# Transboundary Movement of Atlantic Istiophorid Billfishes Among International and U.S. Domestic Management Areas Inferred from Mark-Recapture Studies

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## Introduction

The istiophorid billfishes are large, highly migratory predators, whose range and movements encompass vast geographical areas. For instance, blue marlin, *Makaira nigricans,* and sailfish, *Istiophorus platypterus*, extend to tropical and subtropical waters worldwide, while white marlin, *Tetrapturus albidus*, range throughout the Atlantic Ocean.

Owing to their highly migratory behavior, billfish stocks are often shared among many countries and, therefore, require regional and international management cooperation (Prince and Brown, 1991). In 1966, the International Commission for the Conservation of Atlantic Tunas (ICCAT) was established with a mandate to facilitate cooperative research, data collection, and management of tunas and tuna-like species (e.g. billfishes) within the Atlantic Ocean.

Over recent decades the landings of some Atlantic billfish species have decreased in size and number, a development largely attributed to increased commercial and recreational fishing activities (Restrepo et al., 2003). The most recent ICCAT stock assessments concluded that Atlantic blue marlin biomass is about 40% of the level required to produce maximum sustainable yield, while the situation for white marlin is more dire at about 20% (ICCAT, 2006). Sailfish numbers in the western North Atlantic are presently stable, but those in the eastern Atlantic appear to be decreasing (ICCAT, 2006). In the U.S. Atlantic management area, commercial harvesting of istiophorid billfish species has been prohibited since 1988. However, mortality resulting from incidental bycatch continues as multinational longline fisheries target tunas (Scombridae) and swordfish, *Xiphias gladius*, throughout the Atlantic (ICCAT, 2001; 2004).

Concerns for overexploitation and effective management of these highly migratory predators warrant a thorough understanding of their biology, ecology, and associated movement patterns. Mark-recapture studies using conventional streamer tags have assisted in defining the spatial and temporal characteristics for movement and migration of istiophorid billfish populations worldwide (Squire, 1972; Squire and Nielsen, 1983; Miyake, 1990; Pepperell, 1990a; 1990b; Scott et al., 1990; Van Der Elst, 1990; Prince et al., 2002; Hoolihan, 2003). Mather (1963), Bayliff and Holland (1986), McFarlane et al. (1990), and Prince et al. (2002) provide reviews and tagging technique information.

Conventional tagging of billfish in the United States was initiated in 1954, following development of in-water tagging techniques for large highly migratory species (Mather, 1963; Scott et al., 1990). At present, there are two major constituent-based tagging programs largely responsible for billfish mark-

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*ABSTRACT—Billfish movements relative to the International Commission for the Conservation of Atlantic Tunas management areas, as well as U.S. domestic data collection areas within the western North Atlantic basin, were investigated with mark-recapture data from 769 blue marlin,* Makaira nigricans, *961 white marlin,* Tetrapturus albidus, *and 1,801 sailfish,* Istiophorus platypterus. *Linear displacement between release and recapture locations ranged from zero (all species) to 15,744 km (mean 575, median 119, SE 44) for blue marlin, 6,523 km (mean 719, median 216, SE 33) for white marlin, and 3,845 km (mean 294, median 98, SE 13) for sailfish. In total, 2,824 (80.0%) billfish were recaptured in the same management area of release. Days at liberty ranged from zero (all species) to 4,591 (mean 619, median 409, SE 24) for blue marlin, 5,488 (mean 692, median 448, SE 22) for white marlin, and 6,568 (mean 404, median 320, SE 11) for sailfish. The proportions (per species) of visits were highest in the Caribbean area for blue marlin and white marlin, and the Florida East Coast area for sailfish. Blue marlin and sailfish were nearly identical when comparing the percent of individuals vs. the number of areas visited. Overall, white marlin visited more areas than either blue marlin or sailfish. Seasonality was evident for all species, with overall results generally reflecting the efforts of the catch and release recreational fishing sector, particularly in the western North Atlantic. This information may be practical in reducing the uncertainties in billfish stock assessments and may offer valuable insight into management consideration of time-area closure regulations to reduce bycatch mortality of Atlantic billfishes.*

