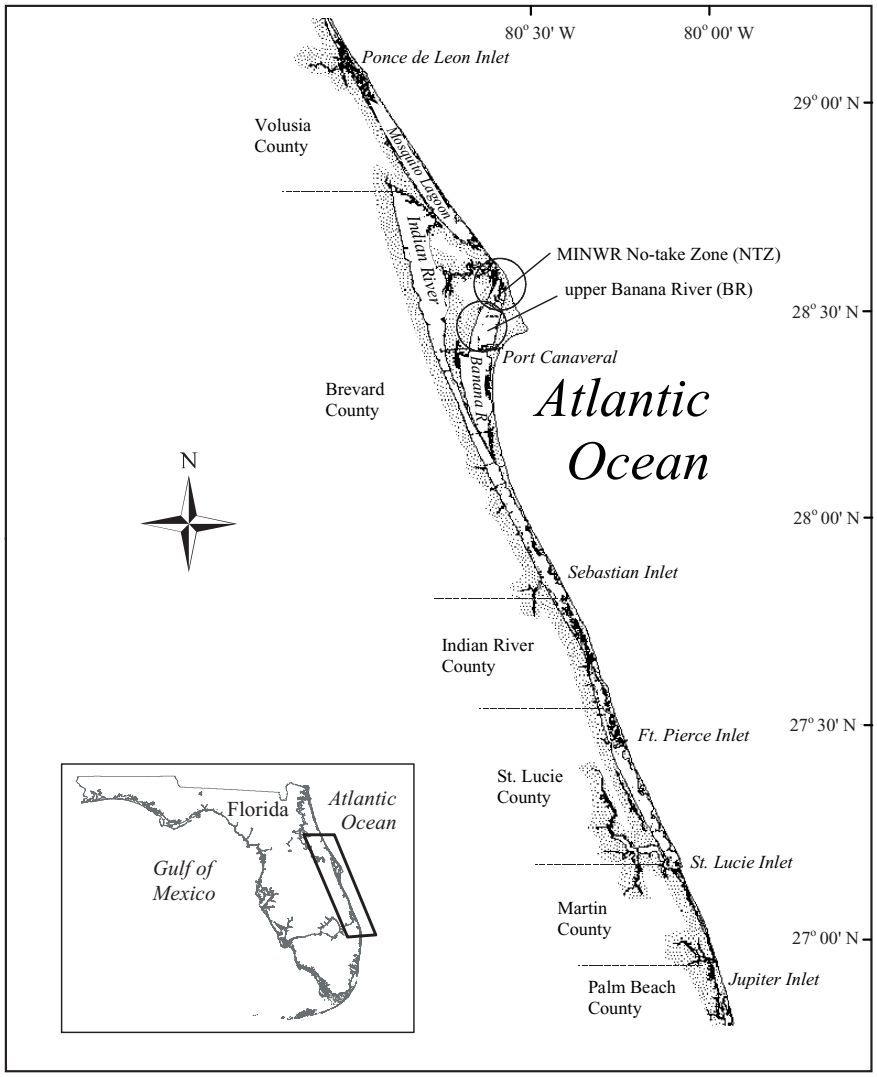


Figure 1
Map of Florida and the Indian River Lagoon study area.

accounted for approximately 20% of our total sampling efforts and averaged approximately 1–2 days/month over the study period.

Fish were tagged by inserting 50-mm, 70-mm, or 100-mm Hallprint dart tags (Halprint Ltd., Victor Harbor, South Australia) into the dorsal musculature; the plastic dart was lodged beneath the pterygiophores of the dorsal fin. Each tag contained a visible external streamer with a unique alphanumeric code and instructions for anglers to contact us with recapture information in order to collect a reward (five dollars or equivalent). Information recorded at the time of initial tagging included the tag number, species tagged, date, location (latitude and longitude), and fish length (standard, fork, and total lengths as appropriate for the species). Recapture information on tagged fish was collected through August 2000 from angler reports and from fish recaptured during FMRI sampling activities. Because of public-access prohibitions, recapture information from inside the MINWR NTZ was gathered exclusively through FMRI sampling efforts. Data requested for recaptured fish included the same information as that recorded at initial tagging; however, in several cases, length or precise location information returned from anglers was considered to be unreliable, which prevented accurate statistical comparisons of relationships involving recapture lengths or distances traveled. Therefore, reported length data are limited to initial tagging information only (total length; TL). To prevent problems with pseudoreplication for individuals recaptured on multiple occasions, we included only the initial tag recovery data in our calculations of recapture percentages.

