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ELEMENTS OF THE ECOLOGY AND MOVEMENT PATTERNS OF HIGHLY MIGRATORY FISH SPECIES OF INTEREST TO ICCAT IN THE SARGASSO SEA

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SUMMARY

This paper provides information on the ecology and movement patterns of a total of 16 different fish species whose distributions include the Sargasso Sea. These species are divided into four groups that broadly correspond with ICCAT species groupings: Group 1 – Principal tuna species including yellowfin tuna, albacore tuna, bigeye tuna, bluefin tuna and skipjack tuna, Group 2 – Swordfish and billfishes including blue marlin, white marlin and sailfish, Group 3 – Small tunas including wahoo, blackfin tuna, Little Tunny (Atlantic black skipjack tuna) and dolphinfish, and Group 4 – Pelagic sharks including shortfin mako, blue and porbeagle. For each species, information is provided on ecology and habitat use in relation to oceanographic parameters such as water temperature, depth preference and dissolved oxygen. In addition, movement and migration patterns are discussed in relation to conventional tag-recapture results and more recent PSAT (Pop-up Satellite Archival Tag) tagging. The importance of Sargassum as essential fish habitat is discussed and is linked to the feeding habits of tunas and other pelagic predators. Flyingfishes are an important prey species in the diet of tunas and billfishes and, as they are largely dependent on Sargassum mats as spawning habitat, the Sargasso Sea plays a fundamental role in the trophic web of these highly migratory, pelagic species. Recent findings from PSAT tagging of several pelagic shark species has revealed the importance of the Sargasso Sea in their life cycles.

RÉSUMÉ

Le présent document fournit des informations sur l'écologie et les schémas de déplacement de 16 espèces de poissons dont les aires de distribution incluent la mer des Sargasses. Ces espèces sont divisées en quatre groupes qui correspondent en gros à la classification des espèces relevant de l'ICCAT : Groupe 1: principales espèces de thonidés, comprenant l'albacore, le germon, le thon obèse, le thon rouge et le listao. Groupe 2: espadon et istiophoridés, incluant le makaire bleu, le makaire blanc et le voilier. Groupe 3: thonidés mineurs incluant le thazard-bâtard, le thon à nageoires noires, la thonine commune et la coryphène commune. Groupe 4 : requins pélagiques, incluant le requin-taupe bleu, le requin peau bleue et le requin-taupe commun. Pour chaque espèce, des informations sont fournies en ce qui concerne l'écologie et l'utilisation de l'habitat par rapport aux paramètres océanographiques, tels que la température de l'eau, la préférence des profondeurs et l'oxygène dissous. En outre, les schémas de déplacement et de migration sont discutés par rapport aux résultats de marquage conventionnel/récupération et du marquage PSAT (marques pop-up reliées à des satellites) plus récent. L'importance des Sargasses comme habitat de prédilection des poissons est abordée, ce qui est expliqué par les habitudes alimentaires des thonidés et d'autres prédateurs pélagiques. Les poissons volants sont une proie importante du régime alimentaire des thonidés et des istiophoridés, et sachant qu'ils dépendent en grande mesure des amas des Sargasses qui constituent leurs habitats de frai, la mer des Sargasses joue un rôle fondamental dans la chaîne trophique de ces poissons grands migrateurs pélagiques. Les récents résultats du marquage PSAT de plusieurs espèces de requins pélagiques ont révélé l'importance de la mer des Sargasses dans leurs cycles vitaux.

RESUMEN

Este documento proporciona información sobre la ecología y los patrones de movimiento de un total de 16 especies diferentes de peces cuyas distribuciones incluyen el mar de los Sargazos. Estas especies se dividen en cuatro grupos que corresponden de manera general a las agrupaciones de especies de ICCAT: Grupo 1: especies de túnidos principales, entre ellas rabil, atún blanco, patudo, atún rojo y listado. Grupo 2: pez espada e istiofóridos, entre ellos aguja azul, aguja blanca y pez vela. Grupo 3: pequeños túnidos entre ellos peto, atún aleta negra, bacoreta y dorado y Grupo 4: tiburones pelágicos, lo que incluye marrajo dientuso, tintorera y marrajo sardinero. Para cada especie, se facilita información sobre la ecología y el

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uso del hábitat en relación con parámetros oceanográficos como la temperatura del agua, la preferencia de profundidad y el oxígeno disuelto. Además, se discuten los patrones de movimiento y migración en relación con los resultados de marcado-recaptura con marcas convencionales y del marcado más reciente con marcas PSAT (marcas archivo pop-up por satélite). Se debatió la importancia del Sargassum como hábitat esencial de los peces y se vinculó con los hábitos alimentarios de los túnidos y otros depredadores pelágicos. Los peces voladores son una especie presa importante en la dieta de los túnidos y marlines, y dado que éstos dependen en gran medida de las malezas de Sargazos como hábitat de reproducción, el mar de los Sargazos desempeña un papel fundamental en la cadena trófica de estas especies pelágicas altamente migratorias. Hallazgos recientes de marcado PSAT de varias especies de tiburones pelágicos han puesto de relieve la importancia del mar de los Sargazos en sus ciclos vitales.

KEYWORDS

Sargasso Sea, Sargassum, Tunas, Swordfish, Billfishes, Sharks, Ecology, Habitat, Oceanography, Movements

Introduction

The Sargasso Sea is located within the North Atlantic sub-tropical gyre and a series of currents define its boundaries with the most influential current being the Gulf Stream in the west. The importance of the Sargasso Sea derives from a combination of factors - oceanographic features, complex pelagic ecosystems, and its role in global ocean processes (Laffoley *et al*., 2012). The Sargasso Sea contains the majority of the world's only pelagic ecosystem based upon floating *Sargassum* which hosts a highly diverse community of associated organisms. *Sargassum* and the Sargasso Sea provides essential habitat for key life history stages of a wide variety of species, some of which are endangered or threatened e.g. four species of sea turtles and the European eel (*Anguilla anguilla*). A variety of oceanographic processes impact productivity and species diversity. *Sargassum* is known to drift through the Caribbean, into the Gulf of Mexico and up the eastern seaboard of the USA in the Gulf Stream. Eddies of water which break away from the southern edge of the Gulf Stream may then spin into the central gyre trapping a significant portion of *Sargassum* (Laffoley *et al*., 2012). Once it has become entrained by the clockwise movement of currents circulating around the gyre, it may remain for long periods.

The importance of the Sargasso Sea as an Ecologically or Biologically Significant Marine Area (EBSA) was recognized by the 11th Conference of the Parties to the Convention on Biological Diversity in 2012. The Sargasso Sea Alliance (SSA) has defined a large portion of the Sargasso Sea as its study area. The proposed study area extends from 22^{o}–38^{o}N and from 76^{o}–43^{o}W, centred on 30^{o}N and 60^{o}W (**Figure 1**). This comprises an area of ~ 4,163,499 km^2 (Laffoley *et al*., 2012).

The Sargasso Sea plays an important role in the ecology and life history of a variety of pelagic fish species, many of which are highly migratory and of both commercial and recreational importance in many countries. The International Commission for the Conservation of Atlantic Tunas (ICCAT) has fisheries management responsibility for many of these large, apex predators which form the basis of significant fisheries in the Atlantic Ocean. These species include the five major tuna species of commercial importance in the North Atlantic as well as swordfish and three species of billfishes. In addition, a number of species (Small Tunas category in ICCAT) which could be categorized as pelagic mesopredators, are monitored but not actively managed. More recently, ICCAT has started to evaluate stocks of some pelagic sharks which can comprise a significant element of longline catches. The focus of this paper is to outline elements of the ecology, oceanography and movement patterns of a total of 16 species (eight of them from the family Scombridae) mentioned above with respect to the Sargasso Sea.

Significance of the Sargasso Sea to pelagic fishes

The overall importance of *Sargassum* for fish life histories has been recognised by the USA as essential fish habitat (SAFMC, 2002). In a study of the feeding ecology of pelagic predators, Ruderhausen et al (2010) examined the dominant prey of blue marlin (*Makaira nigricans*), dolphinfish (*Coryphaena hippurus*), yellowfin tuna (*Thunnus albacares*) and wahoo (*Acanthocybium solandri*) in the North Atlantic. They classified prey into three groups: 1) prey associated with floating *Sargassum* 2) Flying fish (Exocoetidae) - associated with *Sargassum* during spawning and 3) schooling prey, primarily *Auxis* spp. and cephalopods. The dominant prey of yellowfin tuna (>50cm FL) were flying fish, as well as scombrids (mackerels, tunas, wahoo) and cephalopods. Dolphinfish were seen to feed mostly on prey associated with floating structure, mainly *Sargassum*, and flying fish. Blue marlin and wahoo preyed predominantly on scombrids. Thus, flyingfish were a significant component of the diet of these pelagic predators. It is recognized that *Sargassum* is a critical component for reproduction of flying fish (Oxenford et al., 1995) and thus the association of flying fish with *Sargassum* during spawning indicates the significance of this habitat for one of the principal prey groups of tunas, dolphinfish and other pelagic predators. This represents a direct trophic link between *Sargassum* and the diets of tunas and tuna-like species thus again emphasizing the importance of the Sargasso Sea. ICCAT has recently recognized the importance of *Sargassum* as fish habitat and has requested that Contracting Parties assess the ecological status of *Sargassum* as habitat for tunas, billfish and sharks (ICCAT, 2012).

