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Large Pelagic Fishes in the Wider Caribbean and Northwest Atlantic Ocean: Movement Patterns Determined from Conventional and Electronic Tagging

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LARGE PELAGIC FISHES IN THE WIDER CARIBBEAN AND NORTHWEST ATLANTIC OCEAN: MOVEMENT PATTERNS DETERMINED FROM CONVENTIONAL AND ELECTRONIC TAGGING

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ABSTRACT Conventional tagging data has documented long distance movements (including trans-Atlantic movements) in blue marlin (*Makaira nigricans*) and yellowfin tuna (*Thunnus albacares*) within the Atlantic. Swordfish (*Xiphius gladius*) have also been shown to move substantial distances, although primarily in a north-south direction. There is, however, a paucity of data for wahoo (*Acanthocybium solandri*). In the past several years, electronic archival (i.e., data recording) tags have significantly advanced our understanding of the behavior and movement patterns of large pelagic fishes. Data from electronic archival tags have generally corroborated conventional tagging data with respect to long distance movements, as well as the daily vertical movement patterns previously obtained through acoustic telemetry. Taken together, it is now possible to define "habitat envelopes" for pelagic species and to correct nominal catch rates for changes in gear vulnerability due to differences in gear targeting. In general, there is a broad spectrum of vertical movement patterns: blue marlin and yellowfin tuna generally remain within the uniform temperature surface layer (although blue marlin occasionally descend to below 300 m), wahoo have less vertical range and appear to remain above 50 m most of the time, whereas swordfish mirror the vertical movements of the organisms of the deep-scattering layer remaining within about 20–30 m of the surface at night but descending to 700–800 m during the day. Tagging data demonstrates that many large pelagic fish species move through the waters of other jurisdictions thus requiring a regional and international approach to assessment and management. The primary organization which undertakes this function in the Atlantic Ocean is the International Commission for the Conservation of Atlantic Tunas (ICCAT), which is responsible for the assessment and management of tunas, swordfish and billfishes.

INTRODUCTION

A world review of highly migratory species and straddling stocks (FAO 1994) provided a summary of the major fisheries for pelagic species in the world's oceans and their status. In the Atlantic, 5 species of tunas, billfishes and swordfish are listed as the principal species taken by pelagic longline fishing fleets. In the western North Atlantic, the majority of fishing effort for target species is by longliners while surface fisheries (purseseiners and baitboats) predominate in the eastern Atlantic (ICCAT 2006). In the wider Caribbean (including Bermuda), the majority of large pelagic species are taken by artisanal fleets principally by trolling. Despite their economic importance, relatively little is still known about the migratory patterns of the majority of these pelagic species. This lack of knowledge provided the impetus for tagging programs to be instituted to elucidate movement patterns. Understanding movement patterns is an important component of regional and international fisheries management programs.

The first tagging program in the Atlantic (the Cooperative Game Fish Tagging Program) was started in the USA in 1954 at Woods Hole Oceanographic Institute. An account of the origins and history of this program is provided by Scott et al. (1990). The program involves both recreational and commercial fishermen as well as scientists for tag release and recovery activities of a wide range of fish species (Ortiz et al. 2003). An examination of the recapture results from this tagging program (now called the Cooperative Tagging Center (CTC) based at the National Marine Fisheries Service (NMFS) Southeast Fisheries Science Center (SEFSC) in Miami, Florida) indicate that many large pelagic fish species are highly migratory and can make trans-Atlantic crossings. This has been demonstrated in several species including blue marlin (*Makaira nigricans*) (Ortiz et al. 2003) and yellowfin tuna (*Thunnus albacares*) (E. Prince, pers. comm., NMFS, Miami, FL). Tagging effort for blue marlin has been concentrated in the NW Atlantic and, since the 1980s, there has been a growing conservation ethic in the recreational billfish fishery which has resulted in increased tagging effort. The Billfish Foundation (TBF) has actively promoted tagging as part of catch and release fishing for billfish since 1990 (Ortiz et al. 2003).