Overall patterns of fish migrations, including general recapture locations and direction of movements into or away from the NTZ, were described by using data

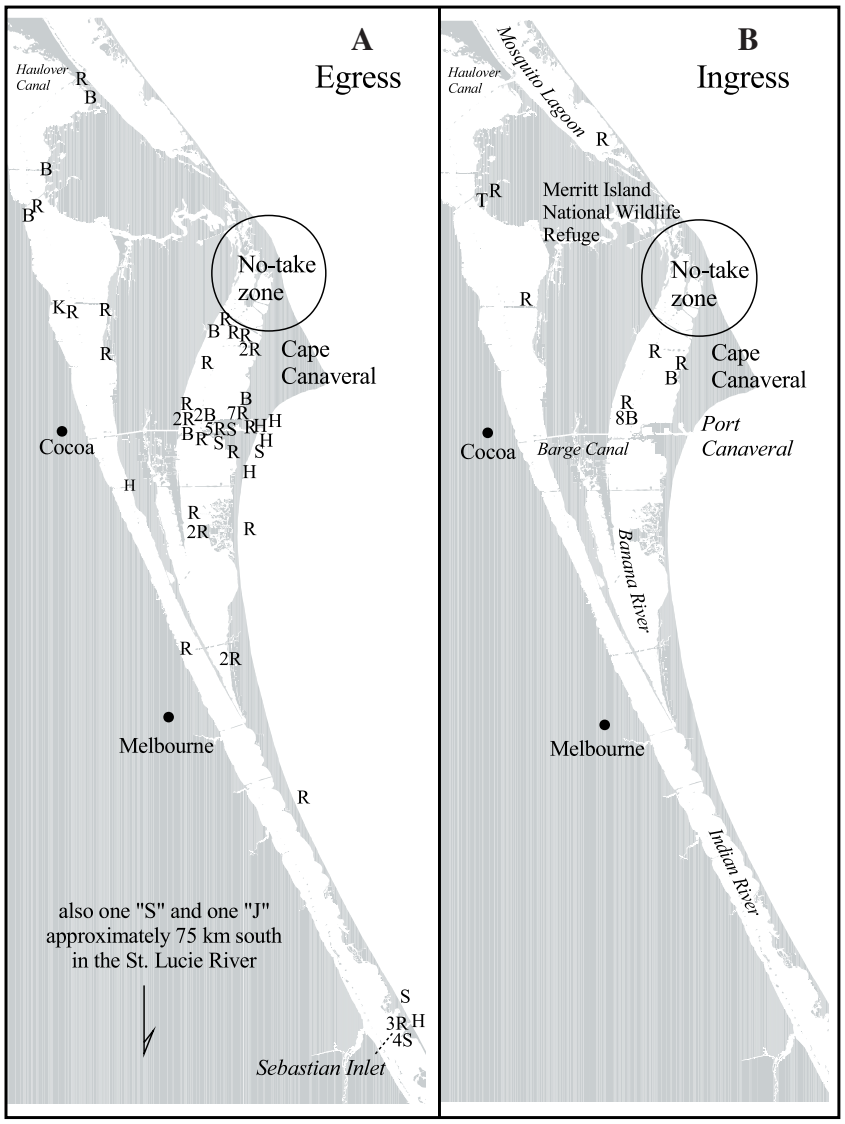


Figure 2

(**A**) Recapture locations of tagged fish that migrated out of the Merritt Island National Wildlife Refuge no-take zone. (**B**) Original tagging locations of fish that migrated into the Merritt Island National Wildlife Refuge no-take zone. R = red drum, B = black drum, S = common snook, H = sheepshead, T = spotted seatrout, J = crevalle jack, K = bull shark. Numbers before species codes (letters) indicate the number of individuals of that species that were captured at that location.

from all available recapture sources. In contrast, we calculated migration rates exclusively from the recapture data collected during FMRI sampling activities. Although this procedure excluded tag-return data from recreational anglers, it permitted a quantitative assessment of recapture rates based on standardized FMRI collection gear, comparable sampling effort, and 100% tag reporting rates. We resolved potential problems related to differences in habitat characteristics and sampling intensity by including only data from the NTZ and a fishable area of a similar size and habitat type in the adjacent Banana River (BR, Fig. 1). This BR zone corresponded precisely to the sampling zone used for population comparisons in Johnson et al. (1999), denoted as "FBR" (fished Banana River) in that study. Species that did not contribute any FMRI recapture information in either of these two areas were excluded from our analyses. Tag recovery and migration rates were calculated separately for the NTZ and BR. For our purposes, "migration" was defined as a directional fish movement across the NTZ boundary from the original tagging location, and we made the assumption that the migration patterns of recaptured fish represented the migration patterns of the overall population. Rela-

Table 1

Summary of tagging and recapture data for seven of the most common sportfish species tagged by FMRI scientists in the northern Indian River Lagoon study area. Locations where tag and recapture data were collected are separated into the no-take zone (NTZ) and the surrounding waters of the Indian River Lagoon (IRL).