In more general terms, Coston-Clements et al (1991) list a number of teleost species as being associated with pelagic *Sargassum* in the North Atlantic. The nature of the association is not always evident but is typically related to food and feeding habits. In the Gulf Stream off North Carolina, Casazza and Ross (2008) found that significantly more fishes (n = 18,799) representing at least 80 species, were collected from samples containing *Sargassum*, than from samples collected from open water habitat (60 species, 2,706 individuals). The majority (96%) of fishes collected in both habitats were juveniles. Underwater video recordings indicated a layered structure of fishes among and below *Sargassum* and that smaller fishes were more closely associated with the algae than larger fishes. Underwater video observations of schooling behaviors of dolphinfish and jacks (Carangidae) were also recorded. Wells and Rooker (2004) studied the distribution and abundance of fishes associated with *Sargassum* mats in the northwestern Gulf of Mexico during the summer months. A total of 36 species (17 families) was identified with seven species comprising over 97% of the catch. A large majority (over 95%) of the species collected were in early life history stages confirming the importance of pelagic *Sargassum* as nursery habitat for some species and suggesting that its presence may influence recruitment success. The early life history stages (primarily juveniles) of a number of pelagic predators associated with *Sargassum* are listed by Coston-Clements et al (1991) and they include dolphinfish, wahoo, swordfish *(Xiphius gladius*), blue marlin, white marlin (*Tetrapterus albidus*) and sailfish (*Istiophorus albicans*). The importance of the Sargasso Sea to various pelagic species is not always directly evident but an evaluation of existing information suggests that its importance rests mainly with its status in relation to one or more of the following: migratory route, spawning area, nursery area and feeding area. In the case of some species of pelagic sharks, it has been shown that the Sargasso Sea is of considerable importance as an overwintering ground or pupping area.

In this paper, the migratory species with a known association with the Sargasso Sea have been divided into four groups, largely along ecological lines although many are apex predators. The groups are: 1) Principal tuna species 2) Swordfish and billfishes 3) Small tuna group as defined by ICCAT 4) Pelagic sharks.

Group 1 – Principal Tuna species

Yellowfin tuna (*Thunnus albacares*)

Ecology and oceanography

The yellowfin tuna is a gregarious species, tending to form schools, either free-swimming or associated with FADs, underwater ridges and different marine animals. For example, the fishery for this species is associated with dolphins in the Pacific Ocean. Adults generally form shoals of specimens of the same size (ICCAT, 2010a). This behaviour also predominates in the juveniles which form shoals with specimens that do not necessarily come from the same breeding group in specific migration periods (ICCAT, 2010a). Free-swimming schools of yellowfin (i.e. not associated with FADs) tend to be made up of large individuals and to be monospecific.

Yellowfin are found across a broad thermal range (18 – 31°C) and vertical distribution is determined by the thermal structure of the water column (Collette and Nauen,1983). In general, yellowfin limit their incursions into depths in which the water temperature does not fall more than 8º C with respect to the temperature of the surface layer. It spends more than 90% of its time in waters with a uniform temperature of around 22º C (ICCAT, 2010a). Although it is known to dive to depths of 350 m, adult and juvenile yellowfin spend most of their time in the surface layer, above 100 m. (ICCAT, 2010a). There are generally insignificant differences in depth distribution between day and night. The level of dissolved oxygen is a limiting factor for the depth distribution of yellowfin, as a concentration of 3.5 ml/ l appears to limit their depth distribution (ICCAT, 2010a).

Migration and movements

Yellowfin tuna is the species of tropical tuna that is considered to make the largest migrations, i.e. periodic and regular movements of a large part of the population (ICCAT, 2010a). As migratory behaviour varies with size (age), it is necessary to examine the migratory patterns of three size – age categories: juveniles (50-65 cm), pre-adults (66-110 cm) and adults (111-170 cm) - in order to better understand the dynamics of this species in the Atlantic Ocean (ICCAT, 2010a). Juveniles (up to 50 cm FL) typically remain in coastal waters and undertake only modest movements. With increase in size, yellowfin movements become more extensive and by the time they reach sexual maturity, trans-Atlantic migrations take place (ICCAT, 2010a). In general, adults make trophic migrations northwards in the summer months and then return to their spawning grounds in the winter months.

Tag- recapture results of yellowfin tuna from tagging locations off the eastern seaboard of the USA indicate a strong west to east movement (Luckhurst, 2007) . The majority of the straight-line tagging vectors suggest a transit across the Sargasso Sea in this migration (ICCAT, 2010a). Other data from the Bermuda Seamount (32°N, 64°W) suggest a seasonal migration in the North West Atlantic in the summer months (Luckhurst *et al*, 2001;Luckhurst, 2007) northward into the Sargasso Sea. Three recaptures of yellowfin tagged in Bermuda also indicate movement through the Sargasso Sea, one was recaptured off Cape Hatteras and the remaining two yellowfin near Puerto Rico (**Figure 2**).

Albacore tuna (*Thunnus alalunga)*

Ecology and oceanography

Albacore is an epi- and mesopelagic oceanic species which seldom comes close to shore and prefers deep, open waters. Temperature is one of the dominant factors determining the distribution of albacore and they prefer cooler sea temperatures than more tropical species such as yellowfin tuna (ICCAT, 2010b). The preferred thermal range for albacore is 10-20ºC although temperatures outside this range can be tolerated for short periods. As a result of this thermal preference, the distribution of areas suitable for albacore in the North Atlantic includes the entire Sargasso Sea area and most of the north Atlantic. Albacore occur mainly in the temperature range of 14-20ºC off North-America and between 16-21ºC in the northeast Atlantic (ICCAT, 2010b). These thermal preferences are thought to act as barriers to movements of albacore across the equatorial zone from different regions and this has resulted in separate populations with the designation of north and south Atlantic stocks (ICCAT, 2010b).

Albacore appear to be searching for an optimum temperature zone when they undertake periodic vertical migrations from warm surface waters to deep cooler waters. In a study in the Northeast Pacific, individuals 3-5 years old spent 80% of the time at 100 m, around the thermocline depth, and moved only occasionally to the mixed surface layer or to deeper waters (ICCAT, 2010b). It was also noted that albacore undertook vertical migrations with larger depth range during the day than during the night. Maximum depth distribution is reported to range from 380-450 m in the Pacific Ocean (ICCAT, 2010b). The swim bladder is not fully developed in juvenile albacore and as a result, juveniles have less ability to undertake vertical migrations in the water column. Tunas have a high metabolic rate with consequent high oxygen demand. The minimum estimated dissolved oxygen concentration for albacore is 3.7 ml/l. and using this tolerance level, a large area of the eastern Atlantic, south of 20ºN latitude and extending westwards towards Brazil, is not suitable for albacore at depths greater than 100m (ICCAT, 2010b).

Migration and movements

Albacore have been documented to migrate from the north Atlantic to the Mediterranean and vice versa as well as making transatlantic migrations (ICCAT, 2010b). However, no migrations from the north to the south Atlantic have yet been recorded. Despite these tagging data, albacore migration routes are still uncertain. In the North Atlantic, both juveniles and adults apparently spend the winter in the central Atlantic area. When the water starts warming up in the spring, young albacore start a trophic migration, heading to highly productive waters in the northeast Atlantic (ICCAT, 2010b). In May, tuna start to concentrate in surface waters near the Azores at 38ºN latitude and begin to move north in waters of 17- 20ºC. In the autumn, albacore start migrating back to the mid Atlantic. The trophic migration takes place for the first four years of their lifetime until they reach sexual maturity (ICCAT, 2010b). In contrast, adult albacore undertake reproductive migrations when summertime approaches. They migrate to their spawning grounds in the western part of the north Atlantic (including the Sargasso Sea) and also to an area offshore from Venezuela (ICCAT, 2010b).

Bigeye tuna (*Thunnus obesus*)

Ecology and oceanography

Bigeye tuna is an epi- and mesopelagic species which generally prefers open waters. Like other tunas, they are gregarious and tend to form schools, either independently or in association with drifting objects, marine animals or seamounts. In the eastern Atlantic, bigeye tuna are frequently associated with a large variety of drifting objects, including dead whales, or with some living animals. Bigeye schools associated with floating objects are comprised primarily of small fish (under 5 kg.) although larger fish are also found. Free schools (not associated to any object) are typically formed by large individuals of the same species (ICCAT, 2010c).

The main environmental factors affecting the vertical distribution of bigeye are the depth of the deep scattering layer and temperature (ICCAT, 2010c). The optimum temperature range for bigeye is 17º- 22ºC and they are not found in waters greater than approximately 29ºC (Collette and Nauen, 1983). However, bigeye have a broad thermal tolerance as they are exposed to temperatures down to about 5ºC when they dive to 500 m depth, i.e. up to 20ºC colder than surface water temperature.

Bigeye exhibits a characteristic behavioural pattern with respect to depth. They remain within the surface layer, at a depth of about 50 m during the night but typically dive to depths of up to 500 m at sunrise (ICCAT, 2010c). Depths of over 1000 m were recorded in a study on bigeye tuna conducted using archival tags in the Coral Sea. The bigeye typically ascends swiftly to the temperate surface layer, probably in order to regulate body temperature or possibly to compensate for oxygen deficiency (ICCAT, 2010c). There appears to be a positive correlation between moonlight intensity and the depth at which bigeye tuna are found, the mean depth increasing as the intensity of lunar light increases.

Dissolved oxygen concentration is also an important ecological factor for tunas because of their high metabolic rate. Bigeye tuna are able to withstand lower concentrations of dissolved oxygen than any other tuna species and, as a result, it is capable of inhabiting deeper waters (ICCAT, 2010c) where oxygen concentrations can be less than 1.5 ml/l.

Migration and movements

Bigeye tuna, in common with yellowfin, undertake very significant migrations. Tag-recapture data indicates that bigeye travel faster than yellowfin tuna. Also in common with yellowfin, bigeye seasonal movement patterns (trophic or spawning) may be characterised by size(age) groups (ICCAT, 2010c). In the eastern Atlantic spawning areas, young individuals (30-70 cm FL) tend to gravitate towards the equatorial area (Gulf of Guinea) forming mixed schools with young skipjack and yellowfin tuna. These fish are taken by purse-seine fleets. In contrast, adults (fish over 100 cm FL) are caught throughout the whole of the tropical and sub-tropical Atlantic with longline gear (ICCAT, 2010c).

