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INVENTORY AND ECOLOGY OF FISH SPECIES OF INTEREST TO ICCAT IN THE SARGASSO SEA

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SUMMARY

This paper provides information on the biology and ecology of a total of 18 different fish species whose distributions include the Sargasso Sea. These species are divided into four groups that 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, Atlantic black skipjack tuna (Little Tunny) and dolphinfish, and Group 4 – Sharks including shortfin mako, blue, porbeagle, bigeye thresher and basking shark. For each species, information and data is provided on distribution, fishery landings, migration and movement patterns, reproduction, age and growth, food and feeding habits and ecology in relation to oceanographic parameters, primarily water temperature. 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 highly migratory, pelagic species.

KEYWORDS

Sargasso Sea, Sargassum, tunas, swordfish, billfishes, sharks, biology, ecology, life history, oceanography

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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. 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 proposed area extends from 22^o – 38^{o}N and from 76^o – 43^{o}W, centred on 30^{o}N and 60^{o}W (**Fig. 1**) and covering 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 many pelagic fish species including many of the species documented here. Coston-Clements et al (1991) list 10 of the 13 species of Teleosts presented in this paper as being associated with pelagic Sargassum in the North Atlantic. The nature of the association is not always evident but is typically involved with food and feeding habits. However, the presence of early life history stages (egg, larvae, juvenile) in association with Sargassum suggests an important function in life cycles as well. Early life history stages (primarily juveniles) are listed for dolphinfish, wahoo, swordfish, blue marlin, white marlin and sailfish (Coston-Clements et al 1991). 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, 2706 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 (Coryphaena hippurus), 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. 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 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, feeding area, overwintering ground or pupping area.

For the purpose of examining the ICCAT databases for the extraction of data, it is useful to locate the 5x5 degree grids used in reporting longline catches in relation to the SSA Area (**Fig. 2**). There are a total of 11 squares which cover the majority of the high seas within the SSA Area. Species specific data extractions for time and area can then be made to assess the relative importance of the SSA Area to species landings levels.
The following species outlines from Groups 1-4 describe the known association with the Sargasso Sea (with emphasis on the SSA Area) and/or with pelagic Sargassum.

Species Inventory

Group 1 – Principal Tunas

Yellowfin tuna (*Thunnus albacares*)

Distribution - Cosmopolitan, distributed in tropical and sub-tropical oceanic waters; in North Atlantic to 45-50° N.

Abundance
Reported longline landings in the western Atlantic by ICCAT between 2000- 2011 range from 9,634 to 16,019 t. (**Table 1**). Landings from other surface gears for the same period range from 2,310 to 7,134 t. Landings reported to FAO for Area 31 (Western Central Atlantic) with all gear types combined range from 10,960 to 27,033 (**Table 1**).

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 considered necessary to examine the migratory patterns of three size – age categories: juveniles (50-65 cm), pre-adults (65-110 cm) and adults (110-170 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.

Reproduction
The yellowfin tuna has an indeterminate pattern of reproduction which implies an asynchronous development of the oocyte, as can be seen in mature individuals, without a clear differentiation in the frequency of the distribution of the states of the oocytes (ICCAT, 2010a).
The spatial-temporal distribution of active reproductive females in the Gulf of Mexico and the southeastern Caribbean Sea indicate two reproductive groups in the central area of the western Atlantic (ICCAT, 2010a). These groups are different in size and in their spawning period; one group (< 150 cm FL) spawns in the Gulf of Mexico from May to August and a second group (150 - 170 cm FL), spawns in the Caribbean Sea from July to November. The females average 46 spawning events per spawning period (ICCAT, 2010a), and the number of oocytes in each spawning event varies between 1.2 million (specimen of 123 cm FL) and 4 million (specimen of 142 cm FL).

Age and growth
The growth model currently used by ICCAT (2010a) is based on the modified von Bertalanffy equation and confirms the existence of two growth stanzas. According to this model, yellowfin tuna have a slow juvenile growth phase (between 40 and 65 cm FL) followed by a stage of more rapid growth to adult size, with an inflection point at

approximately 90 cm FL. The succession of two growth stages seems to be related to the migratory character of yellowfin when they leave the nursery grounds (ICCAT, 2010a), Yellowfin reach sexual maturity at about 100 cm FL. Growth studies have been conducted in the western equatorial Atlantic using direct reading of dorsal fin spines (ICCAT, 2010a). In this study, size at sexual maturity was at 3.4 years and the oldest fish was 6.5 years old (191 cm FL). However, there is some evidence that there may be different growth curves between males and females and, as a consequence, there is still uncertainty about the most appropriate growth model to use.

Food and feeding habits
Yellowfin tuna are opportunistic predators, and therefore diets vary both spatially and temporally. Yellowfin is a euriphagic predator, making no distinction in the type or size of its prey, although micronecton are purported to be the main component of the oceanic diet (ICCAT, 2010a). The broad food spectrum of the yellowfin tuna's diet is evidence of its generalist eating habits in environments with low concentrations of organisms, like the oceanic pelagic environment in which it lives. An example of variations in the composition of the diet according to changing seasons is reported from southern Brazil (ICCAT 2010a). Teleosts and squid are the staple diet during the winter, while hyperiid amphipods are the principal prey in the spring diet.

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 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, a concentration of 3.5 ml/ l limits their depth distribution (ICCAT 2010a).

Albacore tuna (*Thunnus alalunga)*

Distribution - Cosmopolitan, primarily a temperate species widely distributed throughout North Atlantic to 50° N.

Abundance
Reported longline landings by ICCAT for the North Atlantic from 2000-2011 range from 2,625 to 7,699 t. (**Table 1**) with a general declining trend in recent years. FAO reported landings for Area 31 (western central Atlantic) for the same period range from 1,497 to 11,293 t. (**Table 1**).

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 winter time in the central Atlantic area (although they have also been found in the east and the west). When 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 of temperature 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 (Sargasso Sea and offshore Venezuela) swimming at depths of 50-150 m (ICCAT, 2010b).

Reproduction
Albacore are multiple or batch spawners, shedding batches of hydrated oocytes, in separate spawning events, directly into the sea where fertilization occurs. There is a close relationship between spawning and sea surface temperature: temperatures above 24ºC and a deep thermocline seem to stimulate maturation and reproductive activity in tunas (ICCAT, 2010b). Spawning may be synchronised with high water temperatures in order to enhance growth of eggs and larvae. Spawning occurs in roughly the same offshore environments which albacore normally inhabit. Spawning areas in the Atlantic are found in subtropical western areas of both hemispheres and throughout the Mediterranean Sea. Spawning grounds of the North Atlantic stock are found in waters offshore in the Sargasso Sea and off Venezuela (ICCAT, 2010b) as well as in the Gulf of Mexico In the north Atlantic, spawning takes place from April through September but peak spawning occurs around July (ICCAT, 2010b). Nocturnal spawning seems to be common among scombrids although there is no such evidence for albacore (ICCAT, 2010b).

Age and growth
Age determination and growth of albacore in the North Atlantic have been studied by means of different methodologies (i.e. otoliths, scales, vertebrae, spines, size frequency analysis and tagging). Depending on the authors and the methodology used, results vary to some extent (ICCAT, 2010b). Albacore are assumed to reach 50% sexual maturity at age five (90 cm FL). Albacore are believed to have a theoretical life span of about 15 years but tagging experiments have shown that the oldest albacore ever recovered was less than 10 years old. The growth model currently in use by ICCAT uses the results of an analysis of spines. However, when it comes to transforming catch-by-size into catch-by-age, an alternative equation is used derived from size frequency analysis. This model predicts similar mean lengths at age but a new growth model has been proposed integrating spines and tagging information (ICCAT, 2010b).

Food and feeding habits
Albacore are top carnivores and they opportunistically prey on schooling stocks of sardine, anchovy, mackerel and squid. In the northeast Atlantic, albacore diet is mainly composed of fish, mainly Trachurus trachurus and, to a lesser extent, of crustaceans (ICCAT, 2010b).

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 most relevant environmental 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 (**Figure 4)** 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 mixing 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).

Bigeye tuna (*Thunnus obesus*)

Distribution - Found throughout the entire North Atlantic to 50° N

Abundance

Reported longline landings in the entire Atlantic by ICCAT between 2000- 2011 range from 34,182 to 71,193 t. (**Table 1**). Landings reported to FAO for Area 31 (Western Central Atlantic) for all gear types combined are much lower and range from 1,825 to 6,216 t. (**Table 1**). This substantial difference in reported landings is probably due to the high level of landings of this species in the eastern Atlantic which are reported to ICCAT but which would not be included in this FAO figure.

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).

Reproduction

Spawning takes place throughout the entire year in a wide zone in the vicinity of the equator with water temperatures above 24ºC. Spawning takes place in areas of high biological productivity: near the boundaries of localised eddies and local seamounts and along frontal regions of equatorial currents (ICCAT, 2010c). Spawning occurs from the coast of Brazil to the Gulf of Guinea. Spawning is particularly prevalent from January to June to the south of Brazil and from December to April in the Gulf of Guinea. During the third quarter of the year spawning occurs in a wide area near the equator off the north-east coast of Brazil and Venezuela (ICCAT, 2010c). However, in the northeastern Atlantic (Cape Verde Islands, Senegal), the spawning period is reduced to the months of July to September. Bigeye spawning takes place mostly at night. It is estimated that bigeye tuna spawn from 18:00 h. until after midnight, spawning eggs daily (ICCAT, 2010c).

Age and growth

Bigeye exhibit relatively rapid growth reaching 105 cm FL at age three, 140 cm FL at age five and 163 cm FL at age seven; bigeye over 200 cm FL are relatively rare. Bigeye reach sexual maturity at about 100 cm FL between 3-4 years old. The growth equation used by ICCAT up until 2005 which assumed that there was no slow juvenile growth phase (sizes under 60 cm FL) was based on market data (ICCAT, 2010c). More recently, a simple growth equation combining market data and direct reading of age using hard parts was proposed (ICCAT, 2010c). This model encompasses a very broad range of sizes (29-190 cm FL).

Food and feeding habits

In common with other tuna species, bigeye are opportunistic predators, their diet varying in time and space. Bigeye feed on oceanic, mesopelagic communities (migratory and non-migratory), cephalopods, euphausiaceans and mesopelagic fishes and therefore its diet is less affected by latitude or distance from the coast than that of other tuna (ICCAT, 2010c). There are recordings of bigeye moving vertically to forage on organisms from the deep scattering layer (ranging in depth from 200 - 500 m during the day) including cephalopods and some mesopelgic fish species (ICCAT, 2010c). Juvenile bigeye have been observed feeding on small-sized mesopelagic fish in the eastern Atlantic.

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 is therefore capable of inhabiting deeper waters (ICCAT, 2010c) where oxygen concentrations are under 1.5 ml/l.

Bluefin tuna (*Thunnus thynnus*)

Distribution - Found throughout the entire North Atlantic but mostly in temperate waters.

Abundance
Reported longline landings in the western Atlantic by ICCAT between 2000- 2011 range from 186 to 858 t (**Table 1**). Landings from the Sport category for the same period range from 887 to 2,035 t. Landings reported to FAO for Area 31 (Western Central Atlantic) with all gear types combined range from 117 to 644 t. (**Table 1**). A longline fishery for bluefin exists in the Gulf of Mexico during the Spring and these landings would be included in the figures submitted to ICCAT by the USA.

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**).** Migratory routes for bluefin tuna indicate the importance of the Sargasso Sea when fish are migrating from west to east as they may spend considerable time there. Recent PSAT tagging of bluefin in the Gulf of Mexico in May (normally the peak spawning month) indicates that some fish migrate northward through the Sargasso Sea towards the Gulf of Maine (Eric Prince, pers. comm.).

Reproduction
It is generally agreed that bluefin tuna spawning takes place in warm waters (> 24°C) and in specific, restricted locations in the Mediterranean Sea (around the Balearic islands, Sicily, Malta, Cyprus) and in some areas of the Gulf of Mexico. Spawning occurs only once a year in May-June (ICCAT, 2010d). In contrast with tropical tuna species, bluefin reproduce within a small temporal window (Fromentin and Fonteneau, 2001). They appear to spawn when they reach a specific location with evidence of rapid gonadal development possibly related to increasing water temperature in the spawning area (ICCAT, 2010d). It is generally assumed that bluefin tuna spawn every year, but PSAT tagging results, as well as studies conducted on bluefin in captivity, suggest that individual spawning might occur only once every two or three years (Lutcavage et al. 1999).
Bluefin tuna exhibit asynchronous oocyte development and are multiple batch spawners (spawning frequency being estimated at 1-2 days in the Mediterranean). Egg production is age (or size)-dependent: a 5-years old female produces an average of five million eggs, while a 15-20 year old female might produce up to 45 million eggs (ICCAT, 2010d). Average fecundity was recently estimated from stereological quantification at around 93 oocytes/g of body mass for the East Atlantic bluefin tuna (ICCAT, 2010d).

Age and growth
Juvenile bluefin grow rapidly for a teleost fish, those born in June grow to about 30-40cm long and weigh about 1 kg by October. After one year, bluefin reach about 4 kg and 60cm FL (ICCAT, 2010d). Growth in length tends to be slower for adults than juveniles, but growth in weight increases. On average, an individual bluefin tuna is about 200cm and 150kg at 10 years old and reaches about 300cm and 400kg at 20 years (ICCAT, 2010d). An individual of 427cm and 726kg was caught in the Gulf of Maine but of unknown age. The projected lifespan of bluefin is 40 years as indicated by recent radiocarbon deposition studies (ICCAT, 2010d).
The ageing protocol for bluefin has been based mainly on the count of marks on hard structures, but a few studies were also based on length-frequency and mark-recapture data. However, age-size relationships remain uncertain, especially for older (> 8 years) fish (ICCAT, 2010d).

Food and feeding habits
Juvenile and adult bluefin tuna are opportunistic predators. Over 20 species of fish and 10 invertebrate species were found in a study of bluefin stomach contents (ICCAT, 2010d) . The diet can include demersal species such as octopus, crabs and sponges as well as jellyfish and salps. In general, juveniles feed more on crustaceans, fish and cephalopods, while adults feed mostly on fish (herring, anchovy, sand lance, sardine, sprat, bluefish and mackerel (ICCAT, 2010d). Bluefin stomach contents are, however, normally dominated by one or two prey-species, such as Atlantic herring and sand lance in the West Atlantic or anchovy in the East Atlantic and Mediterranean (ICCAT, 2010d). There does not appear to be a clear relationship between prey length and the size of bluefin tuna; both small and large bluefin feed on similar ranges of prey-size. However, the largest prey (those greater than 40 cm FL) are normally only consumed by giant bluefin > 230cm FL (ICCAT, 2010d).