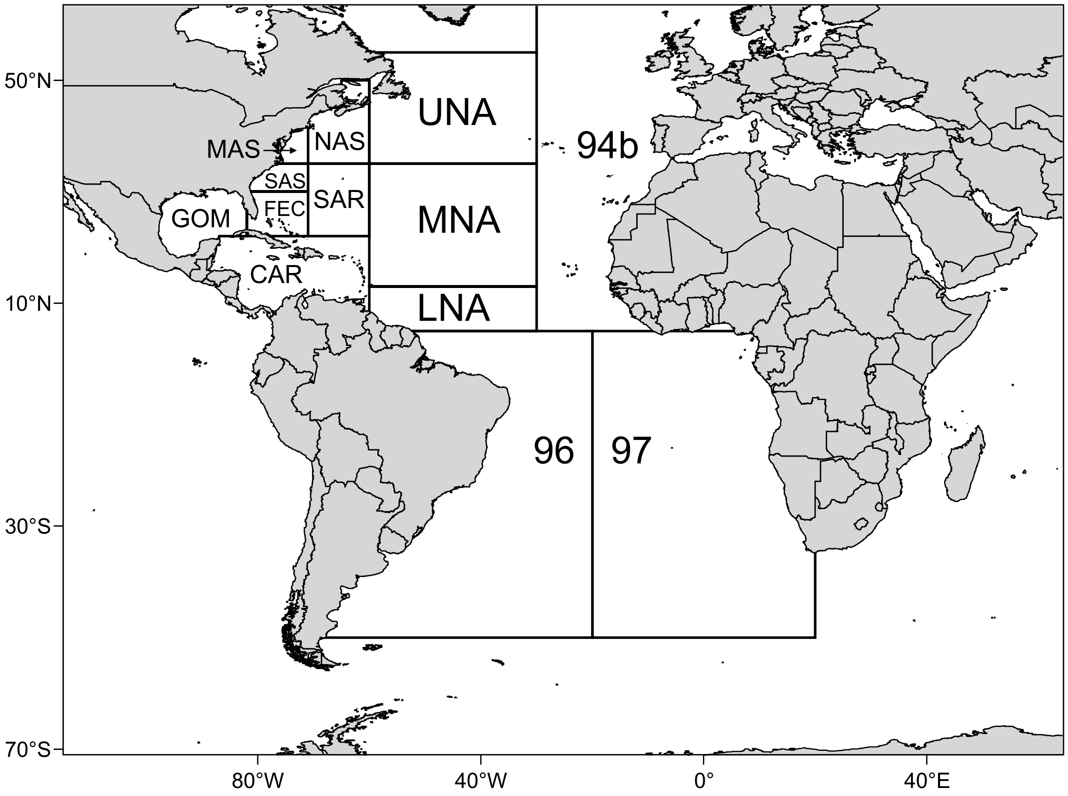


Figure 1.—ICCAT management areas and U.S. domestic submanagement areas used to evaluate movement of Atlantic billfish in this study.

recapture studies in the Atlantic–the Cooperative Tagging Center (CTC), based at NOAA's National Marine Fisheries Service (NMFS), Southeast Fisheries Science Center (Miami, Fla.), and The Billfish Foundation (TBF; Ft. Lauderdale, Fla.). Each program relies on volunteer tagging and recapture reporting by recreational and commercial fishermen.

Worldwide, from 1954 through 2005, these programs and their progenitors have documented the tagging of 266,448 istiophorid billfish. Recapture encounters have revealed Atlantic blue marlin completing transatlantic, transequatorial, and interoceanic movements, while white marlin have demonstrated transatlantic crossings (Ortiz et al., 2003). Sailfish generally remain closely associated with coastal zones having shallow continental shelves, although longline catch records do indicate a nominal presence in some mid-Atlantic offshore areas (Uozumi, 1996; Kim et al., 1998).

**Table 1.—ICCAT Atlantic billfish management areas and associated U.S. domestic sub-management areas within ICCAT boundaries (Fig. 1, 2 show maps).**

| ICCAT Management Area | U.S. Domestic Sub-management Area |
|---|---|
| 91 | GOM = Gulf of Mexico |
| 92 | MAS = Mid Atlantic State, NAS = North Atlantic States, SAS = South Atlantic States, SAR = Sargasso, FEC = Florida East Coast |
| 93 | CAR = Caribbean |
| 94a | UNA = Upper North Atlantic, MNA = Middle North Atlantic, LNA = Lower North Atlantic |
| 94b | N/a |
| 96 | N/a |
| 97 | N/a |

N/a = not applicable.

Currently, ICCAT recognizes single Atlantic-wide stocks for blue and white marlin based on mark-recapture studies and genetic evidence suggesting population mixing (ICCAT, 2006). For sailfish, separate eastern and western stocks are recognized and defined by a boundary loosely associated with the mid Atlantic Ridge (long. 40°W, North Atlantic; long. 20°W, South Atlantic); a decision based on distribution, morphology, genetic analyses, and mark-recapture data (ICCAT, 2006).

ICCAT has managed all Atlantic billfishes by separating presumed stocks along somewhat arbitrary boundaries falling within seven management areas used for statistical data collection purposes (Table 1, Fig. 1). Within some western ICCAT management areas, NMFS has further defined ten "U.S. domestic" subareas, which are targeted by

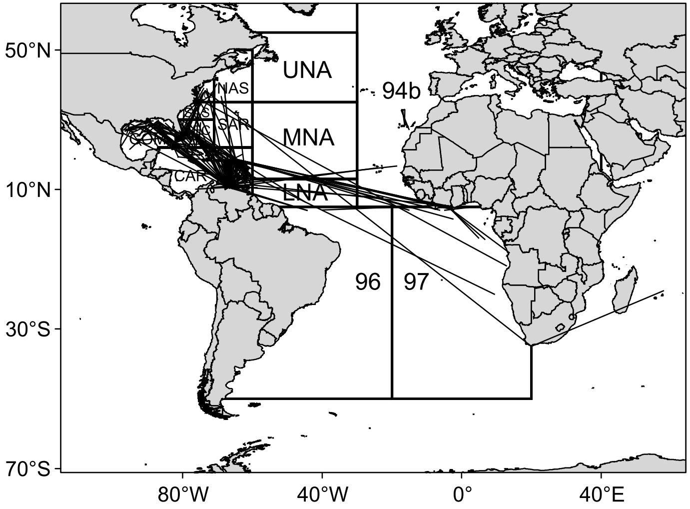
U.S. recreational and commercial fleets and have a finer spatial resolution to suit NMFS requirements for data collection (Table 1, Fig. 1). Istiophorid billfish catches are relatively “rare” events, when compared to large-sized schooling scombrids (Prince and Brown, 1991). Therefore, partitioning data sampling areas into finer-scaled subunits should enhance our comprehension of the spatial distribution and movement patterns of Atlantic billfishes.

Our study was conducted to analyze currently available CTC and TBF mark-recapture data to define and quantify movement patterns and seasonality of Atlantic blue marlin, white marlin, and sailfish in association with ICCAT management areas and U.S. domestic subareas, a relationship not addressed in previous mark-recapture reports. Using mark-recapture data to identify the temporal and spatial distribution of billfish in relation to these management areas can further our understanding of stock structure and migration characteristics that help define essential habitat. In terms of management, this information provides insight into areas of peak abundance, which in turn may lead to reducing uncertainties in stock assessments. This information will also benefit management relative to time-area closure considerations, a method proposed as a means to reduce billfish bycatch mortality (Goodyear, 1999).