	No-take zone			Indian River Lagoon				
		Recapture location			Recapture location			
Species	Tagged inside NTZ	NTZ	IRL	Tagged outside NTZ	NTZ	IRL	Total no. of fish tagged	Total no. recaptured and percent recaptured
Bull shark (*Carcharhinus leucas*)	1		1	24		1	25	2 (8.0)
Common snook (*Centropomus undecimalis*)	104	1	9	406		32	510	42 (8.2)
Crevalle jack (*Caranx hippos*)	55		1	59		1	114	2 (1.8)
Sheepshead (*Archosargus probatocephalus*)	597		6	520		26	1117	32 (2.9)
Spotted seatrout (*Cynoscion nebulosus*)	193	2		171	1	3	364	6 (1.6)
Black drum (*Pogonias cromis*)	637	4	8	831	9	32	1468	53 (3.6)
Red drum (*Sciaenops ocellatus*)	720	30	40	1344	6	190	2064	266 (12.9)
Total	2307	37	65	3355	16	285	5662	403 (7.1)

tive migration rates were calculated as the percentage of recaptured fish that migrated from their original tagging location. These migration rates and their reciprocal (retention rates) were compared between the NTZ and the BR to determine the relative potential for sportfish movements into or away from protected habitats. Chi-square contingency tests for frequency data (with Yates's correction for small sample sizes) were used to test the hypothesis that recapture location was independent of the tagging location.

Results

A total of 5951 fish of 27 species were tagged during FMRI sampling within the IRL between September 1990 and December 1999. However, because 95% of these fish were represented by only seven species (Table 1), which included all fish that migrated across the reserve boundaries, only these seven species were considered further in our analyses. Red drum (*Sciaenops ocellatus*) was the most commonly tagged species (n=2064), followed by black drum (*Pogonias cromis*, n=1468), sheepshead (*Archosargus probatocephalus*, n=1117), common snook, (*Centropomus undecimalis,* n=510), spotted seatrout (*Cynoscion nebulosus,* n=364), crevalle jack (*Caranx hippos*, n=114), and bull shark (*Carcharhinus leucas*, n=25). Approximately 41% (n=2307) of these fish were tagged inside the boundaries of the NTZ. The remainder (n=3355) were tagged in the surrounding lagoon. Through August 2000, 403 tagged fish (7.1% of total) were recaptured and reported either by FMRI staff sampling in the lagoon or by the public. Overall recapture rates were highest for red drum (12.9%), followed by those for common snook (8.2%), bull shark, (8.0%), black drum (3.6%), and sheepshead (3.0%).

Tagged fish were generally representative of the larger mobile members of the species and encompassed the legally exploitable size ranges for species with management restrictions (Table 2). For species except the bull shark and red drum, mean lengths of fish tagged inside the NTZ exceeded those of fish tagged outside the NTZ.

Approximately 25% (n=102) of the 403 total recaptured fish were fish originally tagged inside the NTZ (Table 1). Thirty-seven of these fish were also recovered inside the NTZ, including three red drum that were subsequently recaptured on multiple occasions in the protected area. The remaining 65 recaptured fish were caught after emigrating to outlying waters, including one red drum that was recaptured a second time outside the NTZ. Species that migrated out of the NTZ were red drum (n=40, mean TL=643 mm, SD=135 mm), common snook (n=9, mean TL=570 mm, SD=97 mm), black drum (n=8, mean TL=845 mm, SD=88 mm), sheepshead (n=6, mean TL=398 mm, SD=38 mm), bull shark (n=1, TL=789 mm), and crevalle jack (n=1, TL=628 mm). Recapture distances ranged from 0 km immediately outside the NTZ to approximately 150 km south in the St. Lucie River estuary, but recaptured fish were more abundant closer to the NTZ (Fig. 2A). Most of the recaptured fish were concentrated in areas of high fishing pressure, such as causeways, inlets, and waters near the boundary of the NTZ. Collectively, fish that emigrated from the NTZ did not appear to show a bias for any one direction of movement: recaptured fish were found both northward in the Indian River and southward throughout both the Indian River and Banana River basins of the lagoon. For individual species, red drum that emigrated were distributed throughout the lagoon system and coastal habitats, whereas black drum were predominantly recaptured in the northern

Table 2

Total length (TL) size ranges (in mm) and legal size limits (as of August 2000) for tagged sportfish species from the no-take zone and the outlying Indian River Lagoon study area.