In recent years, the development of sophisticated electronic tags has helped reveal the migration tracks of the species, the speed at which they move, and vertical habitat use. The first dedicated electronic tagging program for large pelagics was directed at bluefin tuna (*Thunnus thynnus*), a highly important species in the North Atlantic and Mediterranean Sea due to strong market demand for sushi-grade tuna. The results of multi-year tagging of bluefin
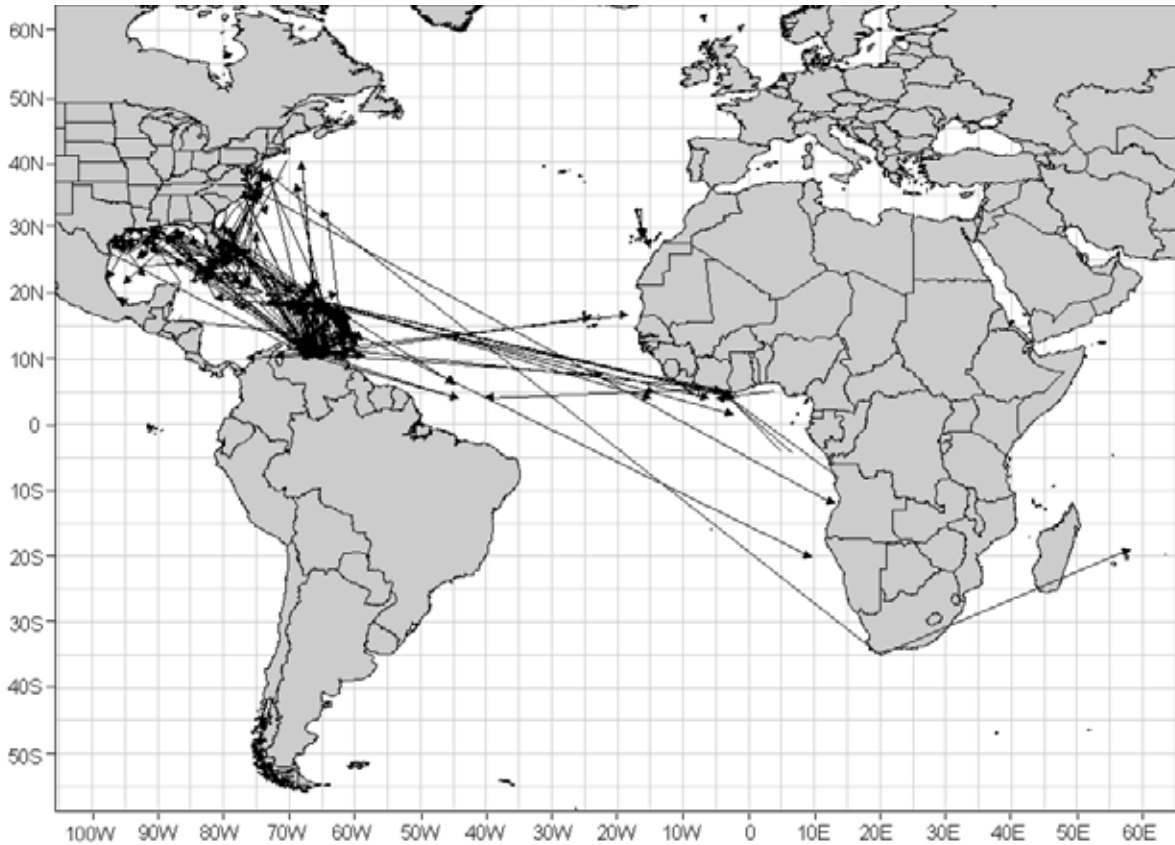
Figure 1. Movement vectors of conventionally-tagged blue marlin (*Makaira nigricans*) in the North Atlantic from 1974-2006. Note number of trans-Atlantic crossings.

tuna have documented numerous trans-Atlantic crossings (Block et al. 2001). The deployment of PSATs (Pop-up Satellite Archival Tags) on blue marlin in the Northwestern Atlantic, primarily through the Adopt-A-Billfish Program, started in 1999 (E. Prince, pers. comm., NMFS, Miami, FL) has revealed extensive movements in relatively short time periods. The tagging of other large pelagic species with PSATs has also been undertaken in the past few years. For example, Sedberry and Loefer (2001) deployed PSAT tags on swordfish (*Xiphius gladius*) off the coast of South Carolina and more recently, Thiesen and Baldwin (In press) PSAT-tagged wahoo (*Acanthocybium solandri*) in the Bahamas. To date, results from these deployments also indicate extensive movements. I have chosen 4 species from 3 separate families, common in the NW Atlantic, to illustrate the scale of movements documented in large pelagic species:

1) Blue marlin—primarily a target species of the recreational fishery in the Western Atlantic but with commercial (artisanal) fisheries off West Africa.

2) Swordfish—exclusively a commercial species taken Atlantic-wide by longliners. Harpoon fisheries for this species have been in decline for some years.

3) Yellowfin tuna—a commercial species Atlantic-wide but with considerable recreational importance in the NW Atlantic.

4) Wahoo—a commercial species in the wider Caribbean but with growing recreational significance in the NW Atlantic.

The focus of my paper is regional, emphasizing data from the wider Caribbean and the Gulf of Mexico (GOM). Thus, references to tagging studies in other oceans are limited. I will examine movement patterns, as revealed by both conventional and electronic tagging, at 2 geographic scales: 1) NW Atlantic and 2) around Bermuda.

In particular, I will attempt to illustrate how these movement patterns provide strong evidence for connectivity between different parts of the Atlantic and why this information is important for regional and international fishery management agencies. I will also illustrate how the data from PSATs has provided invaluable insights into vertical habitat use by blue marlin and swordfish.
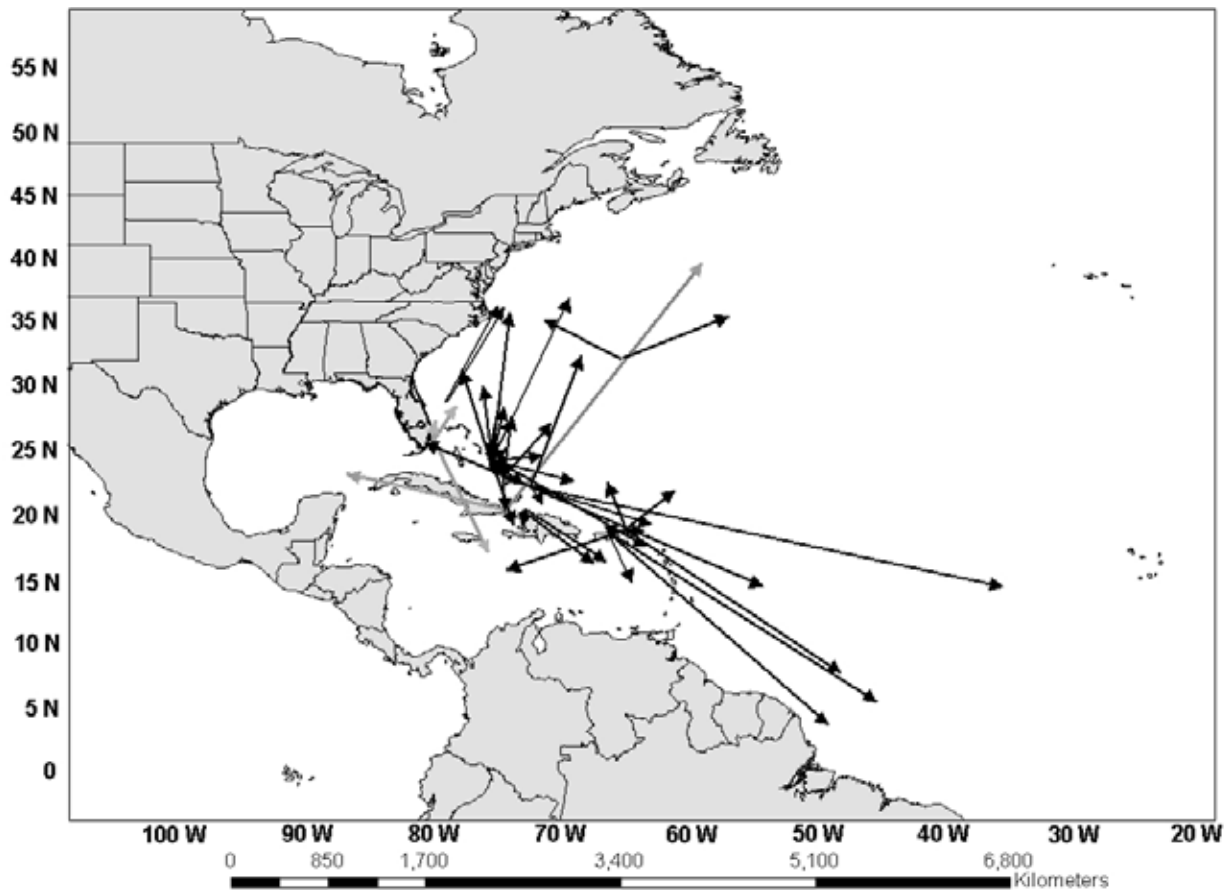
Figure 2. Movement vectors of blue marlin (*Makaira nigricans*) **[dark vectors] and swordfish** (*Xiphius gladius*) **[pale vectors] tagged with Pop-up Satellite Archival Tags (PSATs) in the western North Atlantic from 2002–2006.**