Tagging studies show trans-Atlantic migrations westward from the Gulf of Guinea to the north of Brazil and movements from the Gulf of Guinea along the African coastline. As few tagging studies of bigeye have been conducted in the western Atlantic, data is sparse but trans-Atlantic migrations have been recorded from the eastern seaboard of the US to the Gulf of Guinea as well as along the North-American coast with a few individuals reaching as far as 50ºN latitude (ICCAT, 2010c).

As bigeye are found throughout the entire North Atlantic and have an optimum temperature range of 17- 22ºC, the Sargasso Sea provides a suitable environment for spawning but due to a lack of tagging and research on bigeye in the western central Atlantic, there is little specific information about bigeye in the Sargasso Sea except ICCAT reported landings.

Bluefin tuna (*Thunnus thynnus*)

Ecology and oceanography

Bluefin tuna has the widest geographical distribution of all of the tuna species in the North Atlantic and is the only large pelagic species living permanently in temperate Atlantic waters (Fromentin and Fonteneau, 2001). Bluefin occupy the surface and subsurface waters of both coastal and open-ocean areas, but have been recorded as diving to depths of 500m to 1000m with some frequency (ICCAT, 2010d). Archival tagging data have confirmed that bluefin can sustain a wide range of temperatures (down to 3°C, up to 30°C), while maintaining stable internal body temperatures (ICCAT, 2010d). Similar behaviour has also been reported for other large pelagic species (e.g. bigeye tuna, swordfish) and is generally associated with foraging in the deep scattering layer and possibly to physiological constraints to cool the body temperature (ICCAT, 2010d).

The movement patterns of bluefin tuna and their spatial distribution have, until recently, been hypothesized to be controlled by preferential ranges and gradients of temperature, similar to other tuna species but more recently, it is believed that juvenile and adult bluefin tuna frequent and aggregate along ocean fronts (ICCAT, 2010d). This association appears to be related to foraging as bluefin feed on the concentrations of both vertebrate and invertebrate prey found in these areas. The types of ocean fronts known to be frequently visited by bluefin tuna are upwelling areas, such as the West coasts of Morocco and Portugal, and meso-scale oceanographic structures associated with the general circulation of the North Atlantic and adjacent seas (ICCAT, 2010d). Although there is some agreement amongst scientists about this association, bluefin tuna habitat appears to be more complex than can be explained by these oceanographic features alone.

Migration and movements

Bluefin tuna is a highly migratory species and is found throughout the pelagic ecosystem of the entire North Atlantic and its adjacent seas, mainly the Mediterranean Sea. It is known from the early results of conventional tagging that bluefin undertake transatlantic migrations and subsequent PSAT (Pop-up Satellite Archival Tag) tagging has helped determine the routes and the depths at which they migrate (Wilson and Block, 2009). They display homing behavior and spawning site fidelity in both the Gulf of Mexico and the Mediterranean Sea, which constitute the two main spawning areas (ICCAT, 2010d). Less is known about feeding migrations within the North Atlantic and the Mediterranean but PSAT tagging results indicate that bluefin tuna movement patterns vary considerably between individuals, years and areas (Block et al, 2005**).** Recent PSAT tagging of bluefin in the Gulf of Mexico in May (normally the peak spawning month) indicates that, after leaving the Gulf of Mexico, some fish migrate northward through the Sargasso Sea towards the Gulf of Maine (Eric Prince, pers. comm.) where they are often found during the summer months (Wilson et al, 2005).

As there is no direct evidence of spawning in the Sargasso Sea, these fish are presumed to be feeding, possibly around seamounts, as they travel north. Migratory routes for bluefin tuna PSAT- tagged in the western Atlantic indicate that they transit the Sargasso Sea when migrating eastward to the Mediterranean Sea (Block et al, 2005). Other studies have placed spawning-sized bluefin in an area between Bermuda and the Azores in the central North Atlantic during the spawning period (Lutcavage et al, 1999). These fish were all located above 33°N in the northern sector of the Sargasso Sea and may have been using this area as a foraging ground.

Skipjack tuna (*Katsuwonus pelamis*)

Ecology and oceanography

Skipjack tuna is an epipelagic species generally inhabiting open waters. In common with yellowfin and bigeye tunas, skipjack tend to form schools, either independently or in association with floating objects, marine animals or seamounts. Aggregations of this species tend to be associated with convergences, water mass boundaries, outcrops and other hydrographic discontinuities (Collette & Nauen, 1983). The distribution of skipjack is more tropical than other tunas as they are normally found in waters ranging from 20ºC to 30ºC although they can tolerate temperatures down to 15ºC. They generally dive only to depths where the water temperature is not more than 8ºC below the temperature in the surface layer (ICCAT, 2010e). Although skipjack remain close to the surface during the night (Collette & Nauen, 1983), they are capable of diving to a depth of 260m, a depth considerably less than other tuna species. The minimum values of dissolved oxygen in skipjack tuna habitat have been established at 3.0-3.5 ml/l where temperature is not a limiting factor (ICCAT, 2010e). As a result, this generally restricts skipjack to waters above the thermocline making them more vulnerable to surface gear such as purse seines (ICCAT, 2010e). However, results of acoustic tagging indicate that skipjack can make brief dives down to 400 m with temperatures below 14ºC and an oxygen level close to 1.5 ml l/l.

Migration and movements

The movements of skipjack are influenced by environmental conditions (temperature, salinity, nutrients) and by their tendency to group around floating objects, which may attract other tuna species such as young yellowfin and bigeye (ICCAT, 2010e). The majority of tagging has been done in the equatorial waters of the eastern Atlantic. Results from this tagging effort show that migrations generally follow the coastline, moving both north and south but also with some westward movement. In the western Atlantic, there is very little information from tagging with the only migrations being along the Brazilian coast and minor movements in the Caribbean. For the entire Atlantic, there have been only two East-West transatlantic migrations recorded (ICCAT, 2010e).

Thus there is no known specific association of skipjack with the Sargasso Sea. Skipjack are infrequently caught in Bermuda (located in the western Sargasso Sea) and then only in the summer months when the warmest SSTs occur (Luckhurst, pers. obs).

Group 2 – Swordfish and billfishes

Swordfish (*Xiphius gladius*)

Ecology and oceanography

Swordfish are distributed throughout the Atlantic Ocean and Mediterranean Sea. They spawn mostly in the warm tropical and subtropical waters of the western Atlantic throughout the year but are found in the colder temperate waters during summer and fall months (ICCAT, 2010f). Although swordfish is an oceanic species, it is sometimes found in coastal waters, generally above the thermocline. The swordfish is the species of billfish with the greatest tolerance to temperature (5° to 27°C), but is usually found in surface waters at temperatures above 13°C (ICCAT, 2010f). Adult swordfish are generally solitary and are not known to form schools in the open ocean. Acoustic tagging had earlier shown that swordfish stay near the surface at night, but return to depths of up to 600 m during the day and are presumed to be feeding in the deep scattering layer (ICCAT, 2010f).

A PSAT tag deployed on a small swordfish (59 kg) in the northwest Atlantic provided compelling evidence of this diurnal vertical migration behavior. Throughout the monitoring period, this fish made regular dives to 700–800 m depth during daylight hours (**Figure 3**, inset) while during nocturnal hours, mean depth was much shallower with brief, regular periods spent at the surface (Luckhurst, 2007). This fish moved northward through the Sargasso Sea covering a distance of 2,629 km in 62 days (**Figure 3**).

Migration and movements

Swordfish are known to move through the Sargasso Sea as part of a seasonal migration from the tropical Atlantic to the temperate northwest Atlantic waters (Neilson *et al.*, 2009). The data from conventional tagging based on almost 400 recaptures presented by Luckhurst (2007), indicates that the predominant movement pattern of swordfish in the North Atlantic appears to be north-south, transiting the Sargasso Sea (**Figure 4**), with some east-west movement These recaptures included several trans-Atlantic movements. Although the reasons for this seasonal movement are unclear, it may well be associated with feeding and prey concentrations in thermal boundaries between water masses, suggesting that the Sargasso Sea may be a productive feeding ground (ICCAT, 2010f). In further support of this hypothesis, a swordfish conventionally-tagged from a longliner in the Northwest Atlantic in July 1997 moved in a southerly direction through the Sargasso Sea over 900 km before being recaptured off Bermuda in December, less than six months later (Luckhurst, pers. obs.; E. Prince, pers. comm., NMFS). Data indicating spawning in the north-central Gulf of Mexico and east of the Caribbean islands (ICCAT, 2010f) suggest that the north-south movements may constitute migrations to spawning grounds in warmer waters.

Blue marlin (*Makaira nigricans*)

Ecology and oceanography

Blue marlin is an epipelagic, oceanic species typically found in wide-open, blue waters. Blue marlins are not schooling fish and are considered a rare and solitary species. Adults are mostly found in tropical waters and their distribution appears to be bounded by the 24°C isotherm (ICCAT, 2010g). As habitat preferences of billfish are poorly known compared with tuna, the advent of PSAT tagging has greatly enhanced our understanding of marlin habitat in recent years. Results from PSAT tagging in the western North Atlantic (Graves *et al.* 2002; Kerstetter *et al.* 2003) indicate that blue marlin typically remain where the SST range is 22-31°C. Blue marlins are largely associated with the epipelagic zone and spend over 80% of their time in water temperatures ranging from 26-31°C. They do, however, undertake frequent, short duration dives to depths where the temperature may be as much as 14°C below SST (ICCAT, 2010g). . A study which deployed 79 PSATs in several areas of the Atlantic (Goodyear *et al.* 2006) found that blue marlin showed a mean minimum temperature preference of 17.4°C while other studies suggest that the thermal preference for this species appears to be the warmest waters available in the open ocean (ICCAT, 2010g).