	No-take zone			Indian River Lagoon			Legal size limits
Species	Mean (SD)	min	max	Mean (SD)	min	max	(mm TL)
Bull shark	789 (—)	789	789	974 (135)	684	1180	None
Common snook	570 (106)	330	844	506 (138)	227	944	660–864 (+ 1 over)
Crevalle jack	486 (140)	305	720	443 (113)	264	720	None
Sheepshead	398 (68)	235	614	365 (76)	171	594	305 minimum
Spotted seatrout	415 (129)	185	754	335 (111)	212	678	381–508 (+ 1 over)
Black drum	786 (129)	249	1156	742 (240)	225	1135	356–610 (+1 over)
Red drum	613 (166)	308	1245	624 (229)	203	1210	457–686

estuarine portion of the study area. Sheepshead and common snook were recaptured primarily to the south at inlets or in the adjacent Atlantic coastal waters outside the lagoon.

The remaining 75% (n=301) of the total recaptured fish were from fish originally tagged outside the NTZ (Table 1). The majority of these (n=285) were also recovered in outlying waters, including 16 red drum and 1 sheepshead that were subsequently recaptured on multiple occasions. Sixteen fish were recaptured after they had immigrated into the reserve. These recaptured fish were from three sciaenid species: predominantly black drum (n=9, mean TL=907 mm, SD=66 mm) and red drum (n=6, mean TL=656 mm, SD=170 mm), but also one spotted seatrout (TL=420 mm)(Fig. 2B). The longest migration distances into the NTZ were up to 75 km for red drum and spotted seatrout tagged in southern Mosquito Lagoon and the northern Indian River basins. All black drum that immigrated into the NTZ were tagged in the adjacent Banana River basin.

A relatively large number of red drum, common snook, and sheepshead that were tagged inside the NTZ or in the outlying waters were recaptured in close proximity (0 to 2.75 km distance) to inlet habitats. Recaptured red drum from inlet habitats (n=45, mean TL=647 mm, SD=135 mm) peaked during September through November. Recaptured common snook from inlet habitats (n=13, mean TL=598 mm, SD=111 mm) were distributed throughout much of the year but peaked in late fall. Few common snook were recaptured from inlet spawning habitats during the peak summer spawning months (June–August) when their fishery was closed. Recaptured sheepshead from inlet habitats (n=8, mean TL=373 mm, SD=53 mm) were concentrated in the winter and early spring.

Estimated migration rates were calculated by using only those fish that were tagged and recovered from FMRI sampling in the NTZ and the immediately adjacent upper Banana River (BR). The number of fish tagged in the NTZ (n=1654) was approximately 1.7 times the number tagged in the BR (n=965) (Table 3); however, the overall recapture rates of fish that were originally tagged in each of these two areas were equal (2.4%). Black drum and red drum made up the majority of tagged and recaptured fish in both areas and were the only species recaptured that had migrated both into and away from the NTZ in this comparison. For total sportfish (all species pooled), there was a significant relationship between the tagging location and the direction of fish movements ($\chi^2_{1,\ 0.05}$=13.8, P=0.0002). A total of 40 fish originating from the NTZ were recaptured, but that number included only 2 fish (one red drum and one black drum) that emigrated to the BR (5% overall migration rate). In contrast, 23 fish originating in the BR were recaptured overall, including 12 that immigrated into the NTZ (52% overall migration rate). Species-specific migration rates were highest for black drum, and relative immigration rates (90%) were higher than emigration rates (25%). For this species, the frequency of immigration and emigration were statistically independent of tagging location ($\chi^2_{1,\ 0.05}$=0.01, P=0.9039), which is probably due to the low number of recaptures of fish tagged inside the NTZ (Table 3). For red drum, relative immigration rates (27%) were also higher than emigration rates (3%), but in this case, there was a significant relationship between fish movements and tagging location ($\chi^2_{1,\ 0.05}$=20.58, P<0.0001). Common snook, spotted seatrout, and sheepshead were also recaptured by FMRI scientists in these comparisons, but none of these recaptured fish represented evidence of migrations across the NTZ boundary from their original tagging location.

Discussion

This study demonstrated both the emigration and immigration of sportfish species across the boundaries of an estuarine no-take zone (NTZ). Legal-size large juveniles and adults of six of the recreationally valuable species tagged within NTZ boundaries—red drum, black drum, common snook, sheepshead, bull shark, and crevalle

Table 3

Summary of tag and recapture data from only the Florida Marine Research Institute sampling efforts in the no-take zone (NTZ) and the adjacent fished waters of the Banana River (BR). Species that did not contribute any recapture information were not included in calculations of totals or of migration percentages.