RESULTS

Blue marlin

An examination of the databases (CTC and TBF) of conventional tag deployments on blue marlin indicates that the majority of tagging effort has taken place in the western Atlantic (Ortiz et al. 2003). There have been a total of 52,185 blue marlin releases and 769 recaptures as of the end of calendar 2005, with 18 of these recaptures demonstrating trans-Atlantic movements (E. Prince, pers. comm., NMFS, Miami, FL). Tag recapture rates for blue marlin are generally < 1% throughout the world's oceans; the specific recapture rates for the NW Atlantic are: CTC = 0.91%, TBF =1.74% (Ortiz et al. 2003). The dominant movement patterns for recaptured fish are primarily from west to east and, as blue marlin favor tropical waters, these movements are primarily in the tropical Atlantic (Figure 1). The longest documented movement of a blue marlin (1,108 d at large) was from Delaware, USA to Mauritius in the Indian Ocean (Figure 1), a distance of 14,893 km (Ortiz et al. 2003).

The first PSAT tagging of blue marlin in the NW Atlantic took place in the recreational fishery in Bermuda in 1999 (Luckhurst, pers. obser.). Eight of the 9 tagged blue marlin reported their positions after 5 days and moved distances ranging from 73.8–248.6 km but in all compass directions (Graves et al. 2002). Longer deployments of PSAT tags on blue marlin from commercial longliners in the NW Atlantic demonstrated substantial movement distances (Kerstetter et al. 2003). Two blue marlin tagged with PSATs moved distances of 985 km and 1,968 km in 30 d. During the period 2002–2003, a total of 66 PSATs were deployed (E. Prince, pers. comm., NMFS, Miami, FL), primarily from recreational fishing vessels in the wider Caribbean. These deployments resulted in long distance movements by a number of specimens (Figure 2). The longest movement vector of 4,606 km was of a blue marlin (68 kg) tagged in the Turks and Caicos Islands in 2003 which moved this distance to the eastern tropical Atlantic in 91 d (Figure 3). A detailed analysis of the satellite-transmitted data for this fish indicates that over 40% of its time was spent in the top 25 m of the water column although it made several dives to below 300 m depth
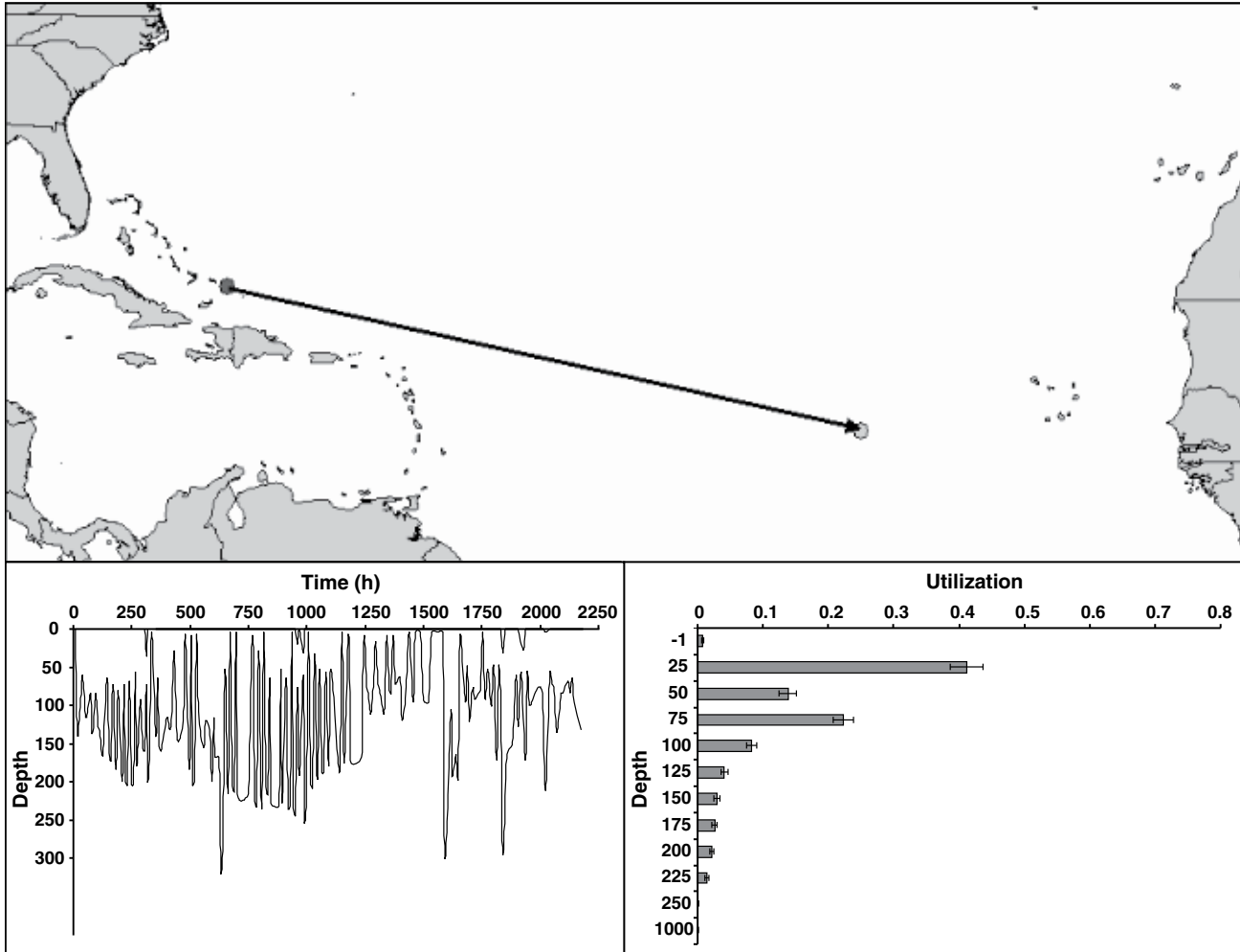
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Figure 3. Movement vector of single blue marlin (*Makaira nigricans*), **estimated at 68 kg, tagged with a PSAT, which moved 4,606 km in 91 d. From insets note that the largest proportion of time** ($\bar{x} \pm s_{\bar{x}}$) **is spent in < 100 m depth.**