Depth distribution data from PSAT tagging has indicated that blue marlin spend most of their time in warm near surface waters (<25 m) in the northwestern Atlantic (Kerstetter *et al.* 2003) but they make frequent, short duration vertical dives from the surface layer to depths >300 m. Goodyear et al. (2006) indicated that blue marlin made deep, short duration dives below 800 m but the mean dive depth for 48 tagged fish was 318.6 m.

Although dissolved oxygen requirements for marlins are poorly known, blue marlin are ram ventilators and require sufficient oxygen to support their high metabolic rates. Prince and Goodyear (2006) proposed that the minimal oxygen concentration for billfish is 3.5 ml/l, defining it as the hypoxic threshold for billfish species. PSAT tagging results from the eastern tropical Atlantic suggest that this minimum oxygen level is indeed a barrier for blue marlin (Prince et al, 2010).

Migration and movements

Blue marlin display extensive movements in the Atlantic Ocean. An examination of the databases of the Cooperative Tagging Center (CTC) and The Billfish Foundation (TBF) of conventional tag deployments 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 (Luckhurst, 2007). Tag recapture rates for blue marlin are generally < 1% throughout the world's oceans (Ortiz et al. 2003). The dominant movement patterns for recaptured blue marlin are primarily from west to east and, as blue marlin prefer warm tropical waters, these movements are primarily in the tropical Atlantic. The few transatlantic and trans-equatorial movements represent about 5% of the documented blue marlin recaptures. However, despite this extensive tagging effort, blue marlin migration routes are still uncertain.

The advent of PSAT tagging has provided many new, important insights into movement and migration as well as habitat use. The first PSAT tagging of blue marlin in the NW Atlantic took place in the recreational fishery in Bermuda in 1999 (Luckhurst, pers. obs.). Eight of the nine tagged blue marlin reported their positions after five 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 days. During the period 2002–2003, a total of 66 PSATs were deployed (E. Prince, pers. comm., NMFS), primarily from recreational fishing vessels in the wider Caribbean. These deployments resulted in long distance movements by a number of specimens (**Figure 5**). The longest movement vector of 4,606 km was of a blue marlin (68 kg) tagged in the Turks and Caicos Islands which moved this distance to the eastern tropical Atlantic in 91 days.

Although blue marlin are principally a tropical species, they do migrate northward into the Sargasso Sea during the summer months and form the basis of a significant recreational fishery in Bermuda (Luckhurst, 1998). Sampling of female blue marlin, principally at tournaments held in July, confirmed that blue marlin were actively spawning in the Sargasso Sea (Luckhurst et al, 2006). This finding significantly extended the northern limit of known spawning areas in the northwest Atlantic into the northern half of the Sargasso Sea at Bermuda's latitude (32°N).

White marlin (*Tetrapterus albidus*)

Ecology and oceanography

White marlin is an epipelagic species that is mostly solitary, although it is known to occasionally form small groups. They generally prefer water >100 m deep with surface temperatures above 22 °C. They often associate themselves with ocean fronts, steep drop offs, submarine canyons, and other features where shoaling of prey species may occur (ICCAT, 2013). Much of the information about habitat use has been gathered in recent years from PSAT tagging. Deployments of these tags in the western Atlantic indicates that white marlin spend most of their time in the epipelagic zone in water 24°-29 °C (ICCAT, 2013). More recent studies have shown that white marlin can expand the temperature range in which they live but they spend almost all their time in the warmest surface layer (97.2% of darkness hours and 80.3% of daylight hours) (ICCAT, 2013). They are capable of short duration deeper dives, which are probably for foraging, but their preference is to stay in the warmest water available. In common with most tropical tunas, billfishes generally do not venture into waters that are more than ~8 °C below the surface temperature (ICCAT, 2013). Depth distributions from PSAT data indicate white marlin spend most of their time in warm near-surface temperatures (<25 m depth) in the western North Atlantic but they make frequent short- duration dives typically in the 100-200 m depth range. As with other billfishes, dissolved oxygen requirements are poorly understood but PSAT tagging data suggests white marlin are limited by a minimum dissolved oxygen concentration of about 3.5 ml/1 (Prince and Goodyear, 2006).

Migration and movements

The majority of information on white marlin movements originates from conventional tag-recapture results mostly from the western North Atlantic. These results indicate a few transatlantic movements, but no transequatorial movements (ICCAT, 2013). The longest linear displacement recorded for a white marlin was 6,517 km (Ortiz *et al.*, 2003). As with blue marlin, white marlin also migrate north in the summer months into the Sargasso Sea and are taken regularly in the recreational fishery in Bermuda but largely on a catch-and-release basis (Luckhurst 1998**).** White marlin are also known to spawn in the Sargasso Sea (NMFS, 2007)

Sailfish (*Istiophorus albicans*)

Ecology and oceanography

Sailfish is an epipelagic species but is the least oceanic of the Atlantic billfishes, as it shows a strong tendency to approach continental coasts, islands and reefs. Sailfish are found in schools during the winter months in the western central Atlantic, in Florida waters, offshore waters of the Gulf of Mexico and the Caribbean Sea (ICCAT, 2010h). It has been suggested that they form schools when the principal prey are abundant schooling species (e.g., clupeids) and they have been documented to hunt cooperatively to concentrate schools of prey species. Fish in Florida waters tend to disperse northward in the summer following the inside edge of the Gulf Stream up the east coast of the US (ICCAT, 2010h). Temperature preferences for sailfish appear to be associated with the seasonal movement of the 28°C isotherm and, as a consequence, they are often found above the thermocline in the surface layer. In the northwestern Atlantic, various studies have shown that sailfish spend most of the time in warm near-surface waters (10-20 m depth) but they also show that sailfish display frequent, short duration dives to depths of 200-250 m, similar to white marlin (ICCAT, 2010h). Prince and Goodyear (2006) proposed that the minimal oxygen concentration for billfishes is 3.5 ml/l, defining it as the hypoxic threshold for these species. PSAT tagging results from the eastern tropical Atlantic tend to support the suggestion that this minimum oxygen level is a depth barrier for sailfish (Prince et al, 2010).

Migration and movements

Sailfish display more restricted movements in the Atlantic than blue or white marlin with no evidence of transatlantic or trans-equatorial movements (ICCAT, 2010h). However, based on minimum distance travelled in tag-recaptured fish, it has been suggested that sailfish in different areas make either cyclic annual movements, exhibit some degree of fidelity, or some combination of the two (Ortiz et al. 2003). Results from the western North Atlantic, where most of the tag and release of sailfish has taken place, indicate significant movements between the Straits of Florida and adjacent waters, and the Gulf of Mexico and the area near Cape Hatteras (35°N). In general, most of the tag- recaptures have occurred in the same general area as the point of release (ICCAT, 2010h). The longest movement recorded was from a sailfish tagged and released off the U.S. northeast coast, and recaptured off Suriname 11 months later having travelled a distance of 3,861 km (Ortiz *et al.* 2003).

Group 3 – Small tunas

Wahoo (*Acanthocybium solandri*)

Ecology and oceanography

Wahoo is an epipelagic,oceanic species which is frequently solitary but may form small loose aggregations rather than compact schools (Collette and Nauen, 1983). Little was known about habitat use until the advent of electronic tagging. Thiesen and Baldwin (2012) deployed PSAT tags on four wahoo in the western North Atlantic which provided data over a total of 198 days. Wahoo spent >90% of their time in water less than 200m depth and > 90% of their time was spent in water temperatures ranging from 17.5 to 27.5°C. Three of the four fish made regular dives to depths greater than 200m (Thiesen and Baldwin, 2012). All four fish displayed significant differences in mean depth in daylight (50.7m) and during darkness (29.7m).

Migration and movements

Relatively little is known about wahoo movement patterns and migration in the western Atlantic and there has been very limited success using conventional tags to define migration patterns (Oxenford et al., 2003). In Bermuda, a small scale wahoo tagging program in 1998 succeeded in tagging only 15 wahoo before the program was forced to conclude. However, one of these tagged wahoo was recaptured 10 months later, 64 km away from the point of release (Oxenford et al., 2003). It is not possible to know if it remained in Bermuda waters during its time at liberty or returned after a seasonal migration. It is conceivable that it followed a migratory route into the western central Atlantic, with the Bermuda Seamount, located in the western Sargasso Sea as a seasonal feeding /spawning area, as has been postulated for yellowfin tuna and blackfin tuna in Bermuda (Luckhurst et al., 2001).

Another form of evidence suggesting a migration pattern in the Sargasso Sea is marked seasonality in landings. In Bermuda, wahoo catches have a strong seasonal pattern with 60–70% of the annual landings consistently occurring in the second and third quarters of the year (April–September) during the period of highest water temperatures (Luckhurst and Trott, 2000). Wahoo are known to actively spawn in Bermuda waters in the summer months (Oxenford et al, 2003). Historically, there are spring (April–May) and fall (August–September) runs of wahoo in Bermuda which vary inter-annually in magnitude and to a lesser degree in timing (Luckhurst and Trott, 2000). However, wahoo landings are consistently lowest (5–8% of annual landings) in the first quarter which coincides with the lowest annual SST (18°C).

The advent of PSAT tagging of wahoo in recent years has provided important insights into movements and migration (Luckhurst, 2007). PSAT tags deployed on four wahoo in the western North Atlantic indicated that straight-line distances moved (deployment to pop-up) ranged from 162.5 to 1,960 km (Thiesen and Baldwin, 2012). The movement patterns of these tagged fish appeared to be largely north-south movements in relation to the Gulf Stream.