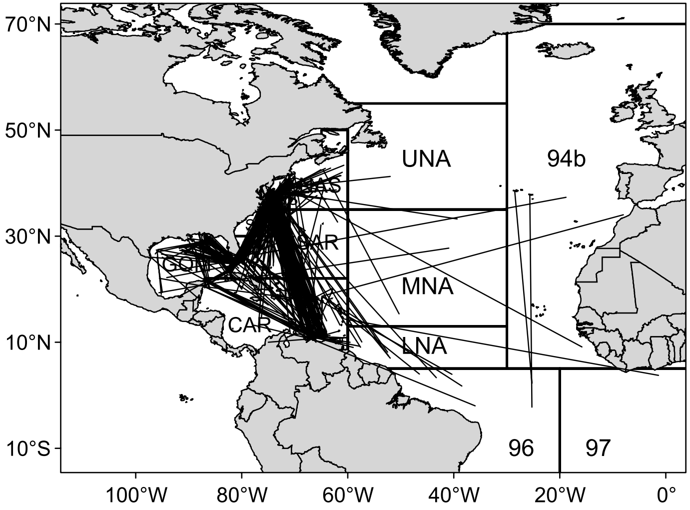
## Methods

We assessed movements of Atlantic istiophorid billfishes among ICCAT and U.S. domestic management areas (Table 2, Fig. 2) using conventional tagging data compiled during 1954–2005 for blue marlin (released = 51,473, recaptured = 769), white marlin (released = 47,662, recaptured = 961), and sailfish (released = 91,125, recaptured = 1,801). Days at liberty, displacement distance moved (km), and transboundary cross-

(a) Blue marlin (*n* = 769)



(b) White marlin (*n* = 961)



(c) Sailfish (*n* = 1801)

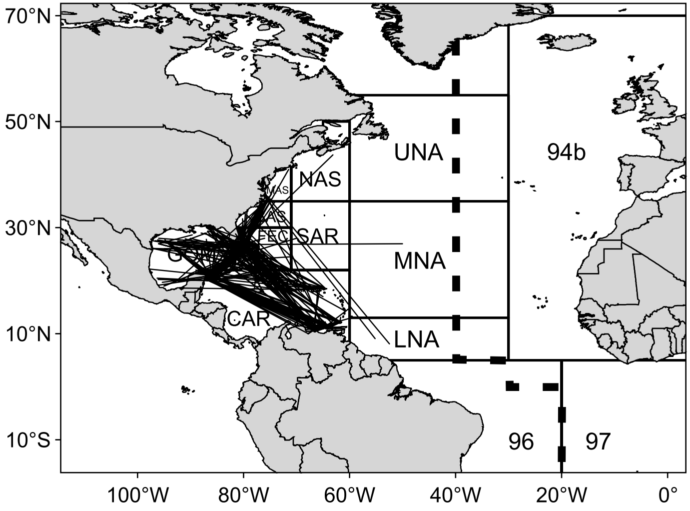


Figure 2.—Movement vectors of mark-recaptured blue marlin (a), white marlin (b), and sailfish (c), depicting shortest reasonable straight-line swimming routes. Specific indicators of release and recapture points have been omitted due to obscurity caused by multiple overlapping lines. Thick dashed line indicates east-west ICCAT stock boundary for sailfish.

**Table 2.—Releases of blue marlin, white marlin, and sailfish by management area (left column), and their respective recapture areas (top row). Dashes indicate none. No recaptures occurred in area 96.**