	No-take zone					Banana River				
	No. of fish tagged	No. fish recaptured		Total	Percent that migrated	No. of fish tagged	No. fish recaptured		Total	Percent that migrated
		NTZ	BR				NTZ	BR		
Red drum	720	32	1	33	3.3	176	3	8	11	27.3
Black drum	637	3	1	4	25.0	495	9	1	10	90.0
Common snook	104	1	0	1	0	62	0	1	1	0.0
Spotted seatrout	193	2	0	2	0	121	0	0	0	—
Sheepshead	597	0	0	0	—	232	0	1	1	0.0
Totals	1654	38	2	40	5.0	965	12	11	23	52.2
Tag recovery (%)				2.4					2.4	

jack—were documented to migrate out of the protected area. Johnson et al. (1999) and Stevens and Sulak (2001) also observed many of these same species emigrating from no-take zones within the same refuge system during the late 1980s, although the species with the highest recapture rates in their studies (common snook) differed from the current study (red drum). This difference may reflect an increase in the popularity of the red drum fishery on Florida's east coast during the current study period. Since 1989, when the recreational red drum fishery reopened under strict management regulations, there has been a significant increase in both the total red drum landings on the Atlantic coast and in the estimated number of fishing trips made by anglers seeking or catching red drum each year (Murphy[2]). Tagging studies in estuarine areas of the Everglades National Park have previously documented emigrations of striped mullet (*Mugil cephalus*), gray snapper (*Lutjanus griseus*), and spotted seatrout away from protected habitats (Bryant et al., 1989; Funicelli et al., 1989). Recent studies suggest that fish moving out of protected areas in the IRL may help to replenish nearby fisheries and may contribute to trophy fisheries in the surrounding system (Johnson et al., 1999; Roberts et al., 2001).

In our study, overall emigration rates were low, but many of the fish that emigrated from the estuarine NTZ moved comparatively large distances. The egress patterns of exploitable species may affect both the species' potential for protection and the degree to which fisheries located adjacent to protected reserves will be enhanced (DeMartini, 1993). In coastal marine and tropical reef systems, where the large majority of reserves have been established, long-distance movements greater than a few kilometers by demersal fishery species are limited to a very small percentage of individuals (Beaumariage, 1969; PDT, 1990 and references therein; Rowley, 1994), and the direct supplementation of nearby fisheries by exploitable species appears to be highly localized (Buxton and Allen, 1989; Russ and Alcala, 1996). The majority of fish that emigrated from the NTZ were recaptured between 10 and 75 km from the boundary, but fish were also recovered as far as 150 km from the NTZ boundary. Our observations on migration distances and recapture locations corresponded well with those reported from previous studies of fish movements out of this same reserve system (Johnson et al., 1999; Stevens and Sulak, 2001), although maximum recapture distances in earlier studies were even greater.

Many of the fish that emigrated from the NTZ—such as red drum, common snook, and sheepshead—were recaptured at inlet locations or in the nearshore coastal waters at sizes that were large enough to include reproductively mature adults (Murphy and Taylor, 1990; Render and Wilson, 1992; Taylor et al., 2000). The seasonality of inlet-associated recaptures was consistent with the seasonality of documented spawning and movement patterns for these species. In Florida, red drum typically spawn in nearshore coastal waters during the fall (Murphy and Taylor, 1990), although spawning within the IRL has also been documented (Johnson and Funicelli, 1991). Spawning by common snook may occur year-round on Florida's east coast (Gilmore et al., 1983), but most spawning takes place between May and October in or near major inlets to the Atlantic Ocean (Taylor et al., 1998). The limited number of common snook recaptured from inlet spawning habitats during the peak summer spawning season (June–August) was likely due to the fishery being closed during those months. Sheepshead move offshore with the onset of cool weather in the late fall (Gunter, 1945; Kelly, 1965), and spawning likely occurs in offshore waters during

[2] Murphy, M. D. 2002. A stock assessment of red drum, *Sciaenops ocellatus*, in Florida: status of the stocks through 2000, 32 p. Florida Fish and Wildlife Conservation Commission Report, Melbourne, FL.

the spring (Springer and Woodburn, 1960; Jennings, 1985; Tucker and Barbera, 1987). In the northern portion of the IRL, where the NTZ is located, the closest access to the coastal environment is through two inlets located approximately 75 km (Sebastian Inlet) and 100 km (Ponce de Leon Inlet) swimming distance away or through an intermittent lock opening at Port Canaveral approximately 12 km to the south. In order to reach nearshore or tidal-pass spawning habitats, species must first migrate to these locations. The coincidence of tag recoveries from these areas during identified spawning or migration periods likely indicated that the relatively long movement distances we observed resulted from a combination of geographical, environmental, and biological factors, including the proximity of the NTZ to habitats that are important for specific life-history requirements of individual species. From a management viewpoint, these relationships can affect the spatial extent of species' migrations in relation to protected habitats, as well as the degree of protection provided to individuals that are migratory, and should be considered carefully in the design of estuarine reserves.