Blackfin tuna (*Thunnus atlanticus*)

Ecology and oceanography

Blackfin tuna is an epipelagic, oceanic species occurring in waters of at least 20° C but is most common in tropical waters. Their distribution is confined to the western Atlantic (Collette and Nauen, 1983). Blackfin frequently form large mixed schools with skipjack tuna. These mixed schools form the basis of an important fishery off the southwest coast of Cuba which uses live-baits and poles (Claro et al, 2001). In a study of blackfin around moored FADs in Martinique, Doray et al (2004) indicated that there is no evidence that moored FADs act as an “ecological trap” for blackfin tuna. There were a small number of juveniles found around the FADs and the authors postulated that these juveniles leave the moored FADs to undergo a trophic migration and then return in the following year as adults to spawn in the area of the Lesser Antilles.

Migration and movements

Very little is known about the migratory patterns of blackfin tuna in the western Atlantic but data from Bermuda suggest that an annual migration to the seamount may occur from the more southerly areas of their distribution, presumably for feeding. However, it is not known if blackfin spawn in Bermuda waters (Luckhurst, pers. obs.). An examination of commercial landings of blackfin in Bermuda between 1987-1998 indicated that the proportion of annual landings taken in the third quarter (July-September) ranged from about 50% to over 70% (Luckhurst *et al,* 2001). This is the period of the warmest SST, a maximum of about 30°C. In contrast, first quarter (January-March) landings are less than 5% of the annual total when the SST is about 18°C (Luckhurst *et al,* 2001). Manooch (1984) reported that blackfin are only found off North Carolina during the warmest months (June- September). Thus, it appears that blackfin may be migrating north as SST warms in the summer months but move south in the fall to stay within their thermal preference zone (Collette and Nauen, 1983).

Another line of evidence is derived from tag-recapture results in Bermuda. The long–term tag-recapture rate of blackfin in Bermuda is 10.7% compared to 3.5% for the western Atlantic (Luckhurst *et al,* 2001). All Bermuda recaptures occurred during the summer months with the largest mode for time-at-liberty at approximately one year. Although the sample sizes are small, a second mode occurred at three years, with single recaptures at two and four years (Luckhurst *et al*, 2001). Taken together these findings tend to support the hypothesis of an annual summer migration through the Sargasso Sea to the Bermuda Seamount. In contrast, a conventional tagging program in the eastern Caribbean which tagged 787 blackfin had only 11 recaptures (1.4%). Despite times at liberty ranging to >3 years, all recaptures were near to or at the original release sites (Singh-Renton and Renton, 2007).

Little Tunny (*Euthynnus alleteratus)*

Ecology and oceanography

Little Tunny is an epipelagic, neritic species which is typically found in coastal waters with swift currents, near shoals and around thermal fronts and upwelling areas. This species is more coastal than other tuna species and is most abundant in the tropical Atlantic where the water temperature is 24º- 30ºC (ICCAT, 2010i). This species lives in schools of similar-sized fish together with other scombrid species, but has a tendency to scatter during certain periods of the year (Collette and Nauen, 1983). In Bermuda, Little Tunny form monospecific schools inshore during the summer months (Luckhurst, pers. obs.) but as water temperatures start to fall they disappear and presumably migrate south. This observation confirms their presence in the western part of the Sargasso Sea but it is not known if their summer distribution extends eastward further into the Sargasso Sea.

Migration and movements

Very little is known about the migratory habits of Little Tunny in the western Atlantic. In Bermuda, schools are taken by seine nets during the summer months to be used for bait (Smith-Vaniz et al, 1999). They appear not to be present during the winter months suggesting that this may be another case of seasonal migration to the Bermuda Seamount. This is consistent with the observations of Manooch (1984) who reported that Little Tunny migrate northward in schools in the coastal waters of the US eastern seaboard in the spring and return southward in the fall.

Dolphinfish (*Coryphaena hippurus*)

Ecology and oceanography

Dolphinfish is an epipelagic, oceanic species which spends most of its time in the surface layer. It is found in tropical and subtropical waters warmer than 20° C (Oxenford, 1999). Dolphinfish are attracted to floating objects of all kinds including windrows or mats of *Sargassum* around which they frequently congregate and feed. They are not known to orient to any particular oceanographic features but rather to floating objects which may be influenced by such features. Small dolphinfish often travel together in schools ranging from several individuals up to 50 fish. Larger adult fish are normally solitary or in pairs.

Migration and movements

Palko *et al* (1982) reported that there was little direct evidence of dolphinfish movements in the western central Atlantic. They believe that migrations and movements are likely to be affected by the movement of drifting objects (including mats of *Sargassum*) in oceanic waters with which dolphinfish are associated. Oxenford and Hunte (1986) proposed two migration circuits of dolphinfish in the northeast and southeast Caribbean, based largely on seasonality of fisheries by location and mean size-at-capture. They suggest a northeastern migration circuit incorporating the northern Caribbean islands, the southeastern US and Bermuda, and a southeast circuit incorporating the southeastern Caribbean islands and the north coast of Brazil. A part of the proposed northeastern circuit is supported by Beardsley (1967) who reported that dolphinfish probably move northward from Florida during spring and summer. Luckhurst and Trott (2000) reported that landings of dolphinfish in the Bermuda fishery from 1987-1997 showed a high level of seasonality with third quarter (July-September) landings comprising 45-60% of annual landings. This is the period with the highest SST and this landings pattern, in common with other species already described, is consistent with a highly migratory species. Off the southeastern US, dolphinfish frequently congregate around *Sargassum* , which serves as both shelter and a source of food (Manooch, 1984). Many of the food types eaten by dolphinfish are found in floating mats of *Sargassum* and this alga is frequently found in their stomach contents.

Group 4 – Pelagic sharks

Shortfin mako (*Isurus oxyrinchus*)

Ecology and oceanography

Shortfin mako is a common, offshore littoral and epipelagic species in coastal and oceanic waters that occurs from the surface down to at least 500 m depth (Kohler *et al*, 2002). The preferred water temperature range of shortfin mako in the North Atlantic appears to be in a narrow range from 17° to 22°C (Kohler *et al*, 2002). An analysis of surface temperature data from almost 2,800 sets of swordfish longline gear between the Gulf of Mexico and the Grand Banks found that the mean minimum and maximum temperatures in which makos were caught were 18.5° and 20.5°C, respectively. The highest catch rates for mako sharks in the Spanish swordfish longline fishery in the North Atlantic also occurred at 18°C and frequently along the margins of the Gulf Stream (Kohler *et al*, 2002). Other evidence on the preferred water temperatures is provided by acoustic tagging. A 160-180 kg mako shark was followed for four days from Florida across the Gulf Stream and into the Sargasso Sea. The shark swam at depths ranging from the surface to 500 m but spent most of its time at depths where the temperature range was between 17° and 22°C (Kohler *et al*, 2002).

A PSAT tag deployed on a shortfin mako off the southeastern US indicated only limited movement (72 km) over 60 days (Loefer *et al,* 2005). The depth range covered during this period was from the surface to 556 m and the water temperature range was 10.4° – 28.6°C. This tagged mako demonstrated a diel pattern of vertical movement defined by greater mean depths during daylight hours (Loefer *et al,* 2005). The tagging data also suggested a seasonal behavioral change in vertical movements with increasing SST.

Migration and movements

In a long term shark tagging program (1962-2000), a total of 5,333 shortfin mako sharks were tagged with 608 being recaptured (11.4%). Distances travelled ranged from no movement to a maximum of 5,310 km (Kohler *et al,* 2002). This maximum distance was a transatlantic migration, the tagged mako moving from the northeastern U.S. and being recaptured 1.4 years later off west Africa. In this tagging study, 75% of the makos travelled less than 926 km from their original tagging location with a mean distance of 737 km (Kohler *et al,* 2002). Times at liberty ranged from 1 day to 12.8 years. This longest-time-at-liberty was a male tagged off North Carolina that was recaptured only 457 km away, off South Carolina. Overall, 75% of tagged makos were at liberty for less than 2 years with a mean of 1.2 years (Kohler *et al* 2002).

Kohler *et al* (2002) proposed a "Sargasso Sea Hypothesis" to explain shortfin mako migrations in the western North Atlantic. In January, shortfin makos are common along the western margin of the Gulf Stream, with at least one area of high abundance off Cape Hatteras, where the Gulf Stream flows near the continental shelf. In April and May, as inshore shelf waters warm, makos appear to move north following the Gulf Stream and begin moving onto the continental shelf between Cape Hatteras and the southern part of Georges Bank. From June through October, makos are caught on the continental shelf between Cape Hatteras and Cape Cod. The continental shelf south of Cape Cod may be the primary feeding grounds for a large part of the juvenile mako population in the western North Atlantic (Kohler *et al*, 2002).

During late fall and early winter (November-December), makos move from the area between Cape Hatteras and the Grand Banks to offshore wintering grounds in the Gulf Stream and the Sargasso Sea. If it is assumed that 18°C Sargasso Sea water represents the preferred habitat for makos, then the core of their distribution in the western North Atlantic covers a latitudinal range between 20° and 40°N, bordered by the Mid-Atlantic Ridge on the east and the Gulf Stream on the west (similar in configuration to the SSA Area – see **Figure 1**). Mako sharks do occur outside of these boundaries at different seasons, and they make trans-Atlantic crossings. However, most of the recaptures can be explained based on a "Sargasso Sea Hypothesis", including those returns from the Caribbean Sea. The distribution of recaptures suggests that the principal wintering grounds of juvenile makos are the western margin of the Gulf Stream and the northern part of the Sargasso Sea (Kohler *et al,* 2002). As shortfin mako have been designated as one of the two major shark species for management focus (ICCAT, 2008), the Sargasso Sea appears to be a very significant area for this species.