| Release area | Species | Total releases | Recapture Area | | | | | | | | | | | | | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | CAR | FEC | GOM | MAS | MNA | NAS | UNA | SAS | SAR | LNA | 94B | 96 | 97 | |
| CAR | Blue marlin | 28,707 | 562 | 4 | 6 | 1 | 4 | 3 | — | — | 1 | 7 | 4 | 2 | 10 | 604 |
| | White marlin | 15,086 | 412 | 1 | 7 | 5 | 1 | 2 | — | 1 | — | 3 | 1 | 3 | 1 | 437 |
| | Sailfish | 29,867 | 289 | 28 | 45 | 1 | — | 1 | — | 1 | — | — | — | — | — | 365 |
| FEC | Blue marlin | 7,108 | 18 | 17 | 12 | 3 | 1 | — | — | — | — | 1 | — | — | — | 52 |
| | White marlin | 2,871 | 9 | 2 | 7 | 11 | — | 4 | — | 1 | — | — | — | 1 | — | 35 |
| | Sailfish | 52,640 | 48 | 1,259 | 56 | 1 | — | — | — | 5 | 1 | — | — | — | — | 1,370 |
| GOM | Blue marlin | 7,084 | 7 | 5 | 47 | 1 | — | — | — | — | — | — | — | — | — | 60 |
| | White marlin | 7,526 | 10 | 7 | 63 | 10 | — | 1 | — | — | — | — | — | — | — | 91 |
| | Sailfish | 4,293 | 8 | 16 | 8 | — | — | — | — | — | — | — | — | — | — | 32 |
| MAS | Blue marlin | 1,556 | 1 | 1 | 1 | 2 | — | — | — | 4 | — | — | — | — | 1 | 10 |
| | White marlin | 18,231 | 78 | 31 | 23 | 188 | 1 | 28 | 1 | 9 | 5 | 5 | — | 1 | — | 370 |
| | Sailfish | 894 | 2 | 10 | 1 | 3 | — | — | — | — | — | 1 | — | — | — | 17 |
| MNA | Blue marlin | 117 | 1 | — | — | — | — | 1 | — | — | — | — | — | — | — | 2 |
| | White marlin | 140 | — | — | — | — | — | 1 | — | — | — | — | — | — | — | 1 |
| | Sailfish | 37 | — | — | — | — | — | — | — | — | — | — | — | — | — | 0 |
| NAS | Blue marlin | 128 | — | 1 | — | — | — | — | — | 1 | — | — | — | — | — | 2 |
| | White marlin | 1,648 | 1 | 3 | — | 7 | — | 3 | — | — | 1 | — | — | — | — | 15 |
| | Sailfish | 30 | — | — | — | — | — | — | — | — | — | — | — | — | — | 0 |
| UNA | Blue marlin | 21 | — | — | — | — | — | — | — | — | — | — | — | — | — | 0 |
| | White marlin | 43 | — | — | — | — | — | — | — | — | — | — | — | — | — | 0 |
| | Sailfish | 5 | — | — | — | — | — | — | — | — | — | — | — | — | — | 0 |
| SAS | Blue marlin | 1,083 | 4 | 5 | — | 3 | — | — | — | — | — | — | — | — | — | 12 |
| | White marlin | 876 | 2 | — | 1 | 3 | — | — | — | 1 | — | — | — | — | — | 7 |
| | Sailfish | 1,187 | 3 | 10 | 1 | 1 | — | — | — | 1 | — | 1 | — | — | — | 17 |
| SAR | Blue marlin | 1,243 | 1 | 1 | — | — | — | — | — | — | 2 | — | — | — | — | 4 |
| | White marlin | 332 | — | — | — | — | — | — | — | — | — | — | — | — | — | 0 |
| | Sailfish | 44 | — | — | — | — | — | — | — | — | — | — | — | — | — | 0 |
| LNA | Blue marlin | 67 | — | — | — | — | — | — | — | — | — | — | — | — | — | 0 |
| | White marlin | 23 | 1 | — | — | — | — | — | — | — | 1 | — | — | — | — | 2 |
| | Sailfish | 20 | — | — | — | — | — | — | — | — | — | — | — | — | — | 0 |
| 94B | Blue marlin | 3,531 | — | — | — | — | 1 | — | — | — | — | — | 16 | 1 | 1 | 19 |
| | White marlin | 673 | — | — | — | — | — | — | — | — | — | — | 1 | 2 | — | 3 |
| | Sailfish | 995 | — | — | — | — | — | — | — | — | — | — | — | — | — | 0 |
| 96 | Blue marlin | 493 | — | — | — | — | — | — | — | — | — | — | — | — | — | 0 |
| | White marlin | 204 | — | — | — | — | — | — | — | — | — | — | — | — | — | 0 |
| | Sailfish | 695 | — | — | — | — | — | — | — | — | — | — | — | — | — | 0 |
| 97 | Blue marlin | 335 | — | — | — | — | — | — | — | — | — | — | 1 | — | 2 | 3 |
| | White marlin | 9 | — | — | — | — | — | — | — | — | — | — | — | — | — | 0 |
| | Sailfish | 418 | — | — | — | — | — | — | — | — | — | — | — | — | — | 0 |

ings of ICCAT and U.S. domestic management areas were determined. Most of the releases occurred in western North Atlantic waters. A few blue marlin and white marlin were marked and released in the eastern Atlantic, but no sailfish. Distance moved was assumed to be the shortest reasonable and direct swimming path between release and recapture locations, calculated as a great-circle arc vector (Earle, 2005). Many of the vectors implied minor land crossings (e.g. Caribbean islands). We opted not to reroute these through adjacent waterways because the change in distance traveled would have been negligible, and the selection of alternate directional paths was considered too arbitrary.

Upon considering Atlantic billfish movement among the 17 management areas (ICCAT, 7; U.S., 10), our preference was to defer (when possible) to the smaller U.S. domestic submanagement areas, which provided a finer spatial scale (Table 1). Therefore, releases and recaptures occurring within U.S. domestic areas were indicated as such, while those outside U.S. domestic areas were assigned to their respective ICCAT areas. Where several U.S. domestic submanagement areas comprise an ICCAT area, that ICCAT area was ignored. This merging procedure reduced our analysis and reporting to a total of 13 management and submanagement areas (Fig. 1) that included ICCAT management areas 94b, 96, 97; and, the U.S. domestic submanagement areas for the Gulf of Mexico (GOM), Mid Atlantic States (MAS), North Atlantic States (NAS), South Atlantic States (SAS), Sargasso (SAR), Florida East Coast (FEC), Caribbean (CAR), Upper North Atlantic (UNA), Middle North Atlantic (MNA), and Lower North Atlantic (LNA).

Hereafter, we apply the term "area" to both management and submanagement areas. "Visit" is defined as release and recapture within the boundaries of a particular area. Visits (putative) were also deemed to have occurred in other management areas falling on a straight line between the release and recapture locations of each tagged fish. Notably, this imposed limitations, since actual swimming tracks are unknown. For individuals released and recaptured in the same area, a single visit was assigned. To derive seasonality, we used release and recapture visits, compiled by month and area, to determine where and when major activity occurred.

## Results

Linear displacement (km) between release and recapture locations ranged from zero (all species) to 15,744 for blue marlin, 6,523 for white marlin, and 3,845 for sailfish. The mean displacements (km) were: 575 (median 119, SE 44) for blue marlin, 719 (median 216, SE 33) for white marlin, and 294 (median 98, SE 13) for sailfish. In total, 2,824 (80.0%) individuals were recaptured in the same management area where released. Days at liberty (DAL) ranged from zero (all species) to 4,591 (12.6 yr) for blue marlin, 5,488 (15.0 yr) for white marlin, and 6,568 (17.9 yr) for sailfish (Fig. 3). The mean DAL values were: 619 (median 409, SE 24) for blue marlin, 692 (median 448, SE 22) for white marlin, and 404 (median 320, SE 11) for sailfish. The proportion of visits (per species) were highest in CAR (blue marlin and white marlin), and FEC (sailfish, Fig. 4). Blue marlin and sailfish were nearly identical when comparing the percent of individuals versus the number of areas visited (Fig. 5). Overall, white marlin visited more areas than either blue marlin or sailfish (Fig. 5).