(Figure 3). Several other blue marlin tagged in the northern Caribbean moved considerable distances to an area off the coast of Brazil (Figure 3).

Swordfish

Conventional tagging of swordfish has taken place since the late 1950s due to its commercial importance and virtually all of the tagging effort has occurred in the western Atlantic and GOM. As of the end of 2006, a total of 10,767 swordfish have been conventionally tagged with 395 recaptures (E. Prince, pers. comm., NMFS, Miami, FL). The predominant movement pattern of tag-recaptured swordfish in the western Atlantic appears to be north–south (Figure 4) although some east–west movement is also evident, including several trans-Atlantic movements. A swordfish conventionally-tagged from a longliner in the NW Atlantic in July 1997 moved in a southerly direction > 900 km before being recaptured off Bermuda in

December, < 6 months later (Luckhurst, pers. obser.; E. Prince, pers. comm., NMFS, Miami, FL).

A relatively small number of PSAT tags have been deployed on swordfish in the NW Atlantic (N < 40, E. Prince, pers. comm., NMFS, Miami, FL). The movement vector of a swordfish (59 kg) tagged with a PSAT tag in the Windward Passage in 2004, indicates a northerly movement of 2,629 km in 62 d (Figure 5). Throughout the monitoring period, this fish made regular dives to 700–800 m depth during daylight hours (Figure 5). During nocturnal hours, mean depth was much shallower but brief, regular periods were spent at the surface (Figure 5).