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-sea 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 (cold down to 3°C, warm up to 30°C), while maintaining stable internal body temperature (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 deep scattering layers 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 current thinking amongst bluefin researchers is 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). Despite the convergence in thinking about this association, bluefin tuna habitat appears to more complex than can be explained by these oceanographic features alone.

Skipjack tuna (Katsuwonus pelamis)

Distribution - Cosmopolitan, distributed in tropical and sub-tropical oceanic waters; in North Atlantic to 35° N

Abundance
Reported longline landings in the western Atlantic by ICCAT between 2000- 2011 range from 13 to 349 t. (**Table 1**). However, landings from other surface gears for the same period are substantially higher ranging from 316 to 1,317 t. Landings reported to FAO for Area 31 (Western Central Atlantic) with all gear types combined range from 1,591 to 7,771 t (**Table 1**). This substantial difference is probably due to the fact that the majority of skipjack landings are taken by purse seiners in Area 31.

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).

Reproduction
Skipjack tuna spawn opportunistically throughout the year over wide areas of the Atlantic. Spawning commences from the age of one. According to various authors, spawning in a school is a synchronised process. Spawning skipjack are observed in all waters where the surface temperature is at least 24ºC (ICCAT, 2010e). Sexual maturation takes place very quickly with consequent rapid oocyte hydration, thus skipjack are able to reproduce as soon as they find favourable water conditions (ICCAT, 2010e). This strategy allows for more efficient utilisation of oceanic regions that are favourable to spawning and larval growth. In the western Atlantic there is a spawning area off Brazil, north of 20ºS latitude, from December to March peaking in January and February. The other known spawning areas are located in the Gulf of Mexico and the Caribbean (ICCAT, 2010e).

Age and growth
Analysis of tagging data from the eastern Atlantic has confirmed that the growth of skipjack varies according to the latitude. In the western Atlantic there are also differences depending on year and zone. In the case of the southeast Caribbean zone, where the sizes caught are larger than in the eastern Atlantic, the growth model used is based on modal progression analysis (ICCAT, 2010e). The maximum age cited for this species is 12 years.

Food and feeding habits
As with other tuna species, the skipjack tuna is an opportunistic predator, and as a result, its diet varies seasonally and by geographic location with the skipjack's principal prey being fish, cephalopods and crustaceans (ICCAT, 2010e). As skipjack actively seeks out its food, which is normally distributed in schools, there may be a predominance of a few species in stomach contents at a given time. For example, skipjack tuna caught by purse seiners in the eastern Atlantic were observed to have fed mostly on small mesopelagic fish (ICCAT, 2010e). A study conducted in the Canary Islands zone in the month of July, showed that in terms of biomass, the predominant prey were fish (99%). Off the Brazilian coast, the main components of the skipjack's diet are two fish species which made up about 60% of stomach contents by volume and a euphausid. Cannibalism is known to occur among skipjack tuna but its occurrence is considered incidental (ICCAT, 2010e).

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). Skipjack are more tropical in distribution and 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.

Group 2 – Swordfish and billfishes

Swordfish (Xiphius gladius)

Distribution - Widely distributed in the Atlantic to 50° N

Abundance
Reported landings of swordfish by all gear types in the entire North Atlantic between 2000 and 2011 range from 9,654 to 12,836 t (**Table 2**). For the same period, reported landings by FAO for area 31 range from 2,018 to 5,135 t (**Table 2**). This discrepancy in landings is probably explained by the fact that there are many swordfish taken in the eastern Atlantic which would not be included in the FAO figures.

Migration and movements 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).

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). These data concur with results given by Luckhurst (2007) on conventional tagging, where the predominant movement pattern of swordfish appears to be north-south, transiting the Sargasso Sea, with some east-west movement, based on almost 400 recaptures (**Figure 5**). 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 concentration in thermal boundaries between water masses, suggesting that the Sargasso Sea may be a productive feeding ground. 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 > 900 km before being recaptured off Bermuda in December, < 6 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 in fact be migrations to spawning grounds.

Reproduction
In common with the principal tuna species, swordfish spawning is strongly influenced by environmental factors, particularly sea surface temperature (SST). . In the Atlantic, swordfish generally spawn in the temperature range 23° to 26°C (ICCAT, 2010f). Due to the influence of SST on spawning, it has been concluded that female reproductive activity is largely restricted to the warm tropical regions of the western Atlantic (ICCAT, 2010f). In the northwest Atlantic, swordfish spawn all year round, with a peak in reproductive activity between December and June. The traditional spawning areas of this species are all found in tropical or sub-tropical waters – including south of the Sargasso Sea, the Gulf of Mexico, east of the Antilles, in the Strait of Florida and along the southeast coast of the United States (ICCAT, 2010f).
There appears to be segregation of the Atlantic swordfish into regions of intense reproduction and regions with sporadic seasonal or non-existent reproduction (ICCAT, 2010f). North Atlantic swordfish mature at a size of 179 cm LJFL (Lower Jaw Fork Length) and an age of 5 years (ICCAT, 2010f) while South Atlantic swordfish reach sexual maturity at about 156 cm LJFL. Males reach maturity a year earlier than females (ICCAT, 2010f).

Age and growth
Swordfish growth has been studied using different methods including the use of otoliths but the most reliable age estimates appear to be from anal fin spines (ICCAT, 2010f). Estimated lengths at age from Multifan analyses of size data have been conducted but all these studies have shown a sexual dimorphism of growth in this species; males grow more slowly and reach a lower asymptotic size than females (ICCAT, 2010f). Growth is very rapid during the first year of the lifecycle and then slows down considerably. Studies have also concluded that Mediterranean swordfish reach a lower asymptotic size than Atlantic swordfish. The maximum age for this species is estimated at 10 years in the Mediterranean but tagging studies have shown that some swordfish can live up to 15 years (ICCAT, 2010f).

Food and feeding habits
Swordfish diet composition studies have been conducted in the North Atlantic, in the Mediterranean Sea and the Pacific (ICCAT, 2010f) . Swordfish change their feeding habits at a very early age, moving from a diet based on

copepods to one based almost entirely on fish. Adult swordfish are diurnal feeders rising close to the mixed surface layer at night and descending to deeper waters during the day to feed on pelagic fish and squid (ICCAT, 2010f).

The adult diet varies considerably with habitats and seasons with fish dominating the diet in some locations whereas cephalopods are predominate in others (ICCAT, 2010f). Smaller prey is generally eaten whole, while larger prey are often observed with slash marks presumably the result of using the sword during feeding (ICCAT, 2010f). In a study of food habits in the Northwest Atlantic, Bowman et al (2000) found that the functional prey groups of swordfish by weight were: squid - 67.4% and fish - 32.5%.

Ecology and oceanography
Swordfish is an oceanic species, but 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 often found in surface waters at temperatures above 13°C (ICCAT, 2010f). Adult swordfish are generally solitary and are not known to form schools in open ocean environments. 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 (ICCAT, 2010f).

A PSAT tag deployed on a small swordfish (59 kg) in the northwest Atlantic provided dramatic 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 6, inset**) while during nocturnal hours, mean depth was much shallower but brief, regular periods were spent at the surface (Luckhurst 2007). This fish moved northward through the Sargasso Sea covering a distance of 2,629 km in 62 day (**Figure 6**).

Blue marlin (*Makaira nigricans*)

Distribution - Tropical and sub-tropical waters to at least 40° N

Abundance
ICCAT landings for all gear types for the North Atlantic for the period 2000-2011 range from 795 to 2156 t (**Table 2**). FAO landings for the western central Atlantic for the same period range from 500 to 951 t (**Table 2**). The majority of ICCAT landings are as by-catch on longliners.

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 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 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 7**). 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.

Reproduction

Blue marlin are batch spawners, shedding batches of hydrated oocytes in separate spawning events (ICCAT, 2010g) directly into the sea where fertilization occurs. Spawning occurs in roughly the same offshore environments which blue marlin normally inhabit. Blue marlin spawning areas in the Atlantic are mainly found in the tropical western areas of both hemispheres. Spawning grounds in the Atlantic are not well known. In the North Atlantic, spawning females and larvae have been found in waters of the Strait of Florida, Puerto Rico, Bahamas, and Jamaica (ICCAT, 2010g). Spawning females have been reported from Bermuda waters (Luckhurst *et al.* 2006) , this being the first documentation of blue marlin spawning in the Sargasso Sea. In addition, spawning sites have been inferred from larval collections from the Straits of Florida and Exuma Sound (Bahamas), and from juvenile fish captured off Jamaica and off Bermuda (Luckhurst *et al.* 2006). Sexual maturity is estimated to occur when females reach 120 kg (237.9 cm LJFL) (ICCAT, 2010g). Based on macroscopic and microscopic assessment of gonad samples from blue marlin caught between 5°N and 25°N, it is estimated that 50% of females are mature at 256.4 cm LJFL (ICCAT, 2010g).

Age and growth

Hard parts (otoliths and dorsal spines) of blue marlin have been used in age and growth studies and significant relationships have been found between length of fish and various measures of hard parts. Larvae grow exponentially and an analysis of daily otolith ring counts of juvenile fish indicates that they can reach 24 cm LJFL in about 40 days, and about 190 cm LJFL in 500 days (ICCAT, 2010g). Blue marlin can reach up to 450 cm TL and exhibit sexually dimorphic growth patterns; females grow much larger than males (ICCAT, 2010g). Somatic growth of males slows at about 100 kg and males do not exceed 150 kg, while females can reach up to 910 kg (ICCAT, 2010g). Pacific blue marlin are estimated to reach ages of 27 years for females and 18 years for males using anal fin spine sections although this spine aging technique has not been validated Tag-recapture results have shown that the longest time-at- large for an Atlantic blue marlin ever recorded was 11 years (Ortiz *et al.* 2003).

Food and feeding habits

Blue marlin are apex predators that feed near the surface and are known to feed in deeper water than other billfish. They opportunistically prey on schools of flying fishes, small tunas, dolphinfish, and squids (ICCAT, 2010g). In the waters off Bahamas, Puerto Rico and the Gulf of Mexico, most prey items include all sizes of dolphinfish (*Coryphaena*), frigate mackerel (*Auxis*), and deep sea fishes (ICCAT, 2010g). Other prey items include scombrid fishes (including bigeye tuna weighting up to 50 kg), snake mackerels, and octopods. In the North and tropical Atlantic, about 85% of the prey were fish and the remainder were cephalopods. Among prey species, fishes of the families Gempylidae followed by the Scombridae comprised about 66% of the total diet (ICCAT, 2010g). followed by the fish families Exocotidae and Alepisauridae. In the western equatorial Atlantic, the most important prey fish for blue marlin was the pomfret, *Brama brama*, the snake mackerel, *Gempylus serpens*, and *Dactylopterus volitans*.

Ecology and oceanography

Blue marlin is an epipelagic oceanic species typically found in wide open blue waters. Blue marlin 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 Atlantic (Graves *et al.* 2002; Kerstetter *et al.* 2003) indicate that blue marlin typically remain where the SST range is 22-31°C. Blue marlin 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).

White marlin (*Tetrapterus albidus*)

Distribution - Tropical and sub-tropical waters to 40° N.

Abundance

ICCAT landings from all gear types for the North Atlantic for the period 2000-2011 range from 136 to 484 t (**Table 2**). FAO landings for the same period range from 119 to 308 t (**Table 2**). In common with blue marlin, the majority of ICCAT landings are as by-catch on longliners.

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 notransequatorial movements (ICCAT, 2013). The longest linear displacement recorded for a white marlin was 6517 km after 474 days-at-liberty (Ortiz *et al.*, 2003).

Reproduction

In common with other billfishes, white marlin do not exhibit sexually dimorphic color patterns or external morphological characteristics. They are batch spawners, shedding batches of hydrated oocytes in separate spawning events (ICCAT, 2013). For fishes between 152 to 172 cm LJFL, the interval between batches has been estimated at 1.5 days (ICCAT, 2013). White marlin spawning areas occur mainly in the tropical western North Atlantic, in the same offshore locations they normally inhabit. Spawning activity has been reported off eastern Florida, the Windward Passage, and north of Puerto Rico and seasonal spawning concentrations have been noted east of Hispaniola and near Puerto Rico (ICCAT, 2013). In the North Atlantic, spawning occurs from April to July, with a peak in May.

Age and growth

White marlin can reach 280 cm TL and exhibit sexual dimorphism, in common with blue marlin, with females growing to a larger maximum size compared to males (ICCAT, 2013). Both otoliths and dorsal fin spines from white marlin have been used in aging studies and more recently, annual periodicity has been described in the annuli formation of anal fin spines. The estimated age of the fish evaluated ranged 1-13 years, though most were aged 3-8 years (ICCAT, 2013). These assigned ages were consistent with a subset of mark-recaptured fish. The results of tag-recapture studies suggest that white marlin are capable of living 15+ years (Ortiz *et al.*, 2003).

Food and feeding habits

White marlin are opportunistic apex predators that prey on schools of flying fishes, small tunas, dolphinfish, and squids. In the tropical North Atlantic, about 57% of the diet consisted of fish prey, with the families Bramidae and Gempylidae comprising over 75% of stomach contents (ICCAT, 2013). The remaining 42% of prey items were composed mostly of cephalopods. In the northeastern United States, major prey items include the round herring, squids and the flying gurnard (ICCAT, 2013). Other prey items included moon fishes, puffer fishes, pomfret fishes, snake mackerels, and deep water red prawns.

In the western equatorial Atlantic, the most important prey species reported for white marlin were pomfrets, squids and the flying gurnard *Dactylopterus volitans* (ICCAT, 2013). The variety and constant presence of prey items have led some authors to suggest that because of the large muscular mass and high active metabolic rates, the space for visceral mass is reduced (including stomach size) forcing the fish to feed constantly to meet their energy needs.

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).