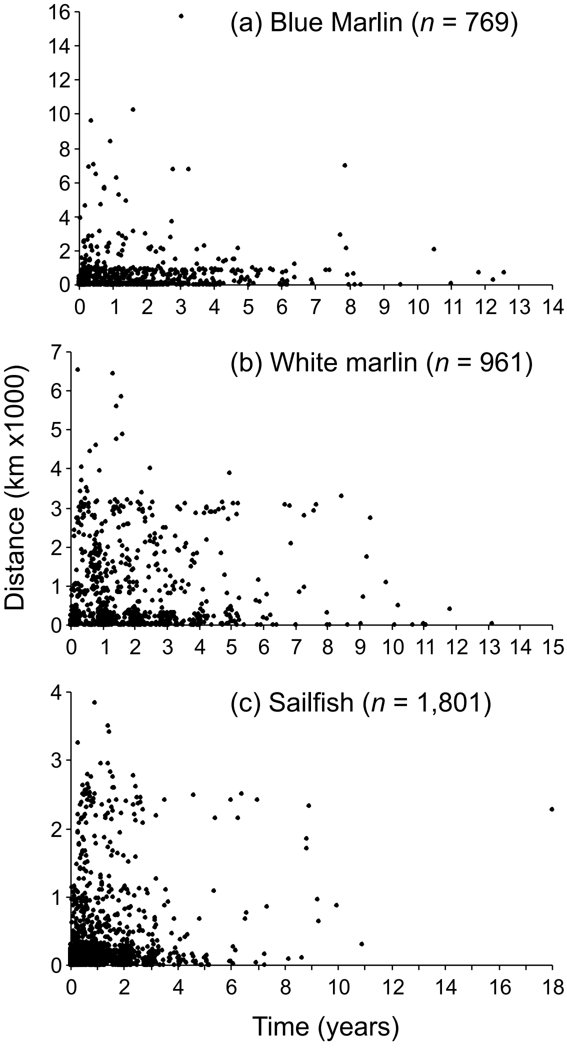


Figure 3.—Distance traveled, in relation to time at large, for mark-recaptured Atlantic blue marlin (a), white marlin (b), and sailfish (c). Distances were calculated as great-circle arc vectors between release and recapture locations.

Blue marlin were associated with all areas except UNA. The number of areas visited by individuals ranged from one to seven (mean 1.30). Of the 769 mark-recaptured blue marlin, 640 (83.2%) were released and recaptured in the same area. The ratio of single area visits to putative visits to other areas between points of release and recapture was 1.88:1. The largest proportion of activity was observed in CAR, which accounted for 64.4% of the total visits to all management or submanagement areas (Fig. 2). Moreover, CAR had the highest number of releases, accounting for 605 (78.7%) specimens. Of these, 562 (92.9%) were also recaptured in CAR. Eighteen blue marlin conducted long distance movements that were transatlantic (i.e. crossing the mid Atlantic Ridge), transequatorial, or both (Fig. 2). One exceptional individual, previously reported by Ortiz et al. (2003), released in MAS, completed transatlantic, transequatorial, and interoceanic movements before being recaptured in the Indian Ocean (Mauritius).

Visits by white marlin were recorded in all the 13 areas included in our study (Fig. 2), while a total of 640 (66.6%) were recaptured in the same area where released. The number of areas visited by individuals ranged from one to seven (mean 1.78), while the ratio of single area visits to putative visits to other areas between points of release and recapture was 0.59:1 Four submanagement areas (CAR, MAS, FEC, and SAS) accounted for 80.0% of all visits. Most of these were released or recaptured inside CAR (31.8%) and MAS (24.0%). Visits to FEC and SAS were largely attributed to transboundary crossings during travel between points of release and recapture from other areas. Two individuals made southerly transequatorial crossings terminating in area 96, representing the first documented transequatorial crossings by white marlin. One originated from CAR and the other from area 94b (Table 2, Fig. 2). These, plus movements of six additional white marlin extended south of lat. 5°N. Five individuals conducted eastward transatlantic crossings, but no interoceanic movements were observed.

Sailfish visited nine areas in total, and were absent from UNA, 94b, 96, and 97 (Fig. 2). The number of areas visited by individuals ranged from one to six (mean 1.19). A total of 1,544 (85.7%) were recaptured in the same area where released. The ratio of single area visits to putative visits to other areas between points of release and recapture was 2.58:1. The area with the greatest proportion (67.9%) of combined visits was FEC. No sailfish were observed making transequatorial, transatlantic, or interoceanic movements. Moreover, no sailfish crossed the boundary line (long. 40°W, North Atlantic; long. 20°W, South Atlantic) used by ICCAT to differentiate between eastern and western stocks. Sailfish seasonality was apparent for many individuals released in FEC during the peak abundance period (winter-spring); then subsequently recaptured (mostly during the summer) after dispersing to other areas (Fig. 6).