Yellowfin tuna

In common with blue marlin and swordfish, the great majority of conventional tagging effort has occurred in the western Atlantic, primarily off the eastern seaboard of the US and, to a lesser extent, in the GOM. There have
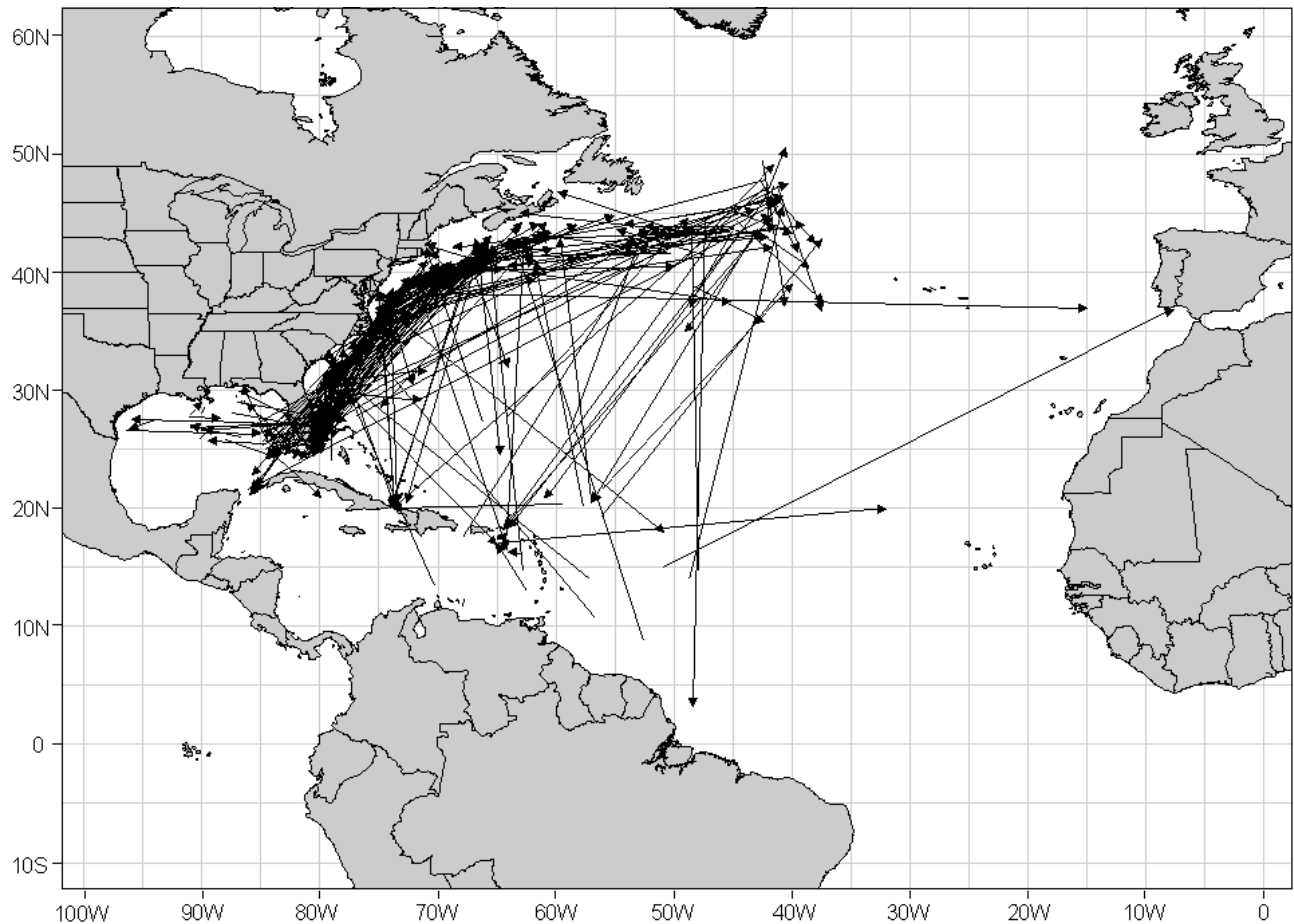
Figure 4. Movement vectors of conventionally-tagged swordfish (*Xiphius gladius*) in the North Atlantic from the CTC database until end of 2006. Note predominantly north-south movements.

been 10, 448 yellowfin conventionally-tagged up until the end of 2006 (E. Prince, pers. comm., NMFS, Miami, FL). Tag-recapture results indicate a strong west to east movement from most tagging locations to the vicinity of the Gulf of Guinea off west Africa (see Prince and Goodyear, this volume, their Figure 3). To a lesser extent, there was also southerly movement from off the US eastern seaboard toward the Caribbean and also within the GOM. Despite this strong migratory tendency, acoustic tagging of yellowfin around oil platforms in the GOM has demonstrated that yellowfin can be resident or seasonally resident within a limited area (Edwards and Sulak 2006).

An examination of movements of conventionally-tagged fish on a limited geographic scale, e.g., around Bermuda, can provide useful insights. To date, there have been a total of 574 yellowfin tuna tagged in Bermuda coastal waters. There have been 91 recaptures of Bermuda-tagged fish for an overall recapture rate of 15.9%. However, only 3 recaptures (3.3%) were outside Bermuda waters (E. Prince, pers. comm., NMFS, Miami, FL). Two recaptures

were off the coast of Puerto Rico and the other was near Cape Hatteras (Figure 6). These 3 fish moved distances of 1,000–1,300 km illustrating connectivity of Bermuda with the larger NW Atlantic region.

An analysis of yellowfin tuna tag-recapture patterns around Bermuda can provide estimates of residence time around the Bermuda Seamount and insights into possible movement patterns. A selection of Bermuda recapture data from the CTC database (Table 1) illustrates the utility of using conventional tagging data. Short term periods at liberty provide an estimate of residence times and longer term periods (on the order of a year) suggest the use of the Bermuda Seamount on a seasonal migratory route in the NW Atlantic (Table 1).