Blue shark (*Prionace glauca*)

Ecology and oceanography

The blue shark is an oceanic-epipelagic and fringe-littoral shark that occurs from the surface to at least 600 m depth (Compagno, 1984). Blue shark movements are strongly influenced by water temperature and this species undergoes seasonal latitudinal migrations on both sides of the North Atlantic. It appears to have a wide thermal tolerance and is caught over a broad range of SST (8°- 29.5°C) but seems to prefer water masses from 12°- 21°C (Kohler *et al*, 2002). In general, larger fish of both sexes are caught over a wider temperature range than smaller sharks and blue sharks demonstrate tropical submergence to remain in the deep, cooler waters in the tropical and equatorial parts of their range (Compagno, 1984). In addition to temperature, reproductive condition and availability of prey strongly influence the distribution and movements of blue sharks (Kohler *et al*, 2002). Documented seasonal migrations to higher latitudes take place on both sides of the North Atlantic. Sizes of blue sharks generally decrease with increasing latitude.

Migration and movements

Based on tagging data, blue sharks in the North Atlantic make frequent trans-Atlantic movements between the western and eastern regions of the Atlantic. They use the major North Atlantic current systems to accomplish these extensive movements. In addition, blue sharks are segregated by sex and size over large areas of the Atlantic with larger, mature fish of both sexes caught in the southern part of their range (Kohler *et al*, 2002). Immature males and females and sub-adult females dominate the northern regions (Henderson et al, 2001). Evidence from tagging studies and catch data suggest that there are distinct seasonal abundances and seasonal latitudinal migrations in blue sharks.

In the western North Atlantic, the winter range of the blue shark is defined as eastward of the northern margin of the Gulf Stream (including the Sargasso Sea**)** where they can be found during all months of the year. Beginning in April-May, as the shelf waters warm, there is a shoreward movement from the Gulf Stream onto the continental shelf from North Carolina to Newfoundland (Kohler *et al*, 2002). Female blue sharks (145-185 cm FL; 3-5 years old) arrive on the mating/feeding grounds of the continental shelf in late May where they interact with adult males (4-5 year olds). A summer breeding season for the blue shark is indicated by the high incidence of mating scars and the presence of sperm in the oviducal gland. Once the females are inseminated, they move offshore typically in November and the sperm is stored until the following spring when they fertilize their eggs (Kohler *et al*, 2002). From May through October, blue sharks are commonly caught on the continental shelf and are also found offshore from the outer edge of the shelf and into the Gulf Stream. According to Kohler *et al* (2002), most blue sharks along the eastern North American coast begin moving south (southeastern United States, Caribbean Sea) and offshore (central Atlantic) in the fall.

Distances traveled for tagged blue shark have ranged up to 6,926 km. This maximum distance moved by a blue shark was from off the coast of New York State to east of Natal, Brazil in 1.4 years (Kohler *et al*, 2002). Over 75% of the tagged blue sharks traveled less than 1,852 km from their original tagging location with a mean distance of 857 km. Times at liberty ranged from 1 day to 9.1 years. Overall, 75% were at liberty for less than 2 years (Kohler *et al*, 2002).

In a recent study of blue shark migration pathways in the northwest Atlantic using PSAT tags, Campana et al (2011) found that all blue sharks tagged on the continental shelf in the autumn (September-October), moved off the continental shelf to the south and/or east. Distances travelled ranged from 141 to 2,566 km (mean = 927 km). Blue shark movements appeared to be closely linked to the current and temperature structure of the water. After encountering the Gulf Stream and, in the subsequent months extending into the winter, the majority of tagged sharks remained in association with the warm waters of the Gulf Stream or its rings. However, nine of the 23 tagged sharks moved southward into the Sargasso Sea (within the SSA Area) with pop-up times mostly ranging from December to March. This appears to provide firm evidence that blue sharks are using the Sargasso Sea as an overwintering ground (Campana et al, 2011).

Porbeagle shark (*Lamna nasus*)

Ecology and oceanography

The porbeagle is a coastal and oceanic shark that inhabits the cold temperate waters of the North and South Atlantic (Compagno, 1984). Porbeagle appear to occupy well-defined and relatively constant temperatures throughout the year (Campana et al, 2010a). Based on fishery data, porbeagle were caught at a mean temperature of 7.4°C, with 50% being caught between 5°-10°C. There was no significant seasonal pattern of temperature preference indicating that porbeagle actively seek out their preferred temperature range (Campana et al, 2010a). In Canadian waters during the spring, porbeagle were caught most frequently in waters immediately adjacent to the frontal edge separating cool Shelf waters from warmer offshore waters but were not associated with fronts in the fall fishery.

Porbeagles are physiologically adapted to live in cold water as they have the ability to conserve metabolic heat and maintain their bodies at considerably warmer internal temperatures than the surrounding water like other members of the family Lamnidae e.g. shortfin mako (Kohler et al, 2002). Body temperatures of 7-10°C above ambient have been recorded for the porbeagle.

Migration and movements

Porbeagle sharks are confined to the colder parts of the North Atlantic and the distances traveled by conventionally tagged porbeagles are considerably less than other pelagic sharks such as the blue shark and shortfin mako which have a broader thermal tolerance. Distances traveled by tagged porbeagles in the northwest Atlantic ranged from 7.4 to 1,859 km (Kohler *et al*, 2002). Over 90% of the porbeagles traveled less than 926 km from their original tagging location with a mean distance of 433 km. Times at liberty ranged up to 9.2 years but almost 75% of tagged porbeagles were at liberty for less than 4 years with a mean of 2.7 years (Kohler *et al*, 2002). On the basis of conventional tagging studies, Porbeagle sharks appeared to be restricted in their distribution to the cold temperate waters of the North Atlantic. However, the results of PSAT tagging of 21 porbeagles off eastern Canada has revealed that males, and immature sharks of both sexes, remained primarily on the continental shelf for periods of almost a year after tagging. However, mature females undertook lengthy migrations of up to 2,356 km through the winter at depths down to 1,360 m beneath the Gulf Stream to a subtropical pupping ground in the Sargasso Sea (Campana et al, 2010 b). These females migrated south from the Canadian Maritimes, mainly through the western part of the Sargasso Sea down to about 20°N (Campana et a,l 2010). In addition to this significant range extension for the species, the location of this critical life history stage in international waters has important implications for the NW porbeagle stock**.** These international waters are largely unregulated but porbeagle sharks fall under ICCAT management, thus making the protection of this southern portion of the Sargasso Sea of considerable importance for managing this stock.

Conclusion

This paper has served to illustrate the importance of the Sargasso Sea in different facets of the life history of a number of highly migratory species in the North Atlantic, many of which are commercially important. In addition to the 13 species of teleosts discussed here, there are also three species of pelagic sharks which have been shown to have significant associations with the Sargasso Sea. Given the broad taxonomic spectrum covered by these species groups, it is clear that the Sargasso Sea plays a fundamentally significant role in the life histories of many species in the North Atlantic Ocean.

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Table 1. Reported landings of five principal tuna species by ICCAT by gear type and total landings reported by FAO for Area 31 Western Central Atlantic (WCA)

	Area / Gear	*2000*	*2001*	*2002*	*2003*	*2004*	*2005*	*2006*	*2007*	*2008*	*2009*	*2010*	*2011*
Yellowfin	ATW - LL	15760	14872	11921	10166	16019	14449	14249	13557	13192	13019	12659	9634
	ATW -SURF	5241	7027	3763	6445	7134	5118	6880	5959	1973	3285	3590	2310
	WCA - FAO	21 548	27 033	18 310	15 785	17 477	10 960	17 570	13 810	11 685	12 755	16 237	13 659
Albacore	ATN - LL	7321	7372	6180	7699	6917	6911	5223	3237	2647	2625	4026	3620
	WCA - FAO	7 431	11 293	9 969	6 187	5 150	3 694	2 419	2 333	1 497	2 094	3 133	2 988
Bigeye	AT - LL	71193	55265	46438	54466	48396	38035	34182	46232	41063	43533	42515	37393
	WCA - FAO	3 928	4 182	2 794	4 125	6 216	3 163	2 452	2 547	1 942	2 428	1 825	1 875
Bluefin	ATW - LL	858	610	730	186	644	425	565	420	606	366	529	743
	ATW (Sport)	1120	1649	2035	1398	1139	924	1005	1023	1130	1251	1009	887
	WCA - FAO	644	117	503	156	262	276	377	326	327	312	396	145
Skipjack	ATW - LL	22	60	349	95	206	207	286	52	49	20	13	31
	ATW -SURF	467	951	398	367	404	316	372	1317	455	950	1104	869
	WCA - FAO	4 143	7 771	3 726	4 449	4 392	2 330	3 245	1 690	1 591	2 973	4 282	7 070

Table 2. Reported landings of swordfish and principal billfishes by ICCAT by gear type and total landings reported by FAO for Area 31 Western Central Atlantic (WCA)

	Area / Gear	*2000*	*2001*	*2002*	*2003*	*2004*	*2005*	*2006*	*2007*	*2008*	*2009*	*2010*	*2011*
Swordfish	ATN - All Gear	11453	10011	9654	11442	12175	12480	11473	12302	11050	12081	11553	12836
	WCA - FAO	3 756	2 782	3 126	4 615	4 517	5 060	2 018	5 080	4 221	4 813	4 087	5 135
Blue marlin	ATN - All Gear	2156	1307	1082	1199	795	1592	832	1078	2126	1610	1695	927
	WCA - FAO	951	769	580	786	594	500	558	704	928	803	905	682
White marlin	ATN - All Gear	484	431	293	253	257	287	196	162	136	203	217	165
	WCA - FAO	243	308	173	186	132	171	163	144	119	169	149	158
Sailfish	ATW - All Gear	575	399	231	42	64	115	56	77	33	46	1	1
	WCA - FAO	Not available											

Table 3. Reported landings of four species of ICCAT Small Tunas category and total landings reported by FAO for Area 31 Western Central Atlantic (WCA)