This study documented the ingress of exploitable estuarine sportfish species into protected habitats and demonstrated that these movements can also cover substantial distances. Species moving towards the NTZ traveled distances of at least 10–75 km. The original tagging locations of these fish were distributed throughout the northern Indian and Banana rivers and southern Mosquito Lagoon, which paralleled the primary region of our tagging efforts. Whether or not fish from more southerly locations in the IRL system would migrate into the NTZ is largely unknown because of the lack of tagging effort in those areas. However, for tropical species such as the common snook, permit (*Trachinotus falcatus*), gray snapper, and others whose abundances increase seasonally in the northern lagoon habitats during the warmer months (Tremain and Adams, 1995), it seems probable that seasonal movements could bring them into contact with the protected habitats. In such cases, these species would benefit only temporarily from fishing protection until their return migrations made them again vulnerable to capture. In contrast, species observed migrating into the NTZ that typically have a high degree of site fidelity during specific life-history stages, such as the red drum (Beaumariage, 1969; Adams and Tremain, 2000), black drum (Murphy et al., 1998), and spotted seatrout (Moffett, 1961), should derive greater long-term benefits from reserve protection following immigration into protected areas.

Tagging studies that examine the transfer of fishery species between reserve and outlying habitats are rare, and we have found only one recent study on any fishery species, the American lobster (*Homarus americanus*), that investigated the effects that multidirectional species migrations may have upon protective reserve functions (Rowe, 2001). Studies in which fish movements have been examined, in both estuarine and marine protected areas, have focused exclusively on fish egress from reserve habitats (Bryant et al., 1989; Buxton and Allen, 1989; Funicelli et al., 1989; Holland et al., 1996; Zeller and Russ, 1998; Johnson et al., 1999, Stevens and Sulak, 2001) or on home ranges of species associated with reserve habitats (Eristhee and Oxenford, 2001; Starr et al., 2002). In the present study, we simultaneously examined both egress and ingress of sportfish in relation to a no-take reserve and the surrounding unprotected waters, and the results provide a starting point to quantitatively discuss the relationship between fish emigration and immigration, as well as the implications of such movements to the resulting functions of replenishment to or withdrawal from nearby estuarine fisheries. When all recapture sources were considered, the ratio of migrating to nonmigrating individuals was much higher for fish tagged inside the NTZ (1.58) than for those tagged outside the NTZ (0.05); this ratio implies that there is a spillover effect from the reserve. However, this difference is less apparent when measured against the large disparity between recapture effort from inside the NTZ (12–24 FMRI sampling days/year + 12–24 angler days/year) and recapture effort from the surrounding lagoon waters of Brevard County (50–100 FMRI sampling days/year + 114,000–181,000 angler days/year [FMRI, unpubl. data]). Furthermore, this direct comparison assumes that recapture potential was the same in protected and unprotected areas, which is unlikely given the differences between the primary recapture gear used in scientific research activities inside the reserve (nets) and the gear used in recreational angling outside the reserve (hook and line). There were no reliable estimates of sportfish species landings available for the limited study region that could have enabled us to intercalibrate for these differences; therefore, we limited further comparisons to only data recovered through FMRI sampling activities in the northern Banana River basin. This limitation came at the expense of important tag-recovery data collected by anglers or collected from more outlying areas of the lagoon but permitted a more quantitative comparison of migration potential that focused comparisons on immediately adjacent areas where the effects of spillover would most likely be realized (Buxton and Allen, 1989; Russ and Alcala, 1996). In these comparisons, a disproportionate number of fish were tagged inside the NTZ, but overall tag-recovery rates for fish originating in both the NTZ and the adjacent Banana River were equivalent. This finding indicated that tagged individuals from both areas were equally susceptible to recapture. However, there were substantial differences in the migration patterns of fish between the two areas. In the vicinity of the NTZ, the relative potential for overall sportfish migrations (primarily for red drum and black drum, which provided the greatest quantity of tag recovery data) towards the NTZ from unprotected habitats (52%) was greater than the potential for migrations out of the NTZ (5%).