Sailfish (*Istiophorus albicans*)

Distribution - Pan-tropical distribution, rarely into sub-tropical waters, a more coastal species than oceanic.

Abundance

ICCAT landings for all gear types in the western Atlantic for the period 2000-2011 range from 1-575 t. with a rapid decline in landings reported after 2002. FAO landings figures were not available for sailfish for the western central Atlantic for this period.

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 sailfish tagged and released off the U.S. northeast coast, and recaptured off Suriname after 332 days at large having travelled a distance of 3861 km (Ortiz *et al.* 2003).

Reproduction

In common with other billfishes, sailfish are batch spawners with spawning occurring in the same environment which they normally inhabit. Sailfish spawning grounds in the Atlantic are less well known than those of blue and white marlin but they are known to be primarily in tropical areas (ICCAT, 2010h). In the North Atlantic, spawning females have been found in shallow waters of the Straits of Florida, and larvae have been collected in the same area. In the western central Atlantic (between 5°N and 13°N) and the southeastern Caribbean Sea, spawning females with hydrated oocytes in their gonads have been recorded (ICCAT, 2010h). In the southwest Atlantic, spawning occurs off the southern coast of Brazil between 20° and 27°S. Spawning of Atlantic sailfish takes place almost year round but in different seasons. In the Straits of Florida and adjacent waters, spawning occurs from April to October, with a peak in late summer and early fall (ICCAT, 2010h). In the western central Atlantic, spawning is recorded from February to September and in the southeastern Caribbean Sea, from June through December in the Caribbean (ICCAT, 2010h).

Age and growth
Sailfish age determination and growth have been studied by means of different methodologies (i.e. otoliths, spines, size frequency analysis and tagging). Depending on the study and the methodology used, lengths of Atlantic sailfish at estimated age 1 range from 108.9 to 141.5 cm LJFL (ICCAT, 2010h). Sailfish grow rapidly in early years and exhibit sexually dimorphic growth patterns with females growing larger than males. Sailfish can reach up to 230 cm LJFL however the common size range is 160-180 cm LJFL (ICCAT, 2010h). Tagging experiments have shown that the longest time-at-large of an Atlantic sailfish was 17 years (Ortiz *et al.* 2003).

Food and feeding habits
Adult sailfish are apex predators and they opportunistically prey on schools of small tunas, jacks, halfbeaks and cephalopods. Adult sailfish in the Straits of Florida and adjacent waters feed on little thunny, *Euthynnus aletteratus*, halfbeaks *Hemiramphus sp*, cutlassfish, *Trichurus lepturus*, rudderfish, *Strongylura notatus*, jacks, *Caranx ruber*, and cephalopods (ICCAT, 2010h). In the southern Caribbean Sea, sailfish diet is composed mainly of the scombrids, *Scomber sp* and *Auxis sp*, followed by *Sardinella aurita*, and *Dactylopterus volitans.* In the tropical North Atlantic, about 75% of the diet was of composed of fish prey and the rest was cephalopods. Among prey fish, species, the most important families were Bramidae and Gempylidae. In the western equatorial Atlantic, the most important fish prey species were also bramids and gempylids.

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 fish (e.g., clupeids), but as the schools of prey disperse, so do the schools of sailfish. 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).

Group 3 – Small tunas

Wahoo (*Acanthocybium solandri*)

Distribution - Cosmopolitan, tropical and sub-tropical waters, distributed in western Atlantic to 35° N

Abundance
Reported landings by all gear types in the northwestern Atlantic by ICCAT between 2000- 2011 range from 0 to 693 t. (**Table 3**). Landings reported to FAO for Area 31 (Western Central Atlantic) for all gear types combined for the same period range from 645 to 1,095 t (**Table 3**).

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 (Oxenford et al. 2003). In Bermuda, a small scale wahoo tagging program commenced in 1998 where only 15 wahoo were tagged and released before the program ended. However, a single 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 in 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 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) (Luckhurst and Trott 2000). 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 water temperature (18°C) .
The advent of PSAT tagging of wahoo in recent years has provided important insights into movements, migration and habitat use (Luckhurst 2007). PSAT tags deployed on four wahoo in the western North Atlantic provided data over a total of 198 days. 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. 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).

Reproduction

Wahoo exhibits early sexual maturity (within the first year) and an extended spawning season (May to October) in the western central Atlantic (Oxenford *et al* 2003). Females are multiple batch spawners and are highly fecund. A female 131 cm FL was estimated to produce about six million eggs per spawning batch (Collette and Nauen 1983).

Both males and females from North Carolina reach sexual maturity during their first year, at about 860 mm total length (TL) and 3.4 kg total weight for males and 1010 mm TL and 5.4 kg for females (Hogarth 1976). In Bermuda, preliminary data for wahoo suggest that size at maturity is around 1020 mm FL for males, while females are smaller (950 mm FL) (SAFMC 1998). These differences between North Carolina and Bermuda may be due to sample sizes. Along the southeastern coast of the US, the spawning period is from June through August (Manooch 1984)., similar to that of Bermuda which is one month longer starting in May (Oxenford *et al* 2003). In a recent study, Jenkins and McBride (2009) determined that wahoo in Florida and northern Bahamas, had a single summer spawning season from June to August. Spawning frequency was every five days and batch fecundity correlated with body size varying from 0.44 to 1.67 million eggs per batch. Size at 50% female maturity was 925 mm FL at an age of 0.64 yrs (Jenkins and McBride 2009).

Age and growth

Limited age and growth studies on wahoo indicate that it is a relatively fast-growing species, has high mortality and probably lives for 5–6 years (Oxenford et al 2003). There is uncertainty involved in aging wahoo, as scales are unreadable and vertebrae annuli are inconsistent (Hogarth 1976). Furthermore, otolith microstructure is complex, and there has been no successful validation of presumed annuli or daily growth checks in otoliths to date. The few studies that have been conducted concur that wahoo is a relatively fast-growing species, particularly in the first year, and estimated size-at-age for wahoo from several locations and/or using different aging techniques produced similar results. Wahoo from the northern Gulf of Mexico and from Bimini in the Bahamas have been tentatively aged using unvalidated annuli in thin-sectioned dorsal fin spines (Franks et al. 2000). From Bimini, there was no difference between the sexes in size-at-age estimates. From the northern Gulf, up to six annuli were detected in the largest specimens and again there was no difference in size-at-age estimates between males and females. Hogarth

(1976) aged wahoo from North Carolina using presumed annuli in whole sagittal otoliths. He used back calculation of lengths at annulus formation to estimate length-at-age and suggested a five year life-span. Presumed annuli as well as apparent daily growth checks were clearly visible on the sagittal otoliths from Bermuda wahoo, under a scanning electron microscope (Luckhurst et al. 1997). However, no size-at-age data were produced in this preliminary study and an attempt to validate the periodicity of the growth checks with an otolith marking (oxytetracycline) tag-recapture program in Bermuda was not successful. However, a single tag-recapture from this study indicated rapid growth from 5 to 15 kg in a wahoo at liberty for 10 months (Nash et al. 2002).

Food and feeding habits

Wahoo are fast and voracious predators that feed primarily on fishes such as frigate mackerel, round herring and butterfish along the southeastern coast of the US (Manooch 1984). This author notes that the most productive fishing areas for wahoo are often in the vicinity of *Sargassum* mats. Wahoo are known to prey upon scombrids, flyingfishes, clupeids, scads and other pelagic fishes and squids (Collette and Nauen 1983). In Bermuda, little tunny (*Euthynnus alletteratus*) and flyingfishes are common fish prey (Luckhurst in Oxenford et al 2003). The groups of key importance to the diet are similar among locations and comprise fast swimming pelagic families (scombrids, exocoetids, clupeids, and cephalopods) as well as those fish families which are generally associated with floating material such as *Sargassum*. This indicates that wahoo forage in open water as well as below floating objects (Oxenford et al 2003). Small items do not appear to feature in the diet, probably because wahoo lack gill rakers, and there is no apparent relationship between predator and prey size since wahoo can bite large prey into pieces.

Ecology and oceanography

Wahoo are 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. Straight-line distances moved (deployment to pop-up) ranged from 162.5 to 1,960 km The movement patterns of these tagged fish appeared to be largely north-south movements in relation to the Gulf Stream. 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).

Blackfin tuna (*Thunnus atlanticus*)

Distribution - Tropical and sub-tropical waters but restricted to western Atlantic to 40° N

Abundance

Reported landings by all gear types in the western Atlantic by ICCAT between 2000- 2011 range from 10 31 to 4,756 t (**Table 3**). Landings reported to FAO for Area 31 (Western Central Atlantic) for all gear types combined range from 1,364 to 4,208 t (**Table 3**).

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 be occurring in the summer months. An examination of commercial landings of blackfin in Bermuda between 1987-1998 indicate that the proportion of annual landings taken in the third quarter (July-September) ranges from approximately 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 above 20°C (Collette and Nauen 1983).

Another line of evidence is derived from tag-recapture results in Bermuda. The tag-recapture rate of blackfin until 1999 was 10.7% compared to 3.5% for the western Atlantic (Luckhurst *et al* 2001). All 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 migration to the Bermuda Seamount.

Reproduction

Collette and Nauen (1983) indicated that blackfin spawning grounds were located well offshore. The spawning season in Florida is reported to be from April to November with a peak in May, while in the Gulf of Mexico it is reportedly shorter (June to September). Along the southeast coast of the US, blackfin are believed to spawn offshore in the warm waters of the Gulf Stream. Ripe females have been collected off North Carolina from June to September (Manooch 1984). Both sexes are believed to reach sexual maturity at age two years (Manooch 1984) and at about 49 cm FL (FishBase). In a study in northeastern Brazil, Vieira et al (2005) found that 50% of females reached maturity at 51cm TL and all were mature by 57.5cm TL. The minimum size of first maturity for the blackfin tuna near Cuba is 39 cm in fork length (Claro et al 2001).

Age and growth

In common with oceanic pelagic species, blackfin are fast-growing and short-lived. The maximum reported size is 108cm FL (FishBase) and the maximum age is probably 5-6 years old. The longest time-at-liberty for a tag-recaptured blackfin in Bermuda was four years (Luckhurst *et al* 2001) thus lending support to the estimate of maximum age. In a study of blackfin tuna caught around moored FADs in Martinique, Doray et al (2004) indicated that blackfin of 32 cm FL were about 7 months old and when they returned as adults the following year they were about 52 cm FL – 1.5 years old. The oldest fish in their study was less than 3 years old.

Food and feeding habits

Blackfin are not primarily piscivorous but also feed on a wide variety of small crustaceans (stomatopod larvae, crab and shrimp larvae). Off North Carolina, the major prey groups of blackfin are crustaceans, juvenile fishes and squid (Manooch 1984).

Predator – prey - Blackfin compete with skipjack tuna for food and they are occasionally preyed upon by skipjack. Other predators of blackfin are blue marlin and dolphinfish (Collette and Nauen 1983).

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. It frequently forms large mixed schools with skipjack tuna (Collette and Nauen 1983). 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 in the size group 35-48 cm FL found around the FADs and it was postulated that these juveniles probably leave the vicinity of moored FADs to undergo a trophic migration and then come back the following year as adults to spawn in the area of the Lesser Antilles.

Little tunny (*Euthynnus alletteratus*)

Distribution - Tropical and sub-tropical waters of Atlantic, to 40° N in the western Atlantic, also in the Mediterranean Sea.

Abundance

Reported landings for all gear types combined in the northwestern Atlantic by ICCAT between 2000- 2011 range from 0 to 3100 t. (**Table 3**). Landings reported to FAO for Area 31 (Western Central Atlantic) for all gear types combined range from 247 to 2,559 t (**Table 3**).

Migration and movements

Very little is known about the migratory habits of Little Tunny in the western Atlantic. They are an epipelagic, neritic species which typically occurs in inshore waters, forming schools of similar-sized fish but they have a tendency to scatter during certain times of the year (Collette and Nauen 1983). In Bermuda, they appear in inshore waters quite suddenly in the summer months where they are taken by seine nets to be used for bait (Luckhurst, pers. obs.). They appear not to be present during the winter months suggesting that this may be a 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 eastern seaboard in the spring and return southward in the fall.

Reproduction

Little Tunny are batch spawners with asynchronous oocyte development and spawning occurs from April to November in the western Atlantic (Collette and Nauen 1983). Little Tunny reach sexual maturity at 35cm FL off Florida. In contrast, spawning occurs from January till May off tropical African coasts and sexual maturity is attained at 44cm FL and 42cm FL in the Gulf of Guinea for males and females respectively (ICCAT, 2010i). Off the eastern seaboard of the US, Little Tunny spawn in all months of the year except December and spawning areas have been identified in offshore waters in depths of 30-100m. Females at age one are capable of spawning (Manooch 1984).

Age and growth

Little Tunny are fast-growing with males attaining larger sizes than females (ICCAT, 2010i). The maximum size recorded for this species is 122cm TL and a maximum weight of 16.5 kg (FishBase). Little Tunny are approximately 35 cm FL at age one and 76 cm FL at age four but they seldom live longer than five years (Manooch 1984). However, a maximum age of 10 years has been reported (FishBase).

Food and feeding habits

Little Tunny are opportunistic predators and feed on virtually any prey group within its range including crustaceans, fishes, squids, heteropods and tunicates (Collette and Nauen 1983). Along the southeastern coast of the US, they feed almost exclusively on small crustaceans, herring, sardines, scad and squids (Manooch 1984) . In a study in the northwest Atlantic, fish dominated as the functional prey group (99%) of Little Tunny (Bowman et al 2000).

Predator-prey - Little Tunny are preyed upon by large yellowfin tuna and billfishes (Collette and Nauen 1983) as well as by wahoo.

Ecology and oceanography

Little Tunny are usually found in coastal waters with swift currents, near shoals and around the warmer waters of thermal fronts and upwelling areas. They are more coastal than other tuna species. It is most abundant in the tropical Atlantic where the water temperature is 24º to 30º (ICCAT 2010i). This species lives in schools by size 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 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 into the Sargasso Sea. This may be of ecological significance as they are an important prey species in the diets of larger pelagic species.