	Area	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**
Wahoo	WCA - FAO	903	1 095	867	760	966	645	966	953	763	747	864	749
	AT + MED	2020	2296	2202	2049	2580	1692	1611	2201	2046	2152	1758	1876
	NW AT	540	560	693	594	600	518	7	0	0	0	0	0
Blackfin tuna	ATW	2465	4034	4756	1303	1926	1031	1937	1927	1669	1442	1516	1462
	WCA - FAO	2 379	4 208	3 588	1 570	1 776	1 364	1 442	1 842	1 565	2 457	2 227	2 168
Little tunny	AT[1]	13189	12484	15750	13065	14347	11148	7248	15668	10064	9513	13721	11051
	NW AT	3100	957	739	691	759	528	0	0	0	0	0	0
	WCA - FAO	2 154	2 201	2 559	630	269	261	323	330	247	401	558	342
Dolphinfish	WCA - FAO	4041	3464	3987	3233	4327	4536	4077	5272	4700	5127	3582	4283

[1] Majority of landings from West Africa

Table 4. Reported landings of five species of sharks by ICCAT and total landings reported by FAO for Area 31 Western Central Atlantic (WCA)

	Area	*2000*	*2001*	*2002*	*2003*	*2004*	*2005*	*2006*	*2007*	*2008*	*2009*	*2010*	*2011*
Shortfin mako	WCA - FAO	15	22	136	76	70	125	117	147	90	282	339	472
	NW AT	122	150	140	114	194	148	101	222	201	278	303	347
Blue shark	WCA - FAO	0	0	14	3	11	1 340	1 984	2 054	884	2 367	5 501	11 036
	NW AT	72	66	22	0	61	51	287	919	683	1816	602	2667
Porbeagle shark	[1] WCA - FAO	0	0	0	0	0	0	0	0	0	13	0	0
	[2] NW AT	902	500	236	142	232	193	192	93	8	0	0	0
Bigeye Thresher	WCA - FAO	N/A											
	NW AT	0	0	0	0	0	0	0	0	10	38	20	8
Basking shark	WCA - FAO	0	0	0	0	0	0	0	0	0	0	0	0
	NW AT	0	0	0	0	0	5	0	0	0	0	0	0

[1] Fishery confined to cold, temperate waters; [2] Canada suspended fishery in 2008.

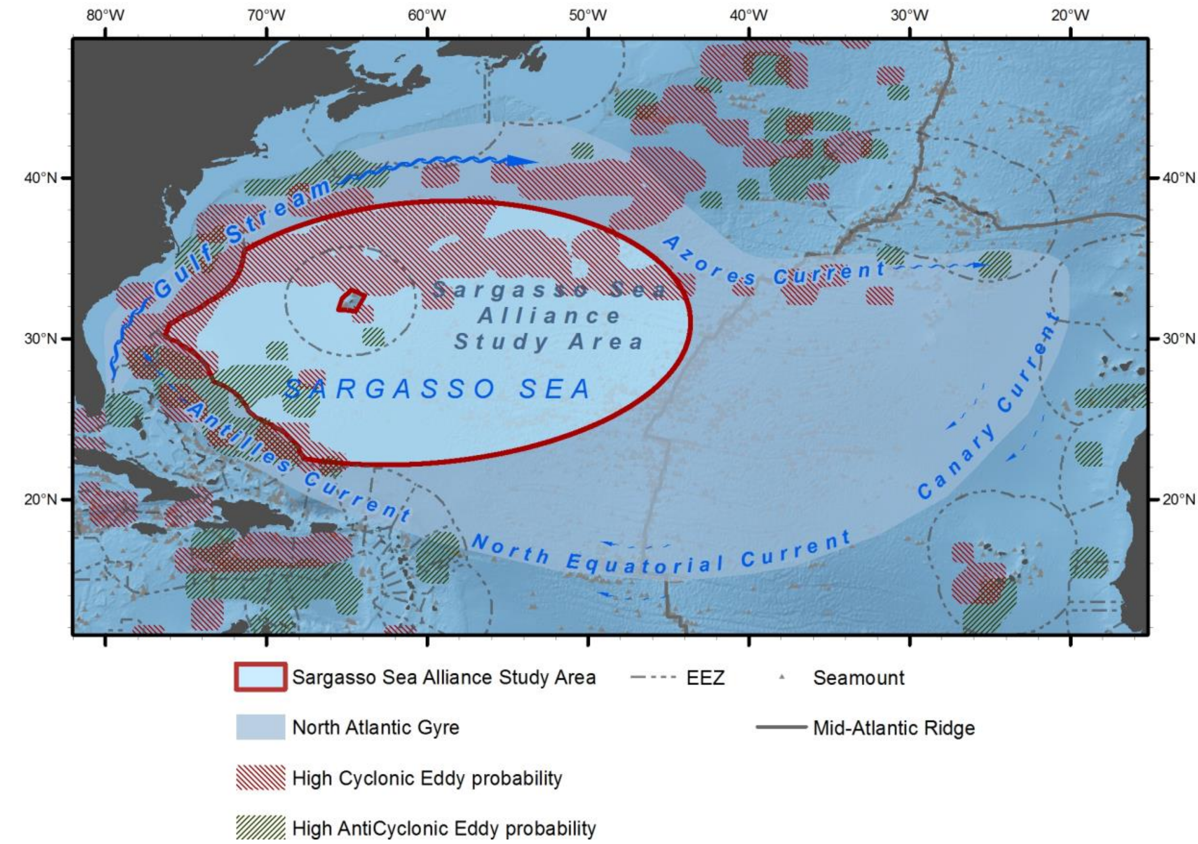

Figure 1. Map of the proposed Sargasso Sea EBSA, including some of the major features that influence overall boundary definition and location (from Laffoley *et al*., 2012).

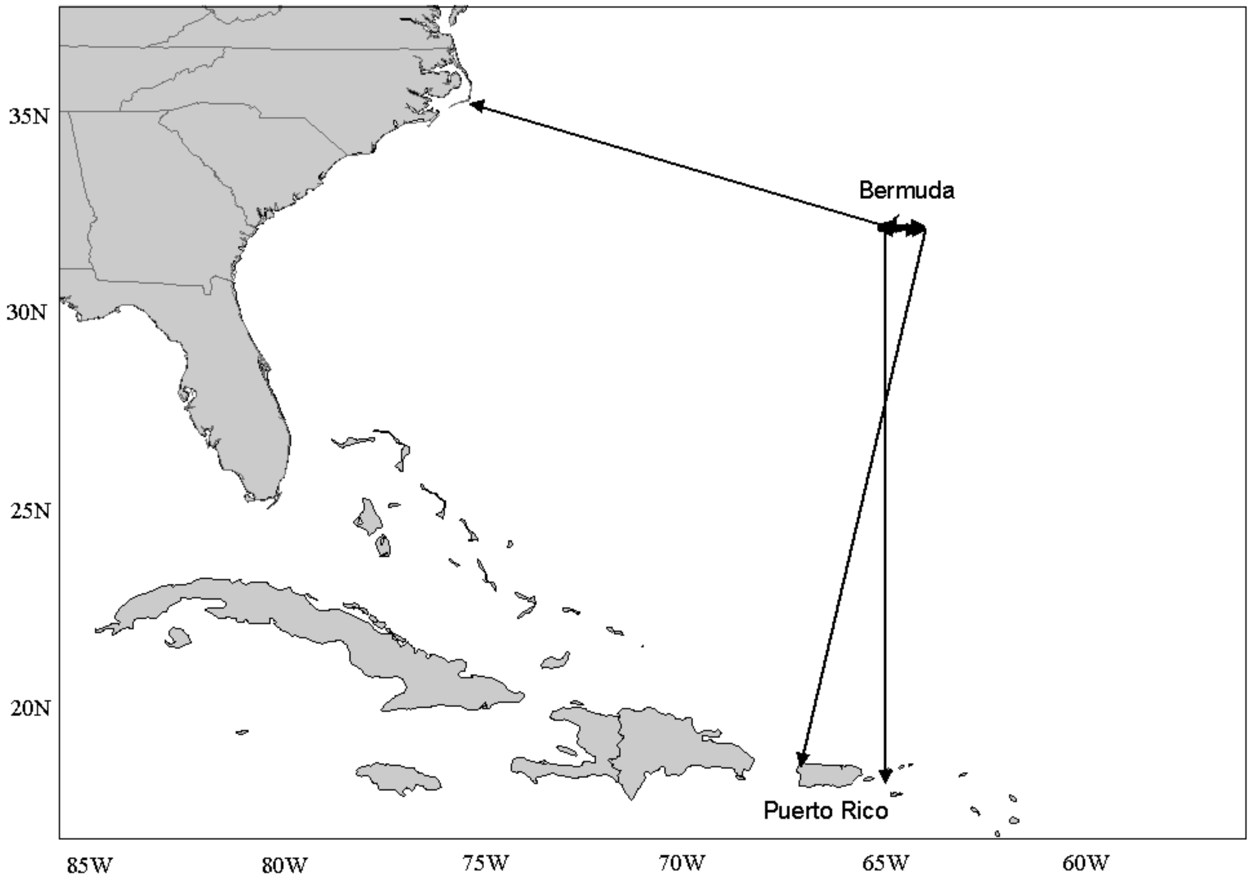

Figure 2. Movement vectors of three conventionally-tagged Bermuda yellowfin tuna (*Thunnus albacares*) recaptured outside Bermuda's EEZ demonstrating demographic connectivity with the wider Caribbean and US eastern seaboard. Straight-line distances moved were between 1,000 and 1,300 km (from Luckhurst 2007).