Two potential limitations must be considered when comparing these migration rates. First, it is possible that recreational fishing in the upper Banana River could have reduced the number of tags available to FM-

RI sampling activities outside the NTZ, leading to lower tag recovery rates from this area. However, several fish from the Banana River study area were recaptured on multiple occasions—a common occurrence in this region where fish are caught and released in fishing practices. Although there is some postrelease cryptic mortality associated with catch-and-release practices, these releases likely limited the effects of local fishing on our analyses. Second, our assumption that the migration patterns of recaptured fish represented the migration patterns of the overall population may not be valid if the respective length frequencies were not also equally represented. The use of multiple gear types and sampling strategies to collect fish for tagging increased the likelihood that the length frequencies of species in our collections represented the available population. Reported recapture length frequencies closely approximated the population length frequencies in our collections for red drum, black drum, and sheepshead but over-represented the frequency of larger individuals for common snook and spotted seatrout. Because red drum and black drum were the principal species that displayed multidirectional migration patterns, we considered the potential for size bias to be minimal in our comparisons of estimated ingress and egress rates.

Ultimately, a determination of the net result of these migration patterns, in terms of replenishment to or withdrawal from adjacent fisheries, would require accurate assessments of species population abundances that were beyond the scope of this study. If there are large enough differences in population densities across the NTZ boundary, either as a result of increased production inside the reserve or high fishing mortality outside, then the relatively low emigration rates that we observed could still result in a net export of exploitable individuals to fished populations in surrounding waters. In trammel-net collections from this same reserve during the late 1980's, Johnson et al. (1999) estimated that in the protected habitats, relative abundances of red drum populations were 6.3 times greater and of black drum were 12.8 times greater than the relative abundances of these populations in adjacent unprotected areas. More recent shoreline haul-seine data from 1997–2000 show that these abundances were only 1.8 times greater for red drum and 1.5 times greater for black drum (FMRI, unpubl. data). To what extent the difference in abundance estimates between these two temporally separate studies is related to fish movements, to stringent changes in management regulations that have occurred, or to the difference in sampling methods used is undetermined. However, if we consider the more recent population level differences between the NTZ and adjacent waters, then the emigration and immigration rates observed in the present study indicate that there is a potential for more substantial movements by these species towards protected habitats than away from them.

One limitation of tag-recapture data is that such data provide only a snapshot view of overall fish movements, and the whereabouts of tagged individuals between the time of tagging and recapture are unknown. It is possible that the movements we observed for red drum and black drum in the vicinity of the NTZ were simply instantaneous views of a more complex series of movements between the NTZ and adjacent waters. One possibility is that these movements could be related to daily or seasonal home ranges that extend across reserve boundaries. Studies that attempt to quantify home ranges for these species at any temporal scale are limited. Carr and Chaney (1976) followed a single red drum, which was fitted with an ultrasonic transmitter, for up to two days after releasing it into the Intracoastal Waterway near St. Augustine, Florida. During that time, fish movements were oriented against the direction of tidal flow but remained within 2 km of the release point. Adams and Tremain (2000) found that large juvenile red drum repeatedly used or were continually associated with a 2-km section of a northern IRL tidal creek for periods of up to 18 months. Tagging studies from estuarine waters generally indicate that the majority of red drum and black drum do not make substantial movements from their release sites, although some individuals are capable of migrating up to several hundred kilometers (Beaumariage, 1969; Osburn et al. 1982; Music and Pafford, 1984; Murphy et al., 1998). During the present study, 20 red drum were recaptured on multiple occasions; however, none of these fish exhibited movements that could provide evidence for home ranges that overlapped the NTZ boundaries. Another possibility for the movement patterns we observed is that they are related to population equilibrium adjustments that occur when the relative attributes of the NTZ and surrounding areas change with respect to each other. For example, beginning in 1990 and coinciding with the onset of the present study, the Banana River adjacent to the NTZ (including much of our BR study area) was closed to motorized boat traffic. Although the area remained open to fishing, it became considerably more difficult to access by fishermen. If this limitation resulted in lower fishing pressure (i.e., predation) and fewer habitat disturbances, then the relative habitat value and rates of migration into this area may have increased during that time. There are no quantifiable estimates of migration rates prior to this study for comparison, but our results do not demonstrate an equilibrium adjustment toward potentially higher quality BR habitats during our study period. If species movements are not equilibrium adjustments, but rather are driven by an attraction to or retention within habitats that offer protective benefits, then ultimately reserve habitats should become saturated. Predicted equilibrium population sizes for queen conch (*Strombus gigas*) and spiny lobster (*Panulirus argus*) were achieved in just three years after the effective creation of a Caribbean reef harvest refuge, but models suggested that relatively minor changes in refuge area and boundary condition (i.e., permeability) could result in major population-level responses by exploited species, depending upon dispersal dynamics and habitat availability (Acosta, 2002). The estuarine no-take zone at

MINWR has been in effect for approximately 40 years, presumably long enough for fish populations to reach equilibrium levels, yet we observed a net movement of fish into protected habitats over the past decade.