Wahoo

Little is known about wahoo movement patterns in the western North Atlantic Ocean because few tagging programs have targeted wahoo. A program in the SE Caribbean tagged a total of 250 fish but there have been
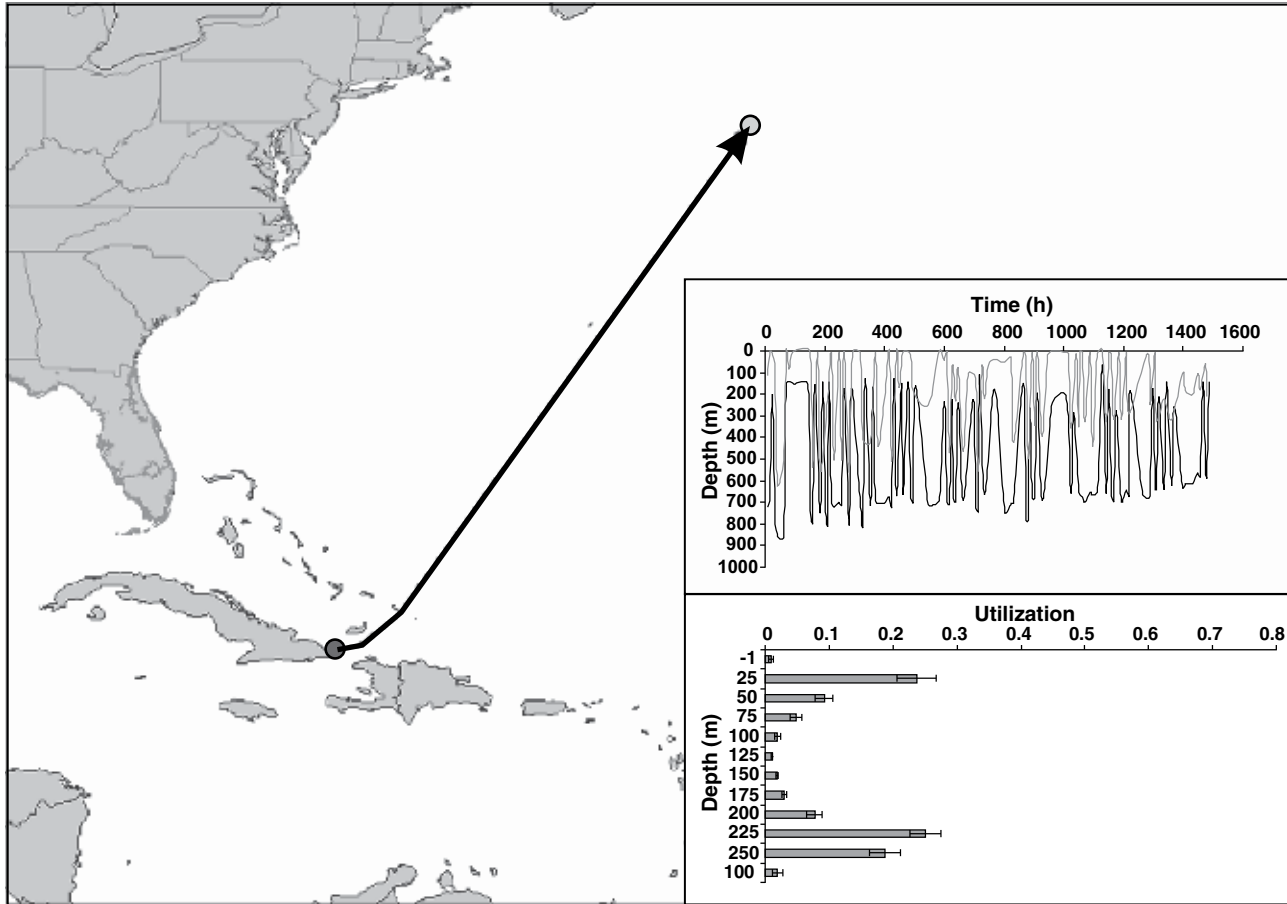
Figure 5. Movement vector of single swordfish (*Xiphius gladius*) estimated at 59 kg, tagged with a PSAT, which moved 2,629 km in 62 d. Inset: Note the number of dives to depths of 700 m or greater and bimodal distribution of time-at-depth (mean ± $s_{\bar{x}}$) reflecting diurnal vertical migration.

no recaptures to date (Singh-Renton 2006). Similarly, the CTC database indicates that a total of 159 wahoo have been tagged but there have also been no recaptures (E. Prince, pers. comm., NMFS, Miami, FL). A small-scale tagging program ($N = 15$) in Bermuda, using a specially-designed tagging cradle for wahoo (Nash et al. 2002), resulted in one recapture after 10 months at liberty. The recapture location was at Challenger Bank, a minimum distance of 65 km from the release site; however, this single recapture provides little insight into the distance actually moved during the time at liberty.

Tagging of wahoo with PSATs has begun only recently and initial results from 3 tagged fish in the NW Atlantic suggest that wahoo move considerable distances (Thiesen and Baldwin In press). The movement patterns of these tagged fish appeared to be largely north-south movements in relation to the Gulf Stream. One tagged fish moved 580 km in 54 d. Satellite-transmitted data from another wahoo, moving along the western edge of the Gulf Stream, indicated that it spent most of its time in the depth range 20–120 m, with almost daily trips to the surface and regular dives to almost 200 m. However, it rarely went below this depth. It also reportedly stayed in a relatively narrow temperature range (20–25° C).

DISCUSSION

The movement data presented here provide convincing evidence that the 4 large pelagic species illustrated in this paper all undertake extensive movements or migrations. Both blue marlin and yellowfin tuna are shown to commonly make trans-Atlantic movements. Similar long-distance movements are also documented for swordfish. The database for wahoo tagging is limited but recent results appear to suggest extensive movements as well (Thiesen and Baldwin In press). The movement patterns of these species demonstrate connectivity between different regions of the Atlantic Ocean.