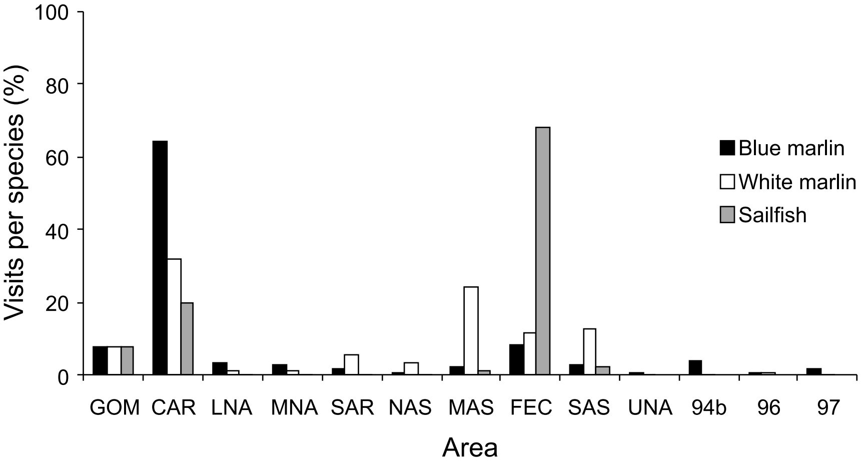


Figure 4.—Occurrence (%), by species, in management areas for blue marlin, white marlin, and sailfish, based on reasonable linear displacement between release and recapture locations.

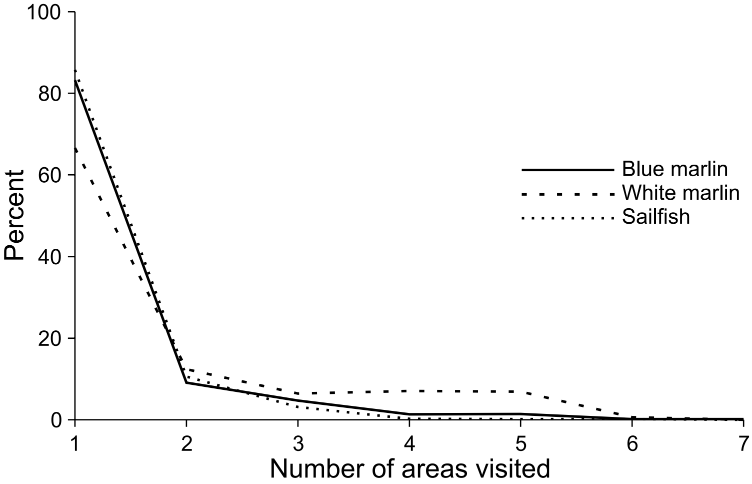


Figure 5.—Percent of visits (by species) for blue marlin, white marlin, and sailfish per management or submanagement area, based on reasonable linear displacement between release and recapture locations.

## Discussion

Much of what is currently understood about the behavior of Atlantic billfishes is derived from conventional mark-recapture efforts. Large numbers of tags deployed over a lengthy period (1954–present) have provided details of movement, range, and longevity that would have been difficult to assess otherwise. Although highly successful, conventional mark-recapture techniques have inherent characteristics that restricted the scope of analyses in our study. For instance, the absence of spatial positioning details (i.e. continuous track path) limited our interpretation of movement to direct linear displacement between points of release and recapture. In contrast, studies monitoring billfish with pop-up satellite tags (PSAT's) revealed that individuals are more likely to meander across large areas, rather than moving in a unidirectional manner (Gunn et al., 2003; Prince et al., 2006). For that reason, the number of areas visited by individuals in our study was probably underestimated.

In addition, our analyses lacked the temporal details of transboundary crossings, a problem further confounded by multiseasonal periods between release and recapture for some billfish. When assigning visit status to various management areas, we were unable to recognize multiseasonal (> 1 yr) movements for most individuals. For example, a sailfish released and recaptured in FEC after 800 DAL was assumed to have remained inside FEC for the full period. The opposite scenario (leaving FEC) is more likely, as this fishery exhibits seasonal abundance variation that is probably a reflection of migratory movement (associated with spawning and foraging behavior) between various locations. Hence, the number of visits calculated for the three species examined is undoubtedly low. Despite these shortcomings, linear tracks offered the best available information and provided estimates for the minimal number of areas encountered by an individual before recapture.

The movements of Atlantic blue marlin, white marlin, and sailfish, derived from the conventional tag recaptures, support the currently accepted ICCAT boundary definitions for delineating stock structure. For example,

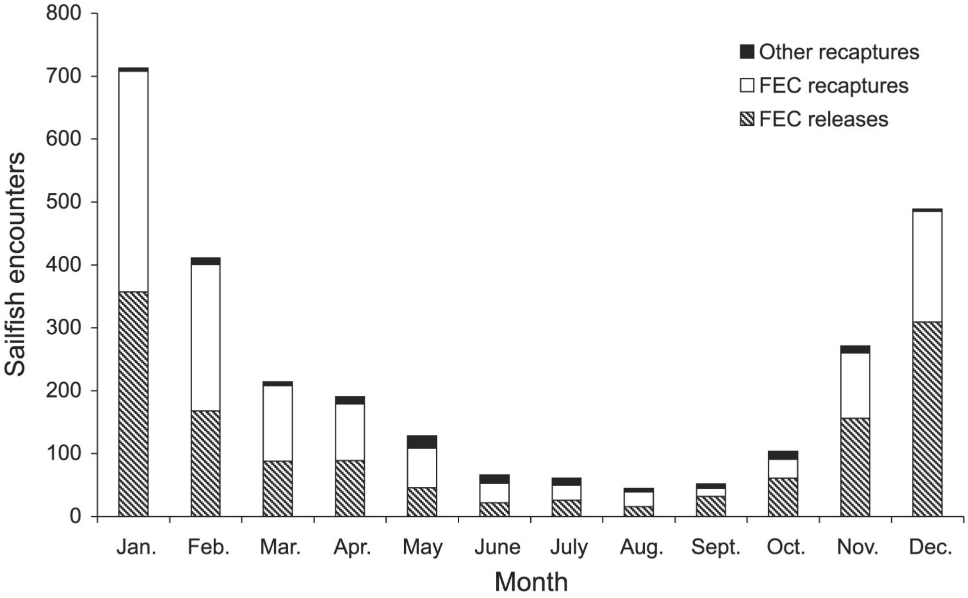


Figure 6.—Total encounters by month for sailfish released in FEC area and subsequently recaptured in FEC and other areas. Recaptures outside FEC suggest seasonal movement.