Dolphinfish (*Coryphaena hippurus*)

Distribution - Cosmopolitan, tropical and sub-tropical waters, distributed across Atlantic to 40° N

Abundance
There are no reported landings of dolphinfish by ICCAT. However, landings reported to FAO for Area 31 (Western Central Atlantic) for all gear types combined for the period 2000-2011 range from 3,233 to 5,272t (**Table 3**).

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 often closely 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 **(Figure 8**). 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 finding is consistent with a highly migratory species.

Reproduction .
There is general agreement among researchers that all dolphinfish in the western central Atlantic reach sexual maturity in the first year of life (Oxenford 1999). The presence of several size classes of eggs in the ovaries indicates that they are batch spawners and probably spawn at least two or three times in each spawning period (Oxenford 1999). Dolphinfish have an extended spawning season which varies with latitude; fish collected in the Gulf Stream off North Carolina were spawning in June and July (Manooch 1984). In a more recent study on dolphinfish conducted off North Carolina, Schwenke and Buckel (2008) reported that the size at 50% maturity was slightly smaller for female (460 mm FL) than male (475 mm FL). Based on monthly length-adjusted gonad weights, peak spawning occurred from April through July. Back-calculated hatching dates from age-0 dolphinfish and prior reproductive studies on the east coast of Florida indicate that dolphinfish spawning occurs year round off the U.S. east coast and highest levels range from January through June. The highest median gonadosomatic index (GSI) values occurred in May for both males and females (Schwenke and Buckel 2008). Length-adjusted mean gonad weights were highest in the late spring and summer and then decreased from midsummer into the fall.

Age and growth
Dolphinfish are fast-growing and probably live less than five years. Males grow faster and live longer than females (Oxenford, 1999). Off North Carolina, mean fork lengths for sexes combined were: age 1 – 86.9 cm FL, age 2 – 110.7 cm FL, age 3 – 127 cm FL, age 4 – 141 cm FL (Manooch 1984). In a more recent study off North Carolina, the estimated average growth rate was 3.78 mm/day during the first six months. The oldest fish sampled in this study was three years old (Schwenke and Buckel 2008). In the Caribbean and the Gulf of Mexico, dolphinfish growth rates are considerably higher than those reported in North Carolina and they are often considered "annual" fish because of their short life span (Oxenford, 1999). The differences in growth curves between various locations in the western central Atlantic (**Figure 9**) are informative.

Food and feeding habits
Dolphinfish seem to be highly attracted to floating objects and off the southeastern US, they frequently congregate around *Sargassum* , which serves as both shelter and a source of food (Manooch 1984). Many of the food types eaten by dolphinfish e.g. small fish, crabs and shrimps are found in floating mats of *Sargassum* and this alga is frequently found in their stomach contents, but this is probably an incidental intake associated with foraging in the *Sargassum* communities. Dolphinfish feed primarily during the day, as they rely upon their vision (as well as their

lateral line system) to detect prey (Oxenford 1999). There is evidence that they may also feed at night when the moon provides ample light. Feeding behavior of dolphinfish varies greatly – sometimes they are voracious predators that pursue and capture fast-swimming prey such as flying fish and mackerels while at other times they simply nibble on small crustaceans found in floating *Sargassum* mats (Manooch 1984).

Predator –prey. The diets of oceanic pelagic species indicate that dolphinfish, particularly juveniles, are an important prey item. Predators of dolphinfish include large tunas – yellowfin, albacore; billfishes – blue marlin, white marlin, sailfish, swordfish and sharks (Oxenford 1999).

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.

Group 4 – Sharks

Shortfin mako (*Isurus oxyrinchus*)

Distribution - Cosmopolitan, tropical and sub-tropical waters, distributed across Atlantic to 50° N. In the Atlantic, it ranges from Newfoundland to Argentina in the west and from Norway to South Africa in the east (Compagno 1984).

Abundance

Reported longline landings in the NW Atlantic by ICCAT between 2000- 2011 range from 101 to 347 t. (**Table 4**). Landings reported to FAO for Area 31 (Western Central Atlantic) with all gear types combined range from 15 to 472 (**Table 4**).

Migration and movements

In a long term shark tagging program (1962-2000), a total of 5,333 mako sharks were tagged. A total of 608 makos were recaptured (11.4%). Distances travelled ranged from no movement to a maximum of 5,310 km (**Figure 10)** (Kohler *et al* 2002). The maximum distance travelled was a transatlantic migration, the tagged mako moving from the northeastern U.S. and recaptured 1.4 years later off west Africa. Approximately 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. The 12.8-year recapture was a male mako 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. From January through April, shortfin makos are seldom taken on the continental shelf north of Cape Hatteras. In April and May, as inshore shelf waters warm and the Gulf Stream moves farther north, mako sharks begin moving northward onto the continental shelf between Cape Hatteras and the southern part of Georges Bank. From June through October, makos are caught by anglers on the continental shelf between Cape Hatteras and Cape Cod and also in southern parts of the Gulf of Maine. 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.

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). 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 route that makos might travel in this water into the Caribbean and then into the Gulf of Mexico and the Florida Straits is consistent with the tag returns from those areas. However, 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).

Reproduction

The shortfin mako is ovoviviparous and oophagous. Earlier studies suggested a gestation period for Atlantic shortfin mako of approximately 12 months but more recent work indicates that it may be up to 3 years (ICCAT, 2008). Parturition occurs mainly in late winter to mid-spring in both hemispheres. The number of young generally ranges from 4 to 18 per litter with a mean litter size of 12.5 (ICCAT, 2008). Litter size is reported to increase with maternal length . Sex ratio at birth is considered 1:1 and size at birth ranges from 59-68 cm FL in the western North Atlantic (Kohler *et al* 2002). Size at maturity for male and female shortfin makos is reported as 179 and 258 cm FL, respectively. A median size at maturity of females from the western North Atlantic is given as 275 cm FL. In a more recent study, Natanson et al (2006) found that size at 50% maturity was 185 cm FL for males and 275 cm FL for females, confirming the earlier estimate for females.

Age and growth

Age and growth estimates were generated using a combination of methods – counts on vertebrae, tag-recapture data and length-frequency analysis. Males were aged to 29 years (260 cm FL) and females were aged to 32 years (335 cm FL) (Natanson et al, 2006). Both sexes grew at a similar rate until age 11(males = 207 cm FL, females = 212 cm FL) at which point the curve for males leveled off and the female curve kept rising (Natanson et al, 2006). Age at 50% maturity for males was 8 years (185 cm FL) and for females 18 years (275 cm FL).

Food and feeding habits

Analysis of the stomach contents of shortfin mako sharks collected from Cape Hatteras to the Grand Banks demonstrated that teleost remains occurred in 67% of the diet with bluefish (*Pomatomus saltatrix*) constituting 78% of the diet by volume (Stillwell and Kohler 1982). Other fish consumed included scombrids, clupeids, alepisaurids and swordfish. Cephalopods comprised 15% of the overall diet by occurrence and were found in specimens taken primarily offshore while bluefish dominated the inshore diet. Food was present in 68% of the stomach samples and averaged approximately 2% of its body weight. Average food volume increased with increasing predator length suggesting that makos may shift to larger prey items such as swordfish as they grow larger (Stillwell and Kohler 1982). Bowman et al (2000) reported only two functional prey groups from the stomachs of shortfin mako taken in the northwest Atlantic, fish (98.2%) and squid (1.4%).

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 lie in a narrow range between 17° and 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 Spanish swordfish longline fishery, which covers an extensive area between Spain and the Grand Banks, also shows the highest catch rates for mako sharks in surface temperatures of 18°C in the region east of the Grand Banks and 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.

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 0–556 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.

Blue shark (Prionace glauca)

Distribution Cosmopolitan, tropical to warm-temperate, distributed across Atlantic to at least 40 deg. N

Abundance
The blue shark is considered the most abundant species among all the pelagic sharks in the Atlantic (Kohler *et al* 2002). Reported longline landings in the NW Atlantic by ICCAT between 2000- 2011 range from 0 to 2,667 t. This range probably reflects a lack of adequate reporting of landings until recent years (**Table 4**). Landings reported to FAO for Area 31 (Western Central Atlantic) with all gear types combined range from 0 to 11,036 t (**Table 4**). There has been growing concern about the status of shark populations in the past 10-15 years and increasingly aggressive attempts to collect more accurate statistics to conduct assessments.

Migration and movements
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 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 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 and 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 the northwestern North Atlantic in late May and early June where they interact with adult males (4-5 year olds). The high incidence of mating scars and the presence of sperm in the oviducal gland indicates a summer breeding season for the blue shark. This process continues as late as November off the northeast coast of the United States. Once the females are inseminated, they move offshore where 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 from North Carolina to the Grand Banks. They are common in shallow water off southern New England and found offshore from the outer edge of the continental shelf and the Gulf Stream. In late summer and fall, most of the blue sharks along the eastern North American coast begin moving south and offshore to areas including the southeastern United States, Caribbean Sea and the central Atlantic (Kohler *et al* 2002).

Distances traveled for tagged blue shark ranged from no movement to 6,926 km. The 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 blue sharks traveled less than 1,852 km from their original tagging location with a mean distance of 857 km (**Figure 11**). 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).

Reproduction

Blue sharks are placentally viviparous and gestation lasts about 12 months (ICCAT, 2008). Size at maturity in the western North Atlantic is reported as 183 cm FL for the males whereas the females pass through a sub-adult phase from 145-185 cm FL (Kohler *et al* 2002). Females mature at an age of 5.5 years and have an expected longevity of 15 years (ICCAT, 2008). In the western North Atlantic, young are born in the spring and summer. The number of young ranges from 4-75 per litter (ICCAT, 2008) with a generally reported sex ratio of 1:1 at birth.

Age and growth

Age and growth for the blue shark has been extensively studied in the Atlantic and Pacific Oceans. Skomal and Natanson (2001) derived a validated age curve for the blue shark in the North Atlantic. They aged males and females at 16 and 13 years, respectively and estimated longevity to be between 20-26 years of age. Using their results, males mature at 4-5 years of age (183 cm FL); subadult females would mature at 3 years of age (145 cm FL), and females would become fully mature by 5 years of age(185 cm FL) (Skomal and Natanson, 2001)

Food and feeding habits

Blue sharks consume cephalopods as a primary component of their diet as well as various species of locally abundant pelagic and demersal teleosts. They also prey upon marine mammals and elasmobranchs (Kohler *et al* 2002). Food was present in 52% of the stomachs sampled in the western North Atlantic where regional and seasonal differences in diet were reported (Kohler *et al* 2002). In a study of food habits in the northwest Atlantic, Bowman *et al* (2000) found three functional prey groups in stomach contents of blue sharks the most important of which was fish (53.9%) followed by squid (33.8%) with the remainder undefined. In a study conducted in the northeast Atlantic, Henderson et al (2001) reported finding the same major prey groups i.e.fish and cephalopods in blue shark stomach contents as in other studies but included seabirds and crustaceans among the contents as well.

Ecology and oceanography

It is generally acknowledged that most shark species segregate by size and sex during various stages of their life history and the blue shark certainly conforms to this pattern. Evidence from tagging studies and catch data suggest that there are distinct seasonal abundances and seasonal latitudinal migrations. Reproductive condition, seasonal variations in water temperature and availability of prey strongly influence the distribution and movements of blue sharks (Kohler *et al* 2002). Based on evidence from 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. Sex ratios of nearly 1:1 are found in the western North Atlantic with primarily females in the northeastern Atlantic and Mediterranean and primarily males in the southeastern region. The one stock hypothesis involving a complex reproductive cycle with mating areas in the northwestern North Atlantic and pupping areas in the eastern North Atlantic is supported by various lines of evidence. Documented seasonal migrations to the higher latitudes take place on both sides of the North Atlantic. Sizes of blue sharks generally decrease with increasing latitude.

Porbeagle shark (Lamna nasus)

Distribution - Cold temperate and subarctic waters (30 -70° N), separate stocks occur in the NW and NE Atlantic. It does not occur in equatorial seas (Compagno 1984),

Abundance

Reported landings by ICCAT of porbeagle shark from the Northwest Atlantic from 2000-2011 declined from 902 t. in 2000 to 8 t. in 2008 when the Canadian fishery was closed due to concerns about overfishing. There are no reported landings by ICCAT from 2009-2011. Reported landings to FAO (Area 31 – Western Central Atlantic) only occurred in 2009 with 13 t. being reported.

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 (**Figure 12**). Times at liberty ranged from 1 day to 9.2 years and this longest recapture was of a male porbeagle tagged off the coast of Massachusetts and recaptured to the northeast of Nova Scotia, Canada. Almost 75% of tagged porbeagles were at liberty for less than 4 years with a mean of 2.7 years (Kohler *et al* 2002).

The results of PSAT tagging of 21 porbeagles off eastern Canada has revealed a great deal of new information. Males and immature sharks of both sexes remained primarily on the continental shelf for periods of almost a year after tagging. Mature females, however, undertook lengthy migrations of up to 2,356 km through the winter at depths down to 1,360 m beneath the Gulf Stream to pupping grounds in the **Sargasso Sea** (Campana et al 2010 b).

Reproduction

Porbeagle sharks are ovoviviparous and oophagous and exhibit low fecundity with an average litter size of four in the NW Atlantic. They also have a late age of sexual maturation with females not reaching sexual maturity until age 13 years (ICCAT 2008). Females mature between 205-230 cm FL (age 13) while males mature at a smaller size (160-190 cm FL) and a younger age (8 years) (Campana et al 2010 a). Porbeagles breed on both sides of the North Atlantic. In the western Atlantic, embryos have been recorded from Massachusetts to Atlantic Canada. Research indicates that mating occurs in at least two locations in the Canadian Maritimes: 1) on the Grand Banks, off southern Newfoundland and 2) at the entrance to the Gulf of St. Lawrence (Campana et al 2010 a). Most large females collected in these areas in the late summer or early fall were pregnant, suggesting that mating took place during the summer. Birth apparently occurs in late winter or spring after an 8-9 month gestation period. There is no evidence of an extended latency period after birth, since virtually all sexually mature females are pregnant in the fall indicating a reproductive cycle of one year (ICCAT 2008). The location of the pupping ground had remained unknown until the results of PSAT tagging revealed that it was located in the sub-tropical waters of the Sargasso Sea well south of porbeagles documented range (Campana et al 2010 b).