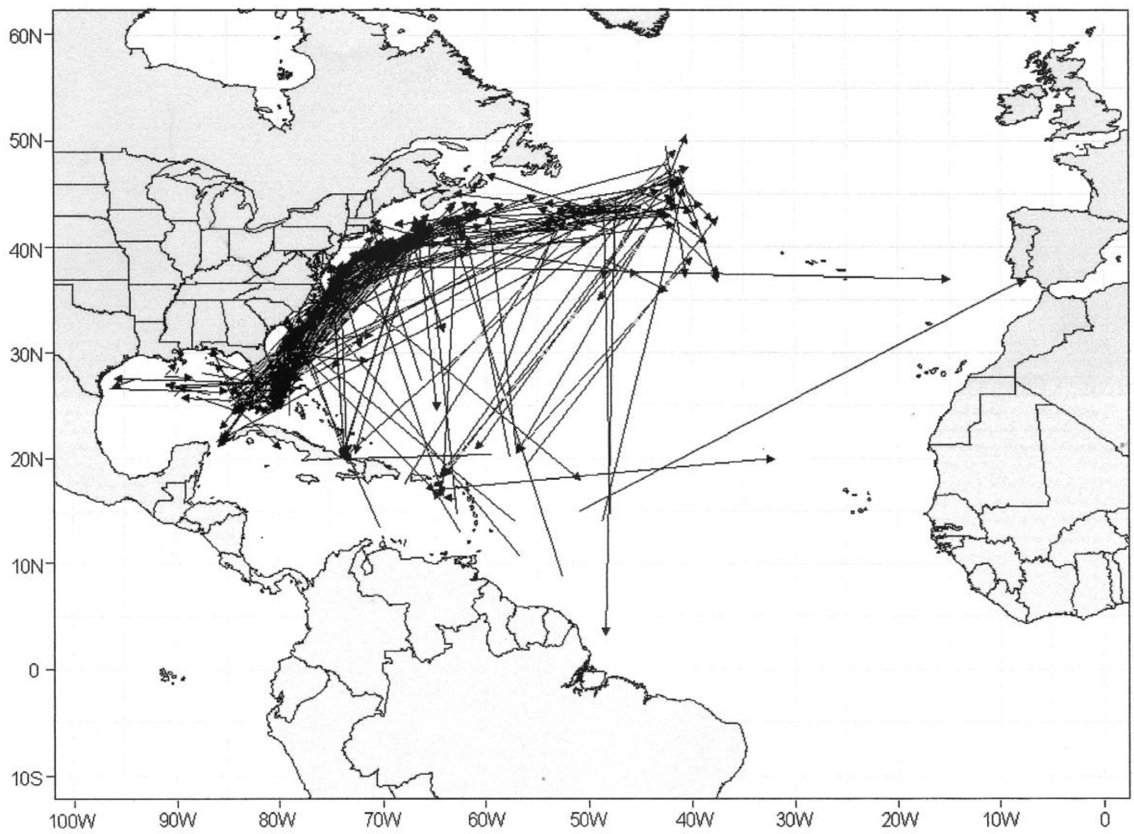

Figure 3. Movement vectors of conventionally-tagged swordfish (*Xiphius gladius*) in the North Atlantic from the CTC database until end of 2006. See text for details. Note predominantly north-south movements (from Luckhurst, 2007).

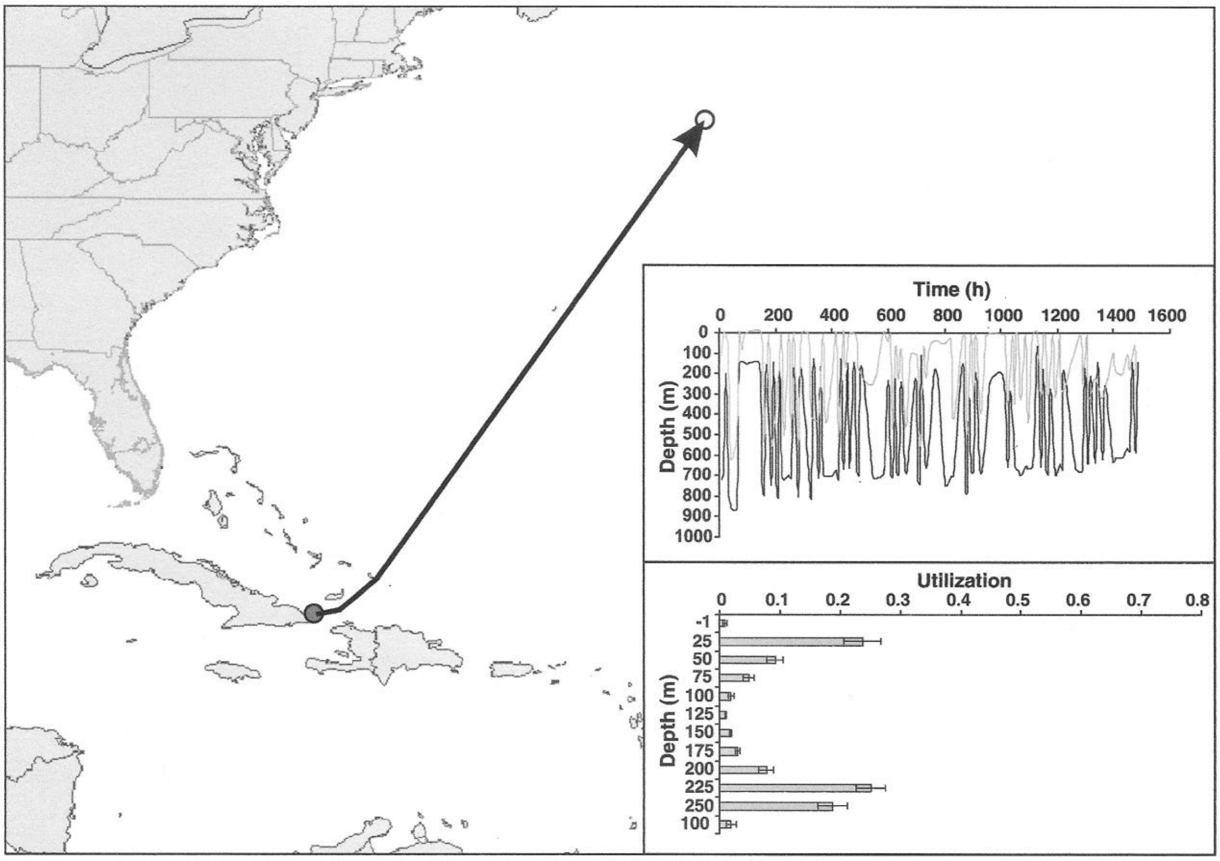

Figure 4. PSAT track of swordfish movement across the Sargasso Sea, illustrating diurnal vertical migration to depths of 850 m (from Luckhurst, 2007).

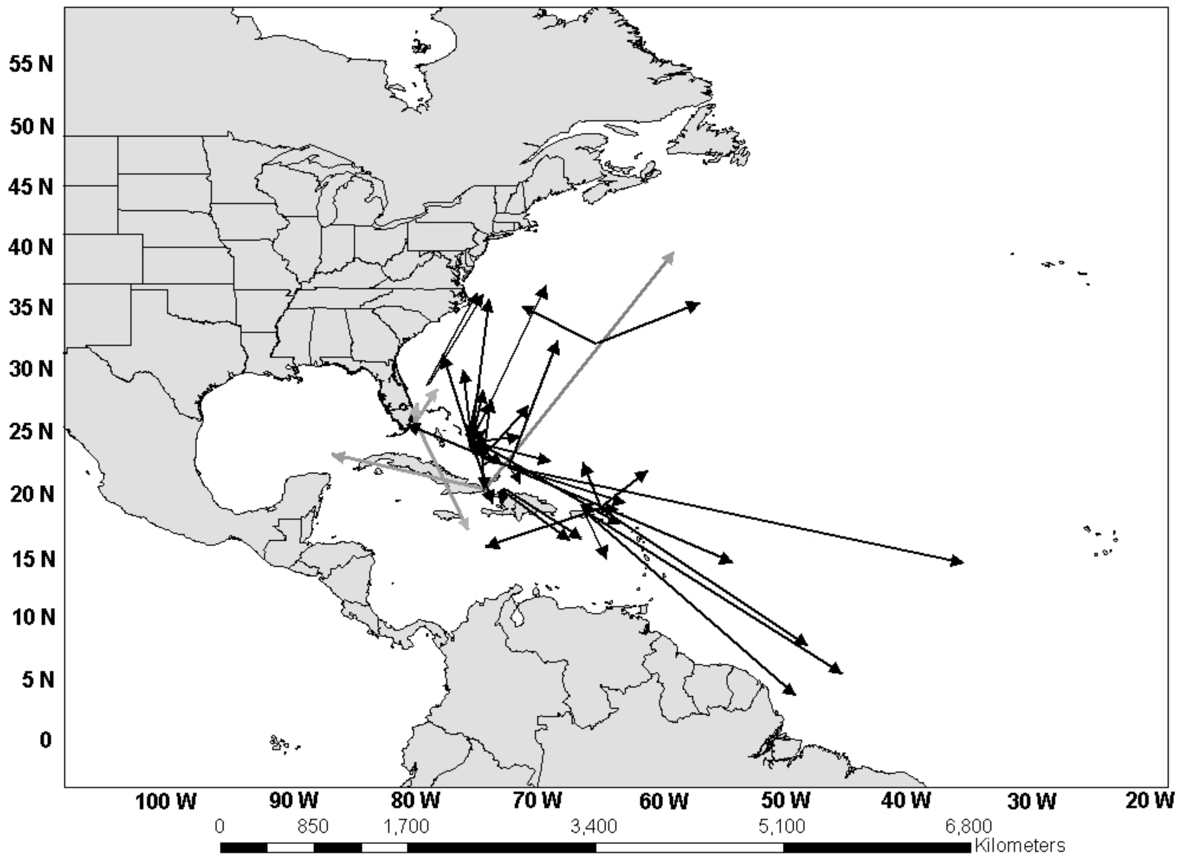

Figure 5. Movement vectors of blue marlin (*Makaira nigricans*) [dark vectors] and swordfish (*Xiphius gladius*) [pale vectors] tagged with PSATs in the western North Atlantic from 2002-2006 (from Luckhurst, 2007).