sailfish exhibited no transboundary movements across the putative boundary lines (long. 40°W, North Atlantic; long. 20°W, South Atlantic) separating eastern and western stocks. In turn, the data also supported single Atlantic-wide stocks for blue marlin and white marlin. Both species exhibited movement across lat. 5°N, the line previously used by ICCAT to differentiate between north and south stocks, although there were few of these examples. However, the spatial distribution of tagging effort throughout the Atlantic was very uneven, a factor probably contributing to the low number of examples.

The currently available information on the genetic stock structure of Atlantic blue marlin, white marlin, and sailfish suggests an absence of within-Atlantic divergence, thereby supporting the likelihood of single stocks for all three species (Graves and McDowell, 1998; 2001). Notably, a few intermingling fish per generation are capable of reducing heterogeneity to a level where genetic population structure is indiscernible (Carvalho and Hauser, 1994). So, while minimal mixing is apparent, it does not necessarily exclude the presence of multiple stocks. Analyses of additional molecular markers may reveal further stock structure.

Distinguishing the presence of multiple stocks also requires a more comprehensive understanding of Atlantic billfish movements. This is particularly relevant for the eastern and southern Atlantic regions, where tagging effort and recapture data are very sparse. Increased tagging effort in these regions is warranted. However, since there is not a well established infrastructure for recreational tag and release in eastern and southern Atlantic regions, in contrast to the western North Atlantic, the deployment of pop-up satellite archival tags may be a more efficient alternative for acquiring more comprehensive and detailed movement information.

Seasonal residency for some management areas was evident from the distribution of mark-recapture data. For white marlin, this was apparent in the MAS area (Fig. 7), where summertime aggregating behavior has been recognized since 1935 (Earle, 1940). Examination of gonads by de Sylva and Davis (1963) showed white marlin moving into MAS in late summer were in post-spawning condition. Subsequent reproductive studies indicated pronounced spawning activity taking place in CAR during April–July (Baglin, 1979; Prince et al., 2005; Arocha et al., 2007). This, plus the relatively high exchange of tagged white marlin between CAR and MAS (Fig. 2), suggests that the seasonal movement to MAS represents a post-spawning foraging migration. Whether the white marlin movements between MAS and CAR are direct, or take more circuitous routes (e.g. via GOM or mid-Atlantic routes), is unclear. However, this is a relevant research question to address. Some recaptures in GOM did occur from both MAS and CAR releases (Table 2); however, this is not necessarily representative of the total population, as movement patterns may vary between sexes, subpopulations, or age groups.

Sailfish released in the FEC exhibited seasonal variation suggesting migratory behavior. Although sailfish releases and recaptures were recorded in every month for the FEC, the majority were concentrated between late fall and early spring, clearly reflecting the seasonality of the recreational fishery. Here, it seems seasonal migration is the norm for this particular population, based on the spatial and temporal characteristics of the recaptures. For example, sailfish released in FEC, but recaptured elsewhere, were mostly recaptured during the summer and not during the period (winter–spring) normally associated with peak abundance in the FEC (Fig. 6). A similar seasonal migration timing was reported by Hoolihan (2003) for sailfish in the Arabian Gulf, using similar mark-recapture techniques.

Sailfish exhibited the maximum time at large (~ 18 yrs.) for the three species in our study, greatly exceeding the maximum age limit estimates from otolith and fin spine studies (Hedgepeth and Jolley, 1983; Prince et al., 1986; Hill et al., 1989; Wilson et al., 1991). Although mark-recapture programs are unable to estimate maximum age, they do provide useful estimates of minimal longevity.

With respect to maximum distances traveled, blue marlin exhibited more cosmopolitan behavior than the other species in our study (Fig. 2, 3). Such extraordinary great distances have also been reported for the Indo-Pacific black marlin, *Makaira indica*, a species of similar somatic size to blue marlin (Ortiz et al., 2003). However, when considering the number of areas visited, white marlin exhibited a ratio of 0.59:1 for single area visits vs. putative visits to other areas between points of release and recapture, clearly exceeding blue marlin (1.88:1) and sailfish (2.58:1). The fact that sailfish showed a higher affinity for remaining in the same area is not surprising considering their close association with coastal areas.