Age and growth

Growth parameter estimates have been calculated for the porbeagle in the western North Atlantic using band counts of vertebral annuli, length-frequency analysis, and tag-recapture data. In earlier work, annual band pair periodicity was validated up to 11 years with oxytetracycline-injected and known age sharks (Natanson et al 2002). Subsequently, it has been determined that Porbeagle age can be most accurately determined from vertebral sections (Campana *et al.* 2010 a). The life span of porbeagle is estimated to be between 25 and 46 years and generation time is about 18 years (Campana *et al.* 2010 a). In both sexes, growth rate appears to decrease slightly at the onset of sexual maturity. Since females mature at an older age than do males, females grow to a larger size.

Food and feeding habits

The porbeagle is primarily an opportunistic piscivore with a diet characterized by a wide range of species. Teleosts occurred in the majority of stomachs and constituted 91% of the diet by weight. Cephalopods were the second most important prey category and were found in 12% of contents (Campana *et al.* 2010a). Diet composition changed seasonally following a migration from deep to shallow water. With increase in shark size, the relative contribution of groundfish increased while that of cephalopods decreased. Other elasmobranchs were occasionally eaten by large porbeagles, but marine mammals and birds were never found in the stomachs (Campana *et al.* 2010a).

In another study of Porbeagle stomach contents in the western North Atlantic, small pelagic schooling fishes such as mackerels, clupeids, gadids, and dogfishes were found as well as squid (Kohler et al 2002). Frequency of occurrence for teleosts was 47% and squid was 12%. In contrast, Bowman et al (2000) found that squid dominated as the functional prey group comprising 99% by weight of stomach contents.

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 even though the thermal preference was similar to that observed in the spring (5-10°C).

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.

Bigeye thresher shark (*Alopias supercilliosus*)

Distribution Cosmopolitan, tropical to temperate, distributed across North Atlantic to at least 40° N

Abundance

There are no reported landings of bigeye thresher in the NW Atlantic until 2008 when 10 t were reported. From 2009 to 2011, the reported landings were 38 t, 20 t, and 8 t respectively. FAO does not report any landings of bigeye thresher in the western central Atlantic.

Migration and movements

Weng and Block (2004) tracked a bigeye thresher shark in the Gulf of Mexico for 60 days, and another in the Hawaiian Archipelago for 27 days, by using PSAT tags. The shark in the Gulf of Mexico moved a straight-line distance of 320 km during the track, starting from the central Gulf in depths exceeding 3000 m and moving to waters 150 km south of the Mississippi Delta where depths were approximately 1000 m. The second shark tagged off Hawaii moved a straight-line distance of 1125 km.

Reproduction

After examining over 1,000 specimens from the northeast Atlantic and western Mediterranean, Moreno and Moron (1992) estimated that size at maturity for males was 276 cm TL based on clasper development while the smallest gravid female was 341 cm TL. Size at birth was estimated to be at least 100 cm TL. Six males measured between 400-410 cm TL,exceeding the previous maximum size for males.

Bigeye thresher have very small litter sizes (mean = 2) and females take a long time to reach sexual maturity (12-13 years) (ICCAT 2008). The reproductive period is about one year and generation time is estimated at 17 yrs. These factors along with a slow growth rate (see Age and Growth), place Bigeye Thresher sharks near the top of the Ecological Risk Assessment list (ICCAT 2008).

Age and growth

Fernandez-Carvalho et al (2011) determined that that band enhancement techniques of vertebrae were necessary in order to use them for age estimation. The total of 117 specimens ranged in size from 101-242 cm FL (176-407 cm TL). Estimated ages of females ranged from 2-22 years and 1-17 years for males. The von Bertalanffy growth model (VGBF) produced the best fit to the data and the estimated growth coefficients confirmed that Bigeye

Thresher sharks are amongst the slowest-growing pelagic sharks making them highly vulnerable to fishing pressure Fernandez-Carvalho et al (2011) An earlier assessment of female longevity estimated it to be 20 years (ICCAT 2008).

Food and feeding habits

Bigeye thresher sharks have a diverse diet and may feed opportunistically on locally and temporally available prey, including epipelagic, mesopelagic, epi-benthic, and deep scattering- layer species. Electronic tracking data demonstrates that the bigeye thresher is predominately a deepwater species, but spends time both within the deep scattering and the mixed-surface layers (Preti et al 2008). In a study of food habits in the northwest Atlantic, Bowman et al (2000) found that the primary functional prey group of this species was fish (83.5%) followed by squid (15.1%).

Ecology and oceanography

An epipelagic and mesopelagic species, it is found primarily in oceanic and neritic waters, over continental and insular shelves where surface temperatures range from 15°–26°C (Compagno 2001). The depth and temperature distribution of a bigeye thresher shark fitted with a PSAT tag and tracked in the Gulf of Mexico for 60 days showed a strong diel movement pattern. This shark spent the majority of the daytime (84%) below the thermocline at depths of 300- 500 m and the majority of nighttime (80%) in the mixed layer and upper thermocline between 10 m and 100 m (Weng and Block 2004), The shark spent most of the daytime (70%) in deeper waters of 6°C to 12°C and most of the nighttime (70%) in shallower waters from 20°C to 26°.

Basking shark (*Cetorhinus maximus*)

Distribution - Basking sharks are found circumglobally in temperate coastal shelf waters but are patchy in distribution (Compagno 2001).

Abundance

Basking sharks have been listed under Appendix 2 of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and IUCN has listed the species as vulnerable globally and endangered in the northeast Atlantic and in the north Pacific. There are effectively no landings of basking shark reported for the northwest Atlantic by ICCAT except for a figure of 5 t in 2005. FAO does not report any landings of basking sharks in the western central Atlantic.

Migration and movements

Movement patterns of basking sharks have been poorly understood because of the difficultly in tracking them. The advent of PSAT tagging has revealed hitherto unknown migrations and habitat use. Basking sharks fitted with PSAT tags off England and Scotland allowed movements to be tracked on seasonal scales (1.7 to 6.5 months). The results showed that they do not hibernate during winter as previously hypothesized but instead undertake extensive horizontal (up to 3400 km) and vertical (>750 m depth) movements to utilise productive continental-shelf and shelf-edge habitats during summer, autumn and winter (Sims et al 2003). They travel long distances (390 to 460 km) to locate temporally discrete productivity'hotspots' at shelf-break fronts, but at no time were there prolonged movements into open-ocean regions away from shelf waters. Basking sharks have a very broad vertical diving range and can dive beyond the known range of planktivorous whales (Sims et al 2003). This study suggests that basking sharks can exploit shelf and slope-associated zooplankton communities in mesopelagic (200 to 1000 m) as well as epipelagic habitat (0 to 200 m). Basking sharks have been assumed until recently to remain in discrete populations with their known distribution encompassing temperate continental shelf areas. Until this study, there was no evidence of trans-Atlantic migration. The results from the tracks and behaviour of two basking sharks tagged off the British Isles, demonstrated a transit of the North Atlantic by one of the sharks covering a horizontal distance of 9,589 km and diving to a record depth of 1264 m (Gore et al 2008). This transit was accomplished in 82 days. The second shark moved over 1800 km in 41 days to a location off the Scottish coast. This result provides the first evidence for a link between European and American populations and indicates that basking sharks make use of deep-water habitats beyond the shelf edge (Gore et al 2008).

In another example of large scale migration, Skomal et al (2009) demonstrated that PSAT-tagged basking sharks make seasonal migrations from temperate feeding areas off the northeast coast of the US to the Bahamas and Caribbean Sea before moving further south to cross the equator into the Southern Hemisphere. When in these equatorial areas, basking sharks descended to mesopelagic depths and, in some cases, remained there for weeks to months Skomal et al (2009). The results of this study demonstrate that tropical waters are not a barrier to migratory connectivity for basking shark populations. A female basking shark PSAT-tagged off the coast of Massachusetts in the autumn moved approximately 800 km south along the continental shelf to North Carolina in 71 days (Skomal et al, 2004). During the tracking period the shark was vertically active covering a depth range of 0-320 m. It showed a marked temperature preference remaining in a narrow temperature range (15-17.5°C) for 72% of the tracking period (Skomal et al, 2004) while associating with the continental shelf and shelf edge.

Reproduction

The life cycle and reproduction of basking sharks are poorly understood, but assumed to be similar to other lamnoid sharks. They are believed to be ovoviviparous, giving birth to live pups during the summer after a gestation period of 2.5-3.5 years (Pauly 2002). Length at birth has been measured in only six embryos from a single litter, where the young were 1.5 to 2 meters in length (Compagno 2001). It is believed that males mature at a length of 4.6 - 6 m (based on clasper development) and an age of 12-16 years. Females presumably reach sexual maturity at a slightly larger size and at an age of 16-20 years. However, the problems associated with age estimation noted by Natanson et al (2008) (see Age and growth section) mean that these estimates must be regarded with caution. Breeding has not been observed but putative mating aggregations have been observed in the southern Gulf of Maine in early September on the warm side of a thermal front and the behaviors exhibited may represent group courtship (Wilson 2004). Sims *et al* (2000a) observed putative courtship behavior of basking sharks off southwest England from May to July along oceanographic fronts, probably as a result of sharks aggregating to forage on rich prey patches before initiating courtship. Many of the social behaviours observed were prolonged and appeared to be consistent with courtship.

Age and growth

Longevity is presumed to be approximately 50 years, but the basis for age estimation in basking sharks is weak. Pauly (2002) analyzed earlier aging data from basking sharks in conjunction with other shark data and concluded that a longevity of 50 yr was likely. Natanson et al (2008) indicated that there were significant problems in aging basking sharks using vertebral growth patterns because band pair deposition may be related to growth and not to time and thus they concluded that basking sharks cannot be directly aged using vertebral counts. Sims *et al* (2000b) estimated a growth increment of 2-4 m in a female basking shark that was re-sighted after three years.

Food and feeding habits

Basking sharks are the second largest fish in the oceans but like whale sharks, they are planktivorous. In a study off the coast of England, basking sharks were tracked in response to zooplankton gradients. The results showed that they are selective filter-feeders that choose the richest, most profitable plankton patches (Sims *et al*, 2000a). They forage along thermal fronts and actively select areas that contain high densities of large zooplankton above a threshold density. They may remain for over a day in rich patches that are transported by tidal currents and move between patches every 1-2 days (Sims *et al* 2000a). Mapping showed that the location of basking sharks indicated the distribution, density and characteristics of zooplankton directly.

Ecology and oceanography

Basking sharks appear to actively seek out thermal fronts, areas that typically contain high densities of zooplankton, to maximize their feeding efficiency (Sims *et al*, 2000a). When their observed mean foraging threshold of 0.62 g/m³ of zooplankton is exceeded, there is a net energy gain and thus basking sharks seek out the most dense zooplankton patches possible. Sims et al (2003) have demonstrated that basking sharks make extensive movements along the continental-shelf to reach productive habitats for feeding during summer, autumn and winter. They also use a broad range of vertical habitats to locate temporally discrete areas of high zooplankton production and selectively feed on them.

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, dolphinfish, yellowfin tuna and wahoo in the North Atlantic. They classified prey into three groups1) prey associated with floating Sargassum , 2) Flying fish (Exocoetidae) - associated with Sargassum during spawning and 3) schooling prey, primarily Auxis sp. and cephalopods. The dominant prey of yellowfin tuna (>50cm FL) were flying fish, as well as scombrids (mackerels, tuna, wahoos) 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 Sargassum habitat for a principal prey group 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 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). The following brief summary highlights the importance of the Sargasso Sea for the species presented in this paper:

Group 1- Principal tunas

Yellowfin tuna
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) 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 3**). In terms of feeding, Manooch and Mason (1983) reported finding *Sargassum* fragments in 26% of yellowfin stomach contents, although they stated that ingestion was probably incidental with their normal prey.

Albacore tuna
The distribution of areas suitable for albacore in the North Atlantic in their preferred thermal range of 10-20ºC. includes the entire Sargasso Sea area and most of the north Atlantic (ICCAT, 2010b). The Sargasso Sea has been identified as a spawning ground for albacore in the North Atlantic (ICCAT, 2010b). Other spawning grounds include offshore waters of Venezuela and the Gulf of Mexico.

Bigeye tuna
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 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
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. Recent PSAT tagging of bluefin tagged in the Gulf of Mexico in May indicates that some fish may enter the Florida Straits and then migrate northward through the Sargasso Sea towards the Gulf of Maine (Eric Prince, pers. com.). 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.

Skipjack tuna
Skipjack are the most tropical of the principal tuna species and most of the research on them has been conducted in the eastern tropical Atlantic. In the western Atlantic, there is very little information from tagging with the only migrations being along the Brazilian coast and with minor movements in the Caribbean. 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.). Reported annual landings of skipjack in Bermuda are generally under 500 kg (Smith-Vaniz et al 1999) indicating a very minor fisheries presence.

Group 2 – Swordfish and billfishes

Swordfish
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). These data support the results obtained from earlier conventional tagging, where the movement vectors of swordfish appeared to be north-south, transiting the Sargasso Sea (Luckhurst, 2007). Although the reasons for this seasonal movement are unclear, it may well be associated with feeding and prey concentration in thermal boundaries between water masses, suggesting that the Sargasso Sea and associated oceanographic features may be a productive feeding ground (ICCAT, 2010f).

Blue marlin
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
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 known to spawn in the Sargasso Sea (NMFS, 2007)

Sailfish
Sailfish are the most tropical of the istiophorid billfishes and are rarely encountered in Bermuda waters. They have no known specific association with the Sargasso Sea.

Group 3 – Small tunas

Wahoo
Wahoo are the most important species in the Bermuda commercial fishery and are seasonally abundant in the second and third quarters (Luckhurst and Trott 2000). They are also known to actively spawn in Bermuda waters in the summer months (Oxenford et al 2003) but there is no evidence of a specific association with the Sargasso Sea.

Blackfin tuna
Blackfin are most abundant in Bermuda waters in the third quarter when water temperatures are warmest (Luckhurst et al 2001). This appears to be a seasonal migration from the more southerly areas of their distribution presumably for feeding but it is not known if blackfin spawn in Bermuda waters (Luckhurst, pers. obs.). Manooch and Mason (1983) found fragments of *Sargassum* in 12% of the stomach contents of blackfin which they examined but believed that the fragments were ingested accidently.