A wide range of factors interact to determine the distributions of large mobile fish in the IRL, where physical environmental conditions (salinity, inlet distance, temperature, etc.) have a primary influence on the species' distributions over a lagoon-wide scale, and where species responses to biological variables (seagrass cover, depth, seasonality, etc.) act secondarily to influence distributions at smaller scales (Kupschus and Tremain, 2001). The specific mechanisms that lead to the greater ingress rates into the NTZ for red drum and black drum in the present study cannot be determined from our data. Possibilities include a behavioral attraction to the NTZ due to the interrelated influences of habitat preference, spawning, and social structure, or due to potentially higher retention rates after migration into the reserve. Red drum and black drum were routinely observed foraging in large schools within both the NTZ and surrounding waters, which suggested that food resources were available in each of these habitats; however, there are few studies that have attempted to quantify differences in resource availability between these areas. Johnson et al. (1999) described the habitat characteristics of their study areas within the same reserve system but found that protection from fishing, and not habitat difference, was the primary factor contributing to differences in the abundance of sportfish species between fished and unfished areas. The availability of suitable spawning habitats within the NTZ may also attract red drum and black drum to the reserve habitats. We observed indications of reproductive behavior by both of these species inside the NTZ that is common among members of the drum family, including concentrations of drumming fish (Mok and Gilmore, 1983) and repeated side-to-side contact among individual fish (Tabb, 1966) in the presence of ripe and running males. Although we did not directly observe these behaviors for either species outside of the NTZ, black drum and red drum are documented to spawn elsewhere within the IRL system (Mok and Gilmore, 1983; Johnson and Funicelli, 1991) and we cannot automatically presume that suitable spawning habitats do not also occur in the surrounding waters. If there is a behavioral attraction to protected habitats, then the subsequent retention of individuals that have immigrated into these areas may be prolonged by the limited boundary permeability of this reserve, which contains only two potential egress pathways back into the adjacent waters. In order to fully understand the protective functions of this estuarine reserve and others, it will be important to identify the biological, behavioral, and physical mechanisms that influence species movements in relation to the reserve boundaries.

The opportunistic nature of our tagging efforts within the design of a larger sampling program precluded statistically valid sample replication, and only one reserve and adjacent fished area were examined; therefore, the results of this study should not be generalized to other areas. Still, the IRL is typical of other bar-built estuaries where access by estuarine fishes to coastal waters through passes or inlets may be limited, and it is reasonable to expect that the geographical, environmental, and biological processes that influence species movements in the IRL would also be important in other estuaries of similar structure. Studies show that no-take areas in estuarine systems can have an effect on species' abundances and size distributions within these protected areas and may indicate that these areas protect species from the effects of fishing pressure (Johnson et al., 1999; FMRI unpubl. data). Whether or not these areas will actually increase fish abundance in adjacent waters or benefit surrounding fisheries through direct supplemental replenishment of exploitable species is less evident. Certainly, some individuals will migrate out of protected areas in response to environmental, biological, or physiological stimuli, and these individuals may contribute to trophy fisheries in surrounding waters (Roberts et al., 2001); however, our data indicated that within estuaries, reciprocal movements over relatively large distances into protected areas also occur and have the potential to extract exploitable individuals from surrounding fisheries. The overall impact of such withdrawals on these fisheries will depend on the degree of retention following migrations into protected areas. If retention rates are high, then increased egg production, larval export, and juvenile recruitment may be more important mechanisms for replenishment of nearby fisheries than spillover of exploitable species, but production and export will be limited unless reserves encompass spawning or nursery habitats (or both) that will support long-term protection and population growth. For estuarine-dependent coastal species that support estuarine fisheries, the benefits obtained within protected areas will be determined, in part, by their specific life-history characteristics, movement patterns, and the reserve design. Although the establishment and study of reserves in marine or coastal systems has increased in recent years, research on the effects of protected no-take reserves in estuarine habitats is still in its infancy. Information on the daily, seasonal, or annual movement patterns of estuarine-resident or estuarine-dependent coastal species is necessary for understanding and designing effective reserve areas in these habitats.

Acknowledgments

We wish to thank the crewmembers and volunteers at FMRI's Indian River Field Laboratory for collecting data and assisting in this study and the many fishermen who willingly provided us with recapture information. We are grateful to U.S. Fish and Wildlife Service personnel for providing access to sampling areas within restricted areas of the Merritt Island National Wildlife Refuge. This paper benefitted from reviews by R. Cody, J. Colvocoresses, L. French, J. Leiby, R. Paperno, J. Quinn,

T. Tuckey, and F. Vose, and two anonymous reviewers. This work was supported in part by funding from the Department of Interior, U. S. Fish and Wildlife Service, Federal Aid for Sport Fish Restoration Grant Number F-43, and by the State of Florida Recreational Saltwater Fishing License monies.

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