The scale of demographic connectivity in pelagic fish populations is generally not well known but important
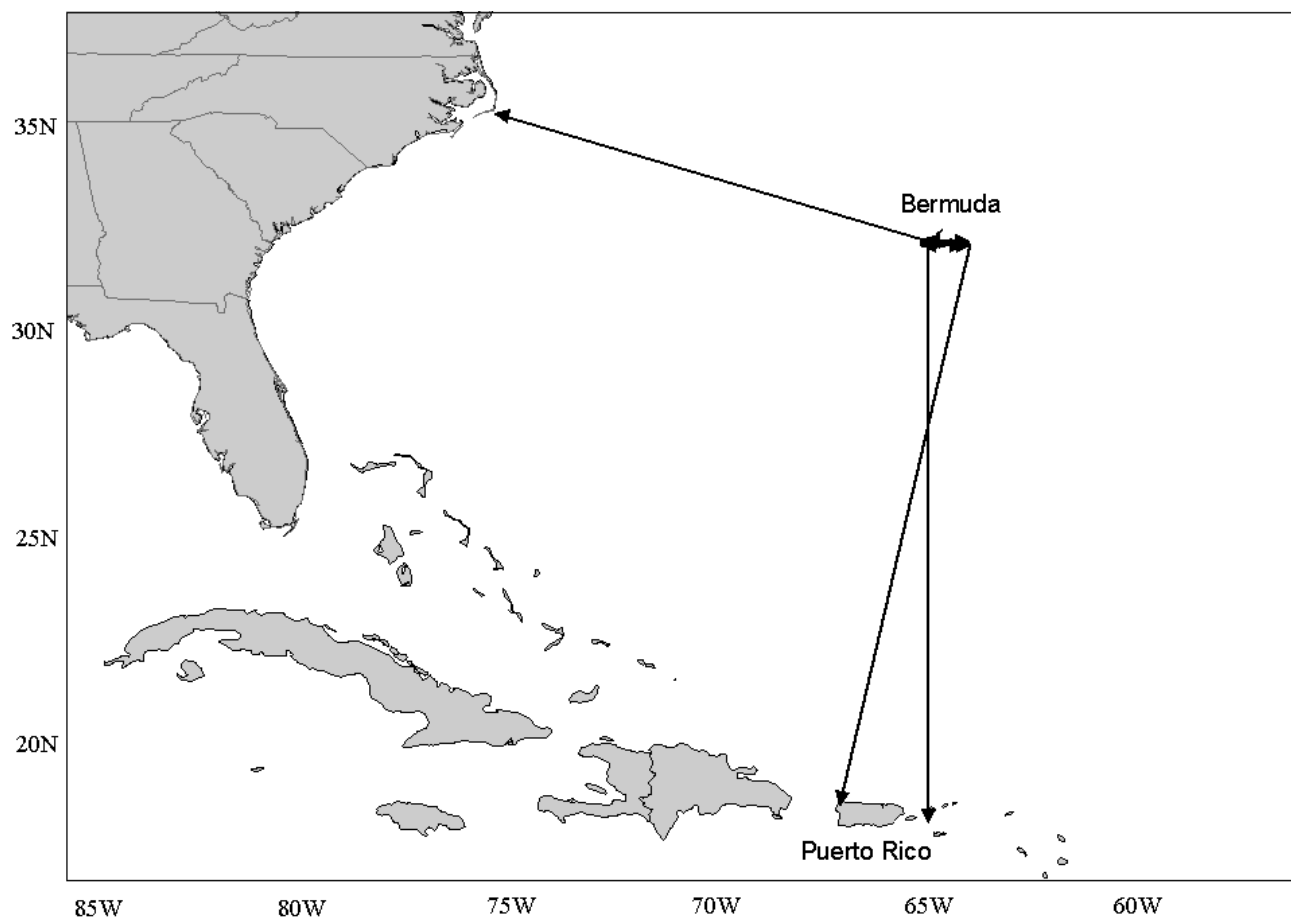
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Figure 6. Movement vectors of three conventionally-tagged Bermuda yellowfin tuna (*Thunnus albacares*) recaptured outside Bermuda coastal waters demonstrating demographic connectivity with the wider Caribbean and US eastern seaboard. Distances moved were between 1,000 and 1,300 km.

insights may be gained using metapopulation concepts which examine changes in population size, age structure and genetic structure (Kritzer and Sale 2004). A number of factors such as larval dispersal potential (Cowen et al. 2006) and spawning site fidelity (Fromentin and Powers 2005) must be evaluated in determining demographic connectivity. The demonstrated scale of movement of the species presented here confirms the need for the management of these highly migratory species by international fishery management agencies. The ICCAT currently regulates the fisheries for pelagic species for its 43 members (contracting parties) having management measures in place for blue marlin, yellowfin tuna and swordfish. However, wahoo, which is included in the small tunas category at ICCAT, is not currently managed. The US is the only jurisdiction which currently has a management plan for wahoo (SAFMC 2004).

Blue marlin

The results of conventional tagging of blue marlin clearly demonstrate that they make trans-Atlantic and trans-equatorial movements. One fish made an inter-ocean movement from the Atlantic to the Indian Ocean (Ortiz et al. 2003). The advent of electronic tagging of blue marlin, particularly since 1999, has provided a wealth of data which has allowed insights into aspects of habitat use which were not possible with conventional tag-recapture data. Kerstetter et al. (2003) found that 2 blue marlin tagged with 30-d PSATs in the NW Atlantic spent the great majority of their time (65.4% and 81.5%) in the upper 5 m of the water column. The integration of detailed temperature-depth-time data from PSAT tagging allows for the definition of "habitat envelopes" (Luo et al. 2006). The use of "habitat envelopes" in conjunction with studies of fishing gear behavior, e.g., pelagic longlines (Luo et al. 2006), can provide important insights into the interaction between fish and fishing gear. This can lead to modifications of fishing strategy and gear deployment which may

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TABLE 1

Selection of tag-recapture results of yellowfin tuna (*Thunnus albacares*) from the Cooperative Tagging Center database, Miami. All data presented are for fish tagged and recaptured at Challenger Bank, Bermuda and indicate the inferences which could be drawn from the days-at-liberty.

Tag No.	Tagging Date	Recapture Date	Days-at-liberty	Inference
R294318	24-May-93	8-Jun-93	15	residence time
R199052	24-May-93	9-Jun-93	16	residence time
R199053	24-May-93	11-Jun-93	18	residence time
R199054	24-May-93	19-Jun-93	26	residence time
R120387	26-May-93	8-Jul-93	43	residence time
R058096	3-Jul-83	8-Jun-84	340	migration route
R058100	3-Jul-83	5-Jul-84	367	migration route
R058102	3-Jul-83	17-Jul-84	379	migration route
R058154	4-Jul-83	19-Jul-84	380	migration route
R058151	4-Jul-83	28-Jul-84	389	migration route
R018715	9-Jul-83	6-Jun-84	332	migration route

help to reduce the level of fishing mortality on by-catch species such as blue marlin.