Little Tunny

Aside from their seasonal presence in Bermuda waters noted earlier, Little Tunny have no known specific association with the Sargasso Sea.

Dolphinfish

Dolphinfish seem to be highly 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 Oxenford and Hunte (1986) proposed that there were two migration circuits of dolphinfish in the central western Atlantic. Their proposed northeastern migration circuit showed dolphinfish migrating through the Sargasso Sea to Bermuda and then moving south on their return to the Caribbean **(Figure 8**). Aside from this hypothesis , it is believed that migrations and movements of dolphinfish are most likely affected by the location and movement of drifting objects in oceanic waters.

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 – Sharks

Shortfin mako shark

Shortfin mako migrations in the western North Atlantic (**Sargasso Sea Hypothesis**). 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 (Kohler *et al,* 2002). 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 (very similar to the SSA Area). 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. As shortfin mako are one of the two major shark species designated by ICCAT, the Sargasso Sea appears to be a very important area for this species.

Blue shark

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 (majority in late September and early 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 (SSA Area) with pop-up times mostly ranging from December to March (**Fig. 13**). This appears to provide firm evidence that blue sharks are using the Sargasso Sea as an overwintering ground (Campana et al 2011).

Porbeagle shark

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 pop-up tagging of 21 porbeagles off eastern Canada has revealed new insights about their movements. . Males and immature sharks of both sexes remained primarily on the continental shelf for periods of almost a year after tagging, but 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). These females migrated south from the Canadian Maritimes, mainly through the western part of the Sargasso Sea down to about 20°N (Campana et al 2010). In addition to this significant range extension , 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 the stock.

Bigeye thresher shark

Although found throughout the North Atlantic, the Bigeye thresher has no known association with the Sargasso Sea.

Basking shark

The basking shark is the only species of shark presented in this paper which is planktivorous. As such, its feeding ecology is different from that of the other four species of sharks which are predators. Basking sharks appear to actively seek out thermal fronts, areas that typically contain high densities of zooplankton, to maximize their feeding efficiency (Sims *et al*, 2000a). Basking sharks are typically seen feeding at the surface along fronts but PSAT tagging has shown that they make regular seasonal movements to the Sargasso Sea and further south during winter months at depths of 200-1000m (Skomal et al 2009).

References

Beardsley, G.L. 1967. Age, growth and reproduction of the dolphin *Coryphaena hippurus* in the Straits of Florida. Copeia 1967: 441-445.

Block, B.A., S. Teo, A. Walli, A. Boustany, M.J. Stokesbury, C.J. Farwell, K.C. Weng, H. Dewar and T.D. Williams. 2005. Electronic tagging and population structure of Atlantic bluefin tuna. Nature 434: 1121-1127.

Campana, S.E, J.F. Gibson, M. Fowler, A. Dorey and W. Joyce. 2010 a. Population dynamics of porbeagle in the Northwest Atlantic with an assessment of status to 2009 and projections for recovery. Collect. Vol. Sci. Pap. ICCAT, 65(6): 2109-2182.

Campana, S.E., W. Joyce, and M. Fowler, 2010 b. Subtropical pupping ground for a cold-water shark. Can J Fish Aquat. Sci. 67:769-773

Casazza, T.L. and S.W. Ross. 2008. Fishes associated with pelagic *Sargassum* and open water lacking *Sargassum* in the Gulf Stream off North Carolina. Fish. Bull. 106: 348-363.

Claro, R., K.C. Lindeman and L.R. Parenti eds. 2001. Ecology of the marine fishes of Cuba. Smithsonian Press, 253 p.

Compagno, L.J.V. 1984. FAO species catalogue. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 1. Hexanchiformes to Lamniformes. FAO Fish Synop. No. 125, Vol. 4; 250 pp.

Compagno, L. J. V. 2001. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Volume 2: Bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes). FAO Species Catalogue for Fisheries Purposes No. 1, Vol. 2: 269 p. Food and Agriculture Organization of the United Nations. Rome. 269 p.

Coston-Clements, L., L.R. Settle, D.E. Hoss and F.A. Cross. 1991. Utilization of the *Sargassum* habitat by marine invertebrates and vertebrates – a review. NOAA Tech. Memo. NMFS-SEFSC-296, 24 p.

Doray, M., B. Stequert and M. Taquet. 2004. Age and growth of blackfin tuna (*Thunnus atlanticus)* caught under moored fish aggregating devices, around Martinique Island. Aquat. Living Resour. 17: 13-18.

Fernandez-Carvalho, J., R. Coelho, K. Erzini and M. N. Santos. 2011. Age and growth of the Bigeye Thresher shark, *Alopias supercilliosus,* from the pelagic longline fisheries in the tropical northeastern Atlantic Ocean, determined by vertebral band counts. Aquat. Liv. Res. 24: 359-368.

Franks, J.S., N.J. Brown-Peterson, M.S. Griggs, N.M. Garber, J.R. Warren, and K.M. Larsen. 2000. Potential of the first dorsal fin spine for estimating the age of wahoo, *Acanthocybium solandri*, from the northern Gulf of Mexico, with comments on specimens from Bimini, Bahamas. Proc. Gulf Caribb. Fish. Inst. 51:428–440.

Gore, M.A., D. Rowat, J. Hall, F.R. Gell and R.F. Ormond. 2008. Transatlantic migration and deep mid-ocean diving by basking shark. Biol. Lett. 4: 395-398.

Graves, J.E., B.E. Luckhurst and E.D. Prince. 2002. An evaluation of pop-up satellite tags for estimating post-release survival of blue marlin (*Makaira nigricans*) from a recreational fishery. Fish. Bull. 100: 134-142.

Henderson, A.C., K. Flannery and J. Dunne. 2001. Observations on the biology and ecology of blue shark in the North-east Atlantic. J. Fish Biol. 58: 1347-1358.

Hogarth, W.T. 1976. Life history aspects of wahoo, *Acanthocybium solandri* (Cuvier and Valenciennes) from the coast of North Carolina, Thesis, North Carolina State University, 107 p.

ICCAT. 2008. Report of the ICCAT shark stock assessments meeting, SCRS/2008/017, 89 p.

ICCAT. 2010a. ICCAT Manual, chapter 2.1.1 yellowfin tuna, 26 p.

ICCAT. 2010b. ICCAT Manual, chapter 2.1.4 albacore tuna, 18 p.

ICCAT. 2010c. ICCAT Manual, chapter 2.1.2 bigeye tuna, 25 p.

ICCAT. 2010d. ICCAT Manual, chapter 2.1.5 bluefin tuna, 19 p.

ICCAT. 2010e. ICCAT Manual, chapter 2.1.3 skipjack tuna, 22 p.

ICCAT. 2010f. ICCAT Manual, chapter 2.1.9 swordfish, 18 p.

ICCAT. 2010g. ICCAT Manual, chapter 2.1.6 blue marlin, 15 p.

ICCAT. 2013.. ICCAT Manual, chapter 2.1.7 white marlin, 15 p.

ICCAT. 2010h.. ICCAT Manual, chapter 2.1.8.1 sailfish, 14 p.

ICCAT. 2010i.. ICCAT Manual, chapter 2.1.10.5 Atlantic Black Skipjack, 8 p.

ICCAT, 2012. ICCAT Resolution on the Sargasso Sea.

Jenkins, K.L.M. and R.S. McBride. 2009. Reproductive biology of wahoo, *Acanthocybium solandri*, from the Atlantic coast of Florida and the Bahamas. Marine and Freshwater Research 60: 893-897.

Kerstetter, D.W., B.E. Luckhurst, E.D.Prince and J.E. Graves. 2003. Use of pop-up satellite archival tags to demonstrate survival of blue marlin (*Makaira nigricans*) released from pelagic longline gear. Fishery Bulletin. 101: 939-948.

Kohler, N.E., P.A. Turner, J.J. Hoey, L.J. Natanson and R. Briggs. 2002. Tag and recapture data for three pelagic shark species: Blue shark (*Prionace glauca*), Shortfin mako (*Isurus oxyrinchus*) and Porbeagle (*Lamna nasus*) in the North Atlantic Ocean. Col. Vol. Sci. Pap. ICCAT 54: 1231-1260.

Laffoley, D. d'A, Roe H.S.J. et al., 2011. The protection and management of the Sargasso Sea: The golden rainforest of the Atlantic ocean. Summary science and supporting evidence case. Sargasso Sea Alliance, 71pp.

Loefer, J.K., G.R. Sedberry and J.C. McGovern. 2005. Vertical movements of a shortfin mako in the western North Atlantic as determined by pop-up satellite tagging. Southeastern Naturalist 4: 237-246.

Luckhurst, B.E., J.M. Dean, M. Reichert, M. Cameron, S. Manuel and T. Trott. 1997. Use of microstructure analysis of the sagittal otoliths to estimate age of the wahoo, *Acanthocybium solandri* from Bermuda.

Proc.Gulf Carib. Fish. Inst. 49: 64-70.

Luckhurst, B.E. 1998. Analysis of Bermuda's Marlin Fishery - Catches of blue marlin (*Makaira nigricans*) and white marlin (*Tetrapterus albidus*) during the period 1975 - 1995 with comments on tagging and tournament fishing effort. In: Report of Third ICCAT Billfish Workshop, Madrid, Spain, pp. 131-134.

Luckhurst, B.E. and T. Trott. 2000. Bermuda's commercial line fishery for wahoo and dolphinfish: landings, seasonality and catch per unit effort trends. Proc. Gulf Caribb. Fish. Inst. 51: 404-413.

Luckhurst, B.E., T. Trott, and S. Manuel. 2001. Landings, seasonality, catch per unit effort and tag-recapture results of yellowfin tuna (*Thunnus albacares*) and blackfin tuna (*T. atlanticus*) at Bermuda. In: G.R. Sedberry, ed. Island in the Stream: Oceanography and Fisheries of the Charleston Bump. American Fisheries Society Symposium 25:225–234.

Luckhurst, B.E., E. D. Prince, J.K. Llopiz, D. Snodgrass and E.B. Brothers. 2006. Evidence of blue marlin (*Makaira nigricans*) spawning in Bermuda waters and elevated mercury levels in large specimens. Bull. Mar. Sci. 79: 691-704.

Luckhurst, B.E . 2007. Large pelagic fishes in the wider Caribbean and Northwest Atlantic Ocean: Movement patterns determined from conventional and electronic tagging. Gulf and Caribbean Research 19: 1-10.

Lutcavage, M.E., R.W. Brill, G.B. Skomal, B.C. Chase and P.W. Howey. 1999. Results of pop-up satellite tagging of spawning size class fish in the Gulf of Maine: do North Atlantic bluefin tuna spawn in the mid-Atlantic? Can. J. Fish. Aquat. Sci. 56:173-177.

Manooch, C.S.III and D.L. Mason. 1983. Comparative food of yellowfin tuna, *Thunnus albacares*, and blackfin tuna, *Thunnus atlanticus*, (Pisces: Scombridae), from the southeastern and Gulf of Mexico coasts of the United States. Brimleyana 9: 33-52.

Manooch, III, C.S. 1984. Fisherman's guide – fishes of the southeastern United States. North Carolina State Museum of Natural History, Raleigh, 362 p.

Moreno, J. and J. Moron. 1992. Reproductive biology of the Bigeye Thresher shark, *Alopias supercilliosus* (Lowe, 1939). J. Fresh. Mar. Res. 43:77-86.

Nash A., J. Whiting and B.E. Luckhurst. 2002. A pneumatic cradle for the handling and tagging of wahoo and other large pelagic fishes. American Fisheries Society Symposium 30: 189-194.

Natanson, L.J., J.J. Mello and S.E. Campana. 2002. Validated age and growth of the Porbeagle shark, *Lamna nasus*, in the western North Atlantic Ocean. Col. Vol. Sci. Pap. 54(4): 1261-1279.

Natanson, L.J., N.E. Kohler, D. Ardizzone, G.M. Cailliet, S.P. Wintner and H.F. Mollet. 2006.Validated age and growth estimates for the shortfin mako, *Isurus oxyrinchus*, in the North Atlantic Ocean. Environ. Biol. Fish 77: 367-383.

Neilson, J.D., S. Smith, F. Royer, S.D. Paul, J.M. Porter, and M. Lutcavage, 2009. Investigations of horizontal movements of Atlantic swordfish using pop-up statellite archival tags. In: Neilson JD, Arrizabalaga H., Fragoso N, Hobday A, Lutcavage M, Sibert J, editors. Tagging and tracking of marine animals with electronic devices. New York: Springer, pp. 145-159

NMFS. 2007. Atlantic White Marlin Status Review. Report to National Marine Fisheries Service, SEFSC, Miami.

Oxenford, H.A. and W. Hunte. 1986. A preliminary investigation of the stock structure of the dolphin, *Coryphaena hippurus,* in the western central Atlantic. Fishery Bulletin US 84:451–460.

Oxenford, H.A., R. Mahon, and W. Hunte, 1995. Distribution and relative abundance of flyingfish (Exocoetidae) in the eastern Caribbean. I. Adults. Mar Ecol Prog Ser 117:11-23

Oxenford, H.A. 1999. Biology of the dolphinfish (*Coryphaena hippurus*) in the western central Atlantic: a review Scientia Marina 63:277–301.

Oxenford, H.A., P.A. Murray, and B.E. Luckhurst. 2003. The biology of wahoo (*Acanthocybium solandri*) in the western central Atlantic. Gulf and Caribbean Research 15:33–49.

Palko, B.J., G.L. Beardsley and W.J. Richards. 1982. Synopsis of the biological data on dolphin fishes, *Coryphaena hippurus* Linnaeus and *Coryphaena equisetis* Linnaeus. NOAA Tech. Rep. NMFS Circ. 443, 38 p.

Pauly, D. 2002. Growth and mortality of basking shark *Cetorhinus maximus* and their implications for management of whale sharks *Rhincodon typus*. P. 199-208. In: Fowler, S. L., Reid, T., and Dipper, F. A. [eds] Elasmobranch biodiversity: conservation and management. Occ. Papers IUCN Survival Commission 25. Gland, Switzerland.

Preti, A.,S. Kohin, H. Dewar and D. Ramon. 2008. Feeding habits of the Bigeye Thresher shark (*Alopias supercilliosus)* sampled from the California-based drift gillnet fishery. CalCOFI rep. 49, 10 p.

Prince, E.D. and C.P. Goodyear. 2006. Hypoxia-based habitat compression of tropical pelagic fishes. Fish. Oceanogr. 15:451–464.

Prince, E.D., J. Luo, C.P. Goodyear, J.P. Hoolahan, D. Snodgrass, E.S. Orbesen, J.E. Serafy, M. Ortiz, M.JSchirripa. 2010. Ocean scale hypoxia-based habitat compression of Atlantic istiophorid billfishes. Fish. Oceanogr. 19: 448-462.

Ruderhausen, P.J., J.A. Buckel, J. Edwards, D.P. Gannon, C.M. Butler and T.W. Averett, 2010. Feeding ecology of blue marlins, dolphinfish, yellowfin tuna, and wahoos from the North Atlantic ocean and comparisons with other oceans. Trans Am Fish Soc 139:1335-1359

SAFMC. 1998. Proceedings of the dolphin/wahoo workshop, May 6-8, 1998, SAFMC, Charleston, S.C.

SAFMC. 2002. Fishery Management Plan for Pelagic *Sargassum* Habitat of the South Atlantic Region. SAFMC, Charlston, SC

Schwenke, K.L. and J.A. Buckel. 2008. Age, growth and reproduction of dolphinfish (*Coryphaena hippurus*) caught off the coast of North Carolina. Fish.Bull.106: 82-92.

Sims, D.W., Southall, E. J., Quayle, V. A., and Fox, A. M. 2000a. Annual social behaviour of basking sharks associated with coastal front areas. Proc. R. Soc. Lond. B 267:1897-1904.

Sims, D.W., C. Speedie and Fox, A. M. 2000b. Movements and growth of a female basking shark re-sighted after a three year period. J. Mar. Biol. Assoc.UK 80:1141-1142.

Sims, D.W., E.J. Southall, A.J. Richardson, P.C. Reid and J.D. Metcalfe. 2003. Seasonal movements and behavior of basking sharks from archival tagging: no evidence of winter hibernation. Mar Ecol Prog Ser 248:187-196.

Skomal, G.B., G. Wood and N. Caloyianis. 2004. Archival tagging of a basking shark, *Cetorhinus maximus*, in the western North Atlantic. J. Mar. Biol. Assoc. UK 84:795-799.

Skomal, G.B., S. Zeeman, J Chisholm, E. Summers, H. Walsh, K. McMahon and S. Thorrold. 2009.

Transequatorial migrations by basking sharks in the western Atlantic Ocean. Current Biology 19: 1019-1022.

Smith-Vaniz, W.F., B.B. Collette and B.E. Luckhurst. 1999. The Fishes of Bermuda: History,Zoogeography, Annotated Checklist and Identification Keys. American Society of Ichthyologists and Herpetologists, Special Publication No. 4, Allen Press, Lawrence, Kansas, 424 p.

Stillwell, C.E. and N.E. Kohler. 1982. Food, feeding habits and estimates of daily ration of the shortfin mako (*Isurus oxyrinchus*) in the Northwest Atlantic. Canadian Journal of Fisheries and Aquatic Sciences 39: 407-414.

Thiesen, T.C. and J.D. Baldwin. 2012. Movements and depth/temperature distribution of the ecothermic Scombrid, *Acanthocybium solandri* (wahoo), in the western North Atlantic. Mar. Biol. 159: 2249-2258.

Vieira, K.R., J.L. Oliveira, M. Barbalho and J. Garcia. 2005. Reproductive characteristics of blackfin tuna *Thunnus atlanticus* (lesson, 1831) in northeast Brazil. Col. Vol. Sci. Pap. ICCAT 58(5): 1629-1634.

Wells, R.J.D. and J.R. Rooker. 2004. Spatial and temporal patterns of habitat use by fishes associated with *Sargassum* mats in the northwestern Gulf of Mexico. Bull. Mar. Sci. 74: 81-99.

Weng, K.C .and B.A. Block. 2004. Diel vertical migration of the Bigeye Thresher shark (*Alopias supercilliosus),* a species possessing orbital retia mirabilia. Fish. Bull. 102:221–229 (2004).

Wilson, S.G. 2004. Basking sharks (Cetorhinus maximus) schooling in the southern Gulf of Maine. Fish. Oceanog. 13: 283-286.

Wilson, S.G.,and B.A. Block, 2009. Habitat use in Atlantic bluefin tuna *Thynnus thynnus* inferred from diving behavior. En Sp Res 10:355-367

Figures

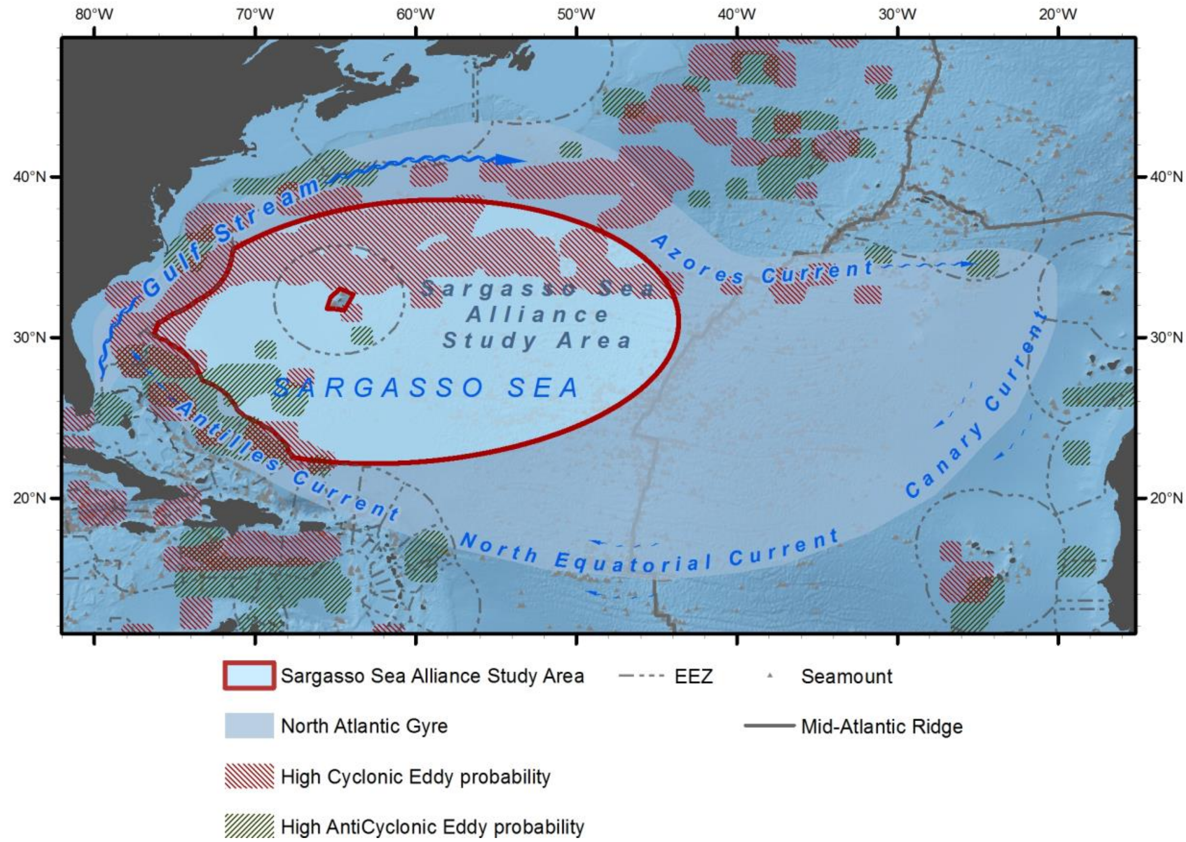


Figure 1. Map of the proposed Sargasso Sea EBSA, including some of the major features that influence overall boundary definition and location (from Laffoley *et al*., 2012).

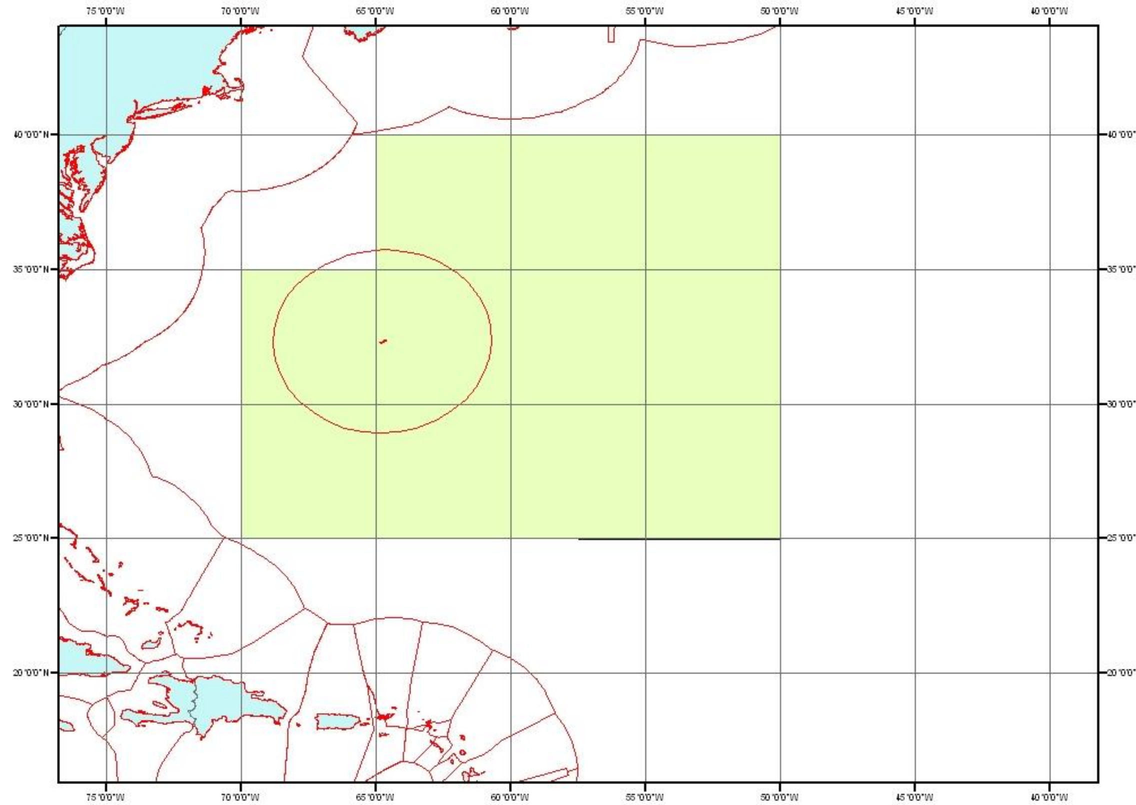


Figure 2 - ICCAT reporting grid (5x5 degrees) in the Sargasso Sea for longline catches of tunas and tuna-like species (map produced by the Sargasso Sea Alliance).

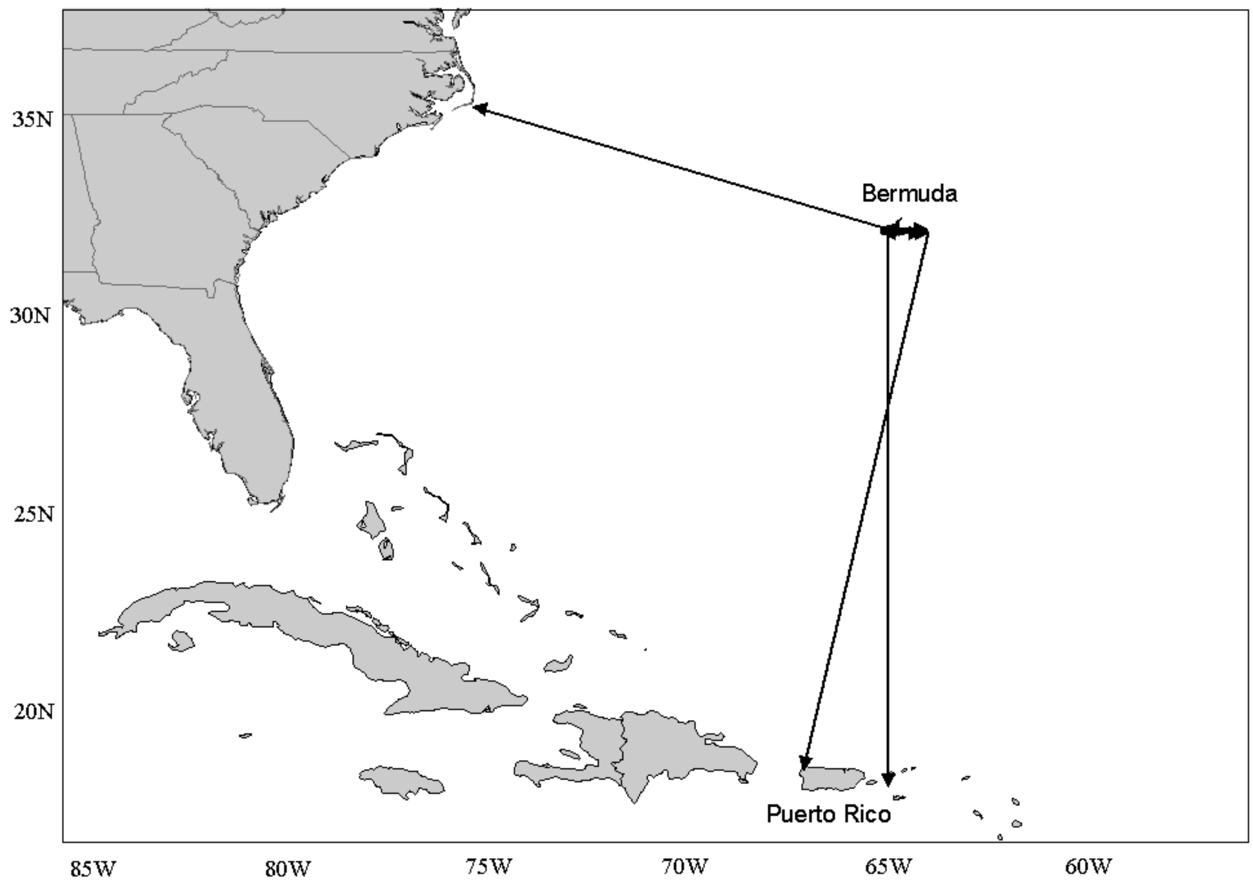


Figure 3. Movement vectors of three conventionally-tagged Bermuda yellowfin tuna (*Thunnus albacares*) recaptured outside Bermuda coastal waters demonstrating demographic connectivity with the wider Caribbean and US eastern seaboard. Straight-line distances moved were between 1,000 and 1,300 km (from Luckhurst 2007).

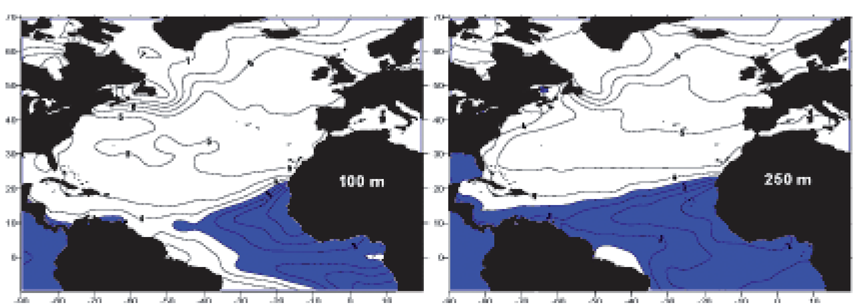


Figure 4. Yearly average temperature (ºC) at 100 m and 250 m depth in the North Atlantic. Areas in blue are not suitable for albacore (after Da Silva *et al.* 1994).

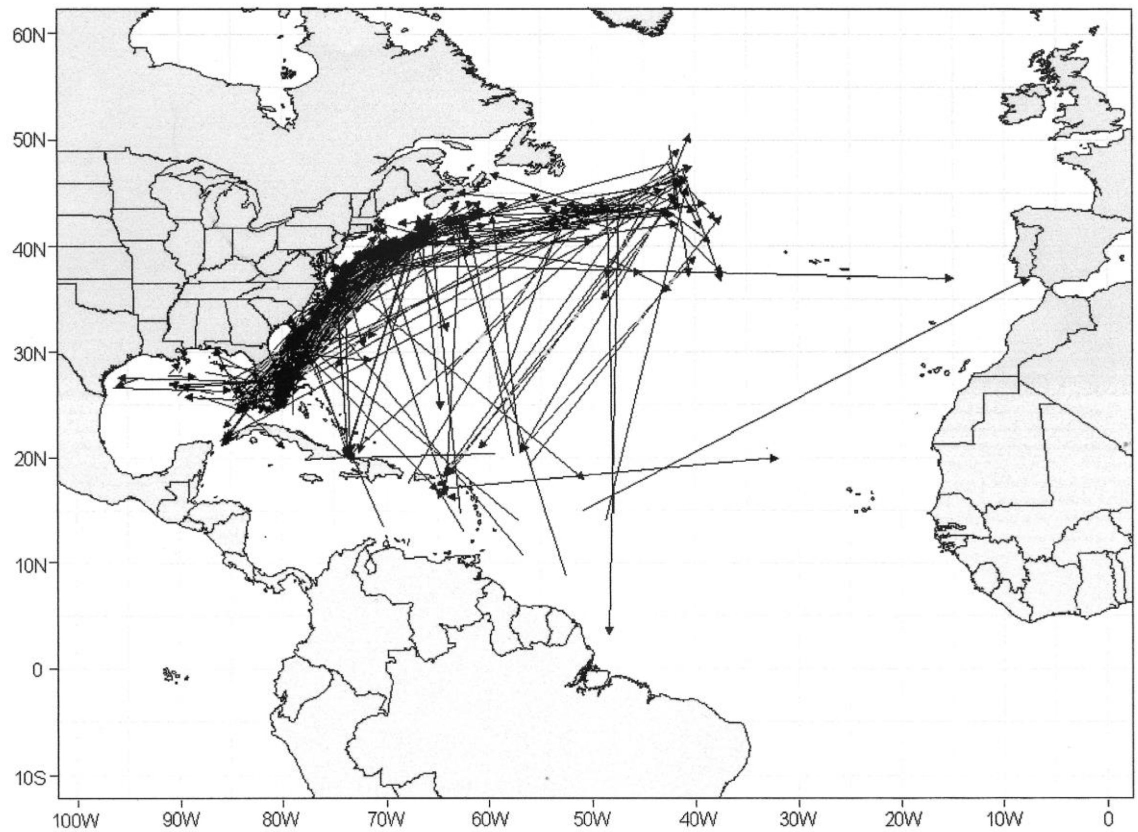


Figure 5. Movement vectors of conventionally-tagged swordfish (*Xiphius gladius*) in the North Atlantic from CTC database until end of 2006. Note predominantly north-south movements (from Luckhurst, 2007)

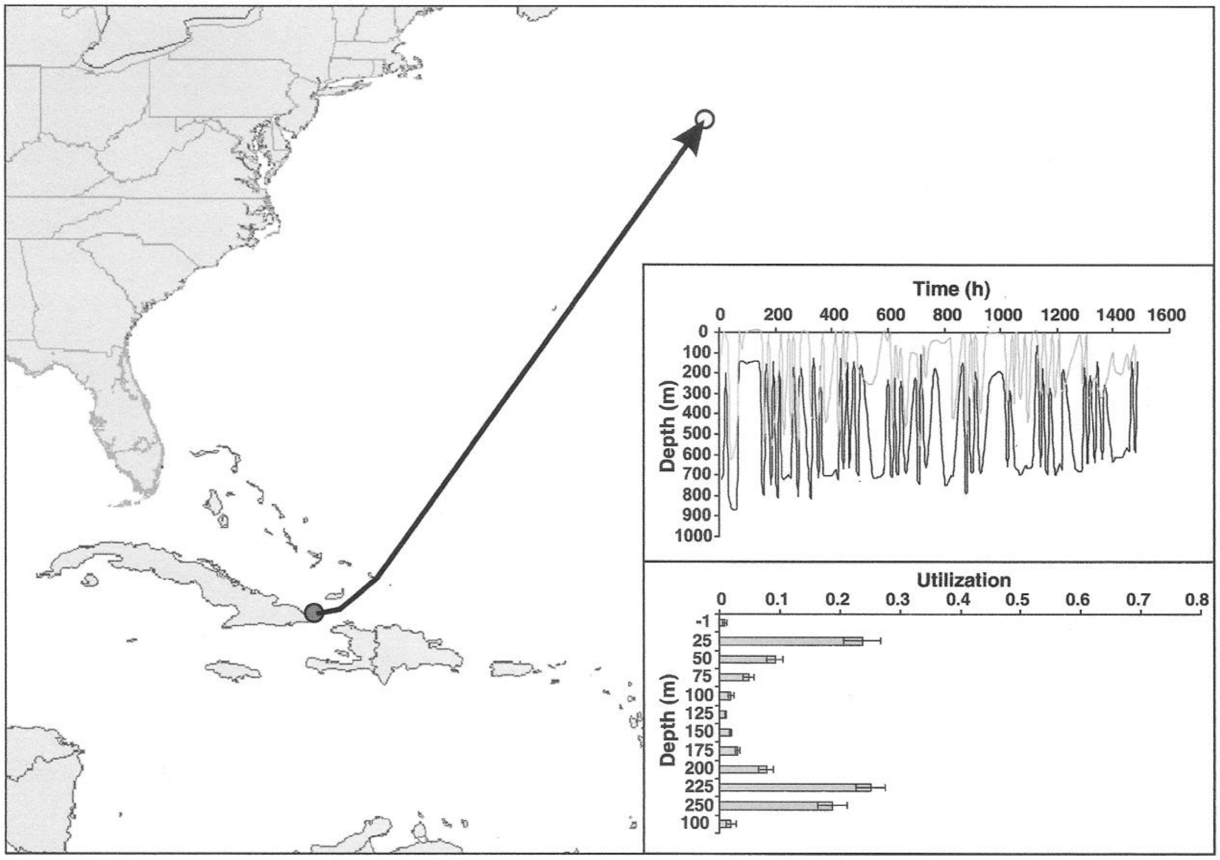


Figure 6 - PSAT track of swordfish illustrating diurnal vertical migration (see text for details).

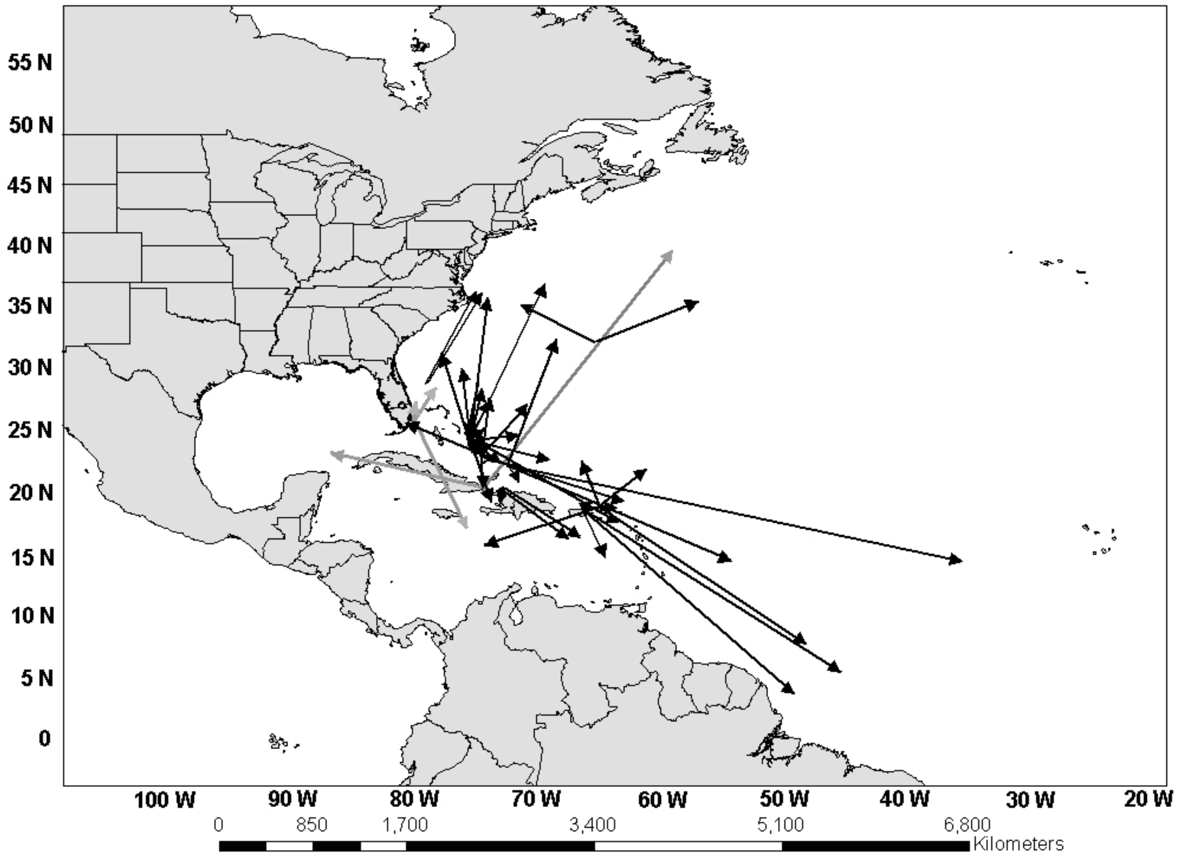


Figure 7. Movement vectors of blue marlin (*Makaira nigricans*) [dark vectors] and swordfish (*Xiphius gladius*) [pale vectors] tagged with Pop-up Satellite Archival Tags (PSATs) in the western North Atlantic from 2002-2006. (from Luckhurst, 2007).

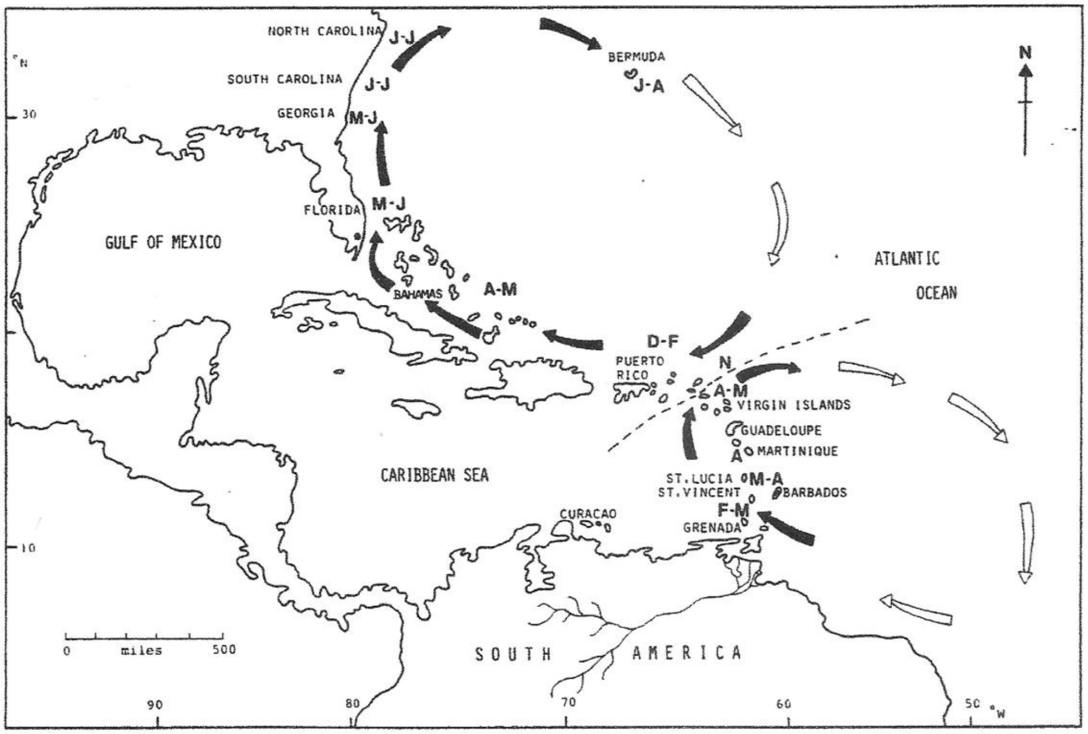