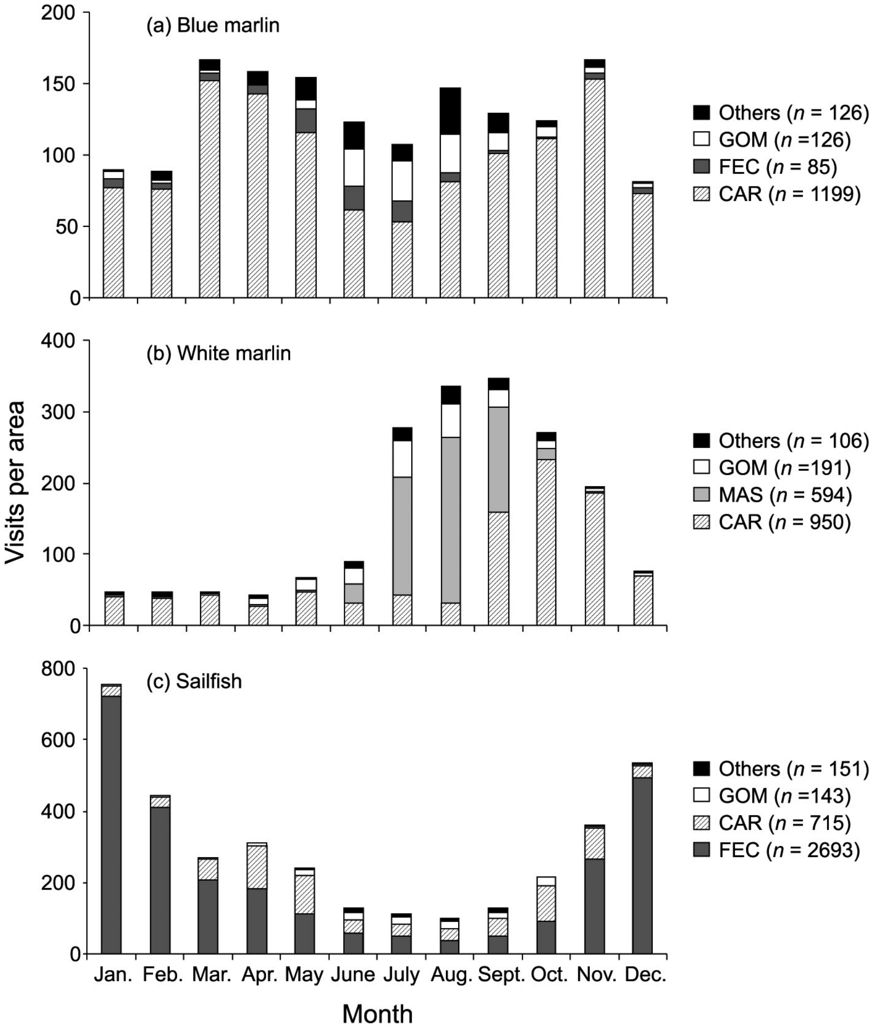


Figure 7.—Number of visits per month by mark-recaptured Atlantic blue marlin (a), white marlin (b), and sailfish (c) to ICCAT management areas and U.S. domestic submanagement areas. One "visit" was assigned to each area of release and recapture. Individuals released and recaptured in the same area were assigned a single visit only. The majority of visits occurred in the U.S. domestic sub-management areas GOM (Gulf of Mexico), FEC (Florida East Coast), MAS (Mid Atlantic States), and CAR (Caribbean). The remainder of visits to other areas were pooled in the group "others" (Table 2 shows releases and recaptures by area).

Use of time-area closures has been shown, in theory, to be a feasible method of reducing longline bycatch mortality of Atlantic billfish (Goodyear, 1999); and, may be an increasingly important approach to rebuilding depleted stocks of Atlantic billfish. The results of the present study enhance existing knowledge regarding distribution, aggregation behavior, and transboundary movements for Atlantic istiophorids that would benefit management planning for time-area closures. For example, mark-recapture information for seasonality and aggregation of white marlin, in relation to spawning activity, would be an important consideration if time-area closures were instigated to protect critical habitat for this overexploited species.

The spatial distribution of mark-recaptured Atlantic billfish presented in our study reflects the successes, and limitations, of a constituent based conventional tagging program (Ortiz et al., 2003). Releases primarily occurred in the western North Atlantic, reflecting the long-term popularity of recreational tag and release fishing in the domestic U.S. submanagement areas. Additionally, nearly all of the mark-release events took place near coastlines, a factor influenced by vessel limitations and trip durations typical of the recreational fishery. Given these limitations, it should be noted that the recreational billfish fishery of the western North Atlantic is extensive and long standing. As such, this suggests that the conventional tagging data offers a reasonable representation of the temporal and spatial coastal abundance for these species. In other words, it is unlikely that the seasonal or geographical occurrence of large numbers of billfish have eluded the recreational fleet.

The CTC and TBF conventional tagging programs have provided useful information about Atlantic billfish movement and migration. At the same time, these programs have formed an association between scientists and recreational fishermen, providing valuable information on local fisheries. Shortcomings in the conventional tagging programs have highlighted two points warranting further investigation. Firstly, enlarging the scope of the tagging effort to include a more comprehensive coverage of the eastern and southern Atlantic billfish habitat is needed. This may present a problem, as these areas lack the active catch and release recreational fisheries that are so prevalent in the western North Atlantic. ICCAT's enhanced research program for billfish, originally developed in 1986 (Prince et al., 1987), included an objective to accomplish more mark-recapture activities in the East Atlantic. However, progress on this objective has been slow to develop.

Secondly, the obvious lack of spatial positioning during DAL when using conventional tags prevents an accurate assessment of track path, or management area usage. Both of these concerns can be ameliorated with well designed PSAT studies. PSAT units can provide track path estimates based on light level geolocation algorithms, thus providing a more realistic portrayal of billfish movement tracks (Arnold and Dewar, 2001). Because PSAT's are "fisheries independent" (i.e. do not require recapture), far fewer are needed in comparison to conventional tags.

The efficacy of using PSAT's to determine movements of large pelagic species is well established (for review, see Arnold and Dewar, 2001). One example is the recent work of Prince et al. (2006), whereby PSAT data from 41 sailfish were used to describe transboundary movements on the Pacific side of central America. However, PSAT's have their own inherent drawbacks and are unlikely to match some of the larger spatial and temporal displacements divulged by conventional tagging. Presently, PSAT's are costly, and they have not proved suitable for long-term monitoring of multi-seasonal behavior. Many of the more interesting long-term displacements, revealed with conventional tags (Fig. 2), would be unobtainable using pop-up satellite tags. We suggest that greater advances will come about if billfish PSAT studies are integrated within the domain of conventional tagging programs, so their respective datasets can complement one another.

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