Swordfish

The reason for the predominantly north-south movements of swordfish in the western Atlantic as generated from conventional tagging is unclear, although it may be associated with seasonal changes in oceanographic productivity. However, it is known that higher densities of swordfish are associated with oceanographic features such as thermal boundaries between water masses where prey species may be more concentrated. These oceanographic features are dynamic systems with low levels of predictability. Sedberry and Loefer (2001) demonstrated that swordfish PSAT-tagged ($N = 29$) in the vicinity of the Charleston Bump moved considerable distances mainly in an E–NE direction. The longest movement documented was 2,497 km. They also determined that these tagged fish were often associated with offshore seamounts or the thermal boundaries of the Gulf Stream. Takahashi et al. (2003) deduced the movements of a PSAT-tagged swordfish off the east coast of Japan by comparing water temperature data from the archival tag with oceanographic data. They showed that the fish moved in a cyclic seasonal pattern between summer and winter periods. In contrast to horizontal movements, tracking vertical movements in the water column generally has more precision as water column structure is more predictable. The pattern of vertical habitat use exhibited by swordfish derived from PSAT tagging indicates that swordfish spend the majority of nocturnal hours in warmer, surface waters where they are vulnerable to longline fisheries. During daylight

hours, they make dives to 700–800 m on a regular basis. A swordfish tagged off Japan made a dive to a maximum depth of over 900 m (Takahashi et al. 2003). The bimodal pattern of vertical habitat use is believed to be associated with diurnal vertical migration which is probably linked to feeding periodicity. It is also linked to metabolic needs as water temperatures at depth are cold and swordfish are thought to spend nocturnal hours in surface waters to warm up after excursions to depth.

Yellowfin tuna

Conventional tagging of yellowfin tuna, since the early 1960s, has been conducted in the western Atlantic, primarily by recreational fishermen (E. Prince, pers. comm., NMFS, Miami, FL). Although recreational fishing effort has increased over the past few decades, yellowfin tuna are taken mainly by industrial fisheries. Tag recaptures usually reflect where the fishery is most intensive and, in the Atlantic, the major fishery is the purse seine fishery in the Gulf of Guinea (ICCAT 2006). This is the primary spawning ground for yellowfin tuna but other spawning grounds have been identified in the GOM and the SE Caribbean Sea. This largely accounts for the concentration of movement vectors to these areas (Prince and Goodyear, this volume, their Figure 3).

The tag-recapture patterns of yellowfin tuna around Bermuda can provide estimates of residence time around the Bermuda Seamount and possible movement patterns (Luckhurst et al. 2001). The 3 recaptures outside Bermuda waters (2 off Puerto Rico, one off Cape Hatteras) demonstrate regional demographic connectivity between Bermuda and other areas of the NW Atlantic. These move-

ment vectors confirm the need for regional and international management regimes for such a highly migratory species as yellowfin tuna.

Atlantic patterns of movement in yellowfin tuna are similar to those noted in the Pacific. For example, acoustic tagging of large, adult yellowfin off Hawaii (Brill et al. 1999) evaluated both vertical and horizontal movements. These fish spent 60–80% of their time in the surface layer (< 100 m) and maximum depth appeared to be limited by water temperatures 8° C colder than the surface layer. Horizontal movements were restricted to within 18.5 km of the coast and fish were often associated with floating objects. Acoustical tracking of yellowfin tuna off California (Block et al. 1997) indicated that the fish spent the majority of their time above the thermocline and only made short, periodic dives to deeper, colder water. However, as these fish were only tracked for 2–3 d. it was not possible to make a meaningful assessment of horizontal movements. Klimley at al. (2003) monitored the presence of yellowfin around a seamount in the Gulf of California using acoustical tags and found that 6 of 23 tagged fish were present for periods of 2–6 weeks. Five other tagged fish were seasonally resident at the seamount or were detected regularly for periods of 6–18 months.

Wahoo

Wahoo is one of the most important commercial species in the wider Caribbean but it has attained increased recreational significance throughout the NW Atlantic in recent years. Little is known about wahoo movement patterns in the western North Atlantic but adult wahoo appear to engage in long distance, seasonal movements (Oxenford et al. 2003) apparently extending into cooler waters in the summer months. They almost certainly move across the Exclusive Economic Zones of a number of countries in the Caribbean region.

There are virtually no data with regard to wahoo tag-recaptures in the NW Atlantic. A tagging program in the SE Caribbean (250 tagged fish) produced no recaptures whereas there was one recapture out of 15 tagged fish in Bermuda. However, it is unknown if this tagged wahoo remained in Bermuda waters during its time at liberty (10 months) or moved away and then returned to Bermuda on a seasonal migratory route (Luckhurst et al. 2001). With such limited data, it is not possible to resolve whether this fish was a Bermuda resident or was on an annual migration past Bermuda. It is probable that wahoo found in Bermuda waters are a combination of a resident population with annual pulses of migrating fish using the Bermuda seamount as a feeding station. The strong seasonality of landings of wahoo in Bermuda with peaks in Spring and Fall

(Luckhurst and Trott 2000) tends to support the concept of an annual seasonal migration past Bermuda (Luckhurst et al. 2001).

Recent PSAT tagging results of wahoo confirm that wahoo move considerable distances e.g., 580 km in 54 d (Thiesen and Baldwin In press). The movement patterns of 3 tagged fish were largely north-south and movement tracks appeared to be related to the position of the Gulf Stream. The data also indicated that wahoo spent most of their time in relatively shallow water but made dives to about 200 m. With this limited data set it is not possible to generalize, but preliminary results suggest that wahoo do not dive to the depths observed in blue marlin and swordfish. This in turn may indicate that they have a narrower preferred thermal range than the other species. Thiesen and Baldwin (In press) stated that their fish remained in a narrow 5° C temperature range (20–25° C).

It is thought that further technological developments (including miniaturization) in electronic tags will greatly increase our ability to determine movement patterns of large pelagic species and that the data can be used to better define habitat use in the pelagic environment. This information can be used to enhance our understanding of fishery exploitation patterns and can assist in the formulation of improved management regimes in pelagic fisheries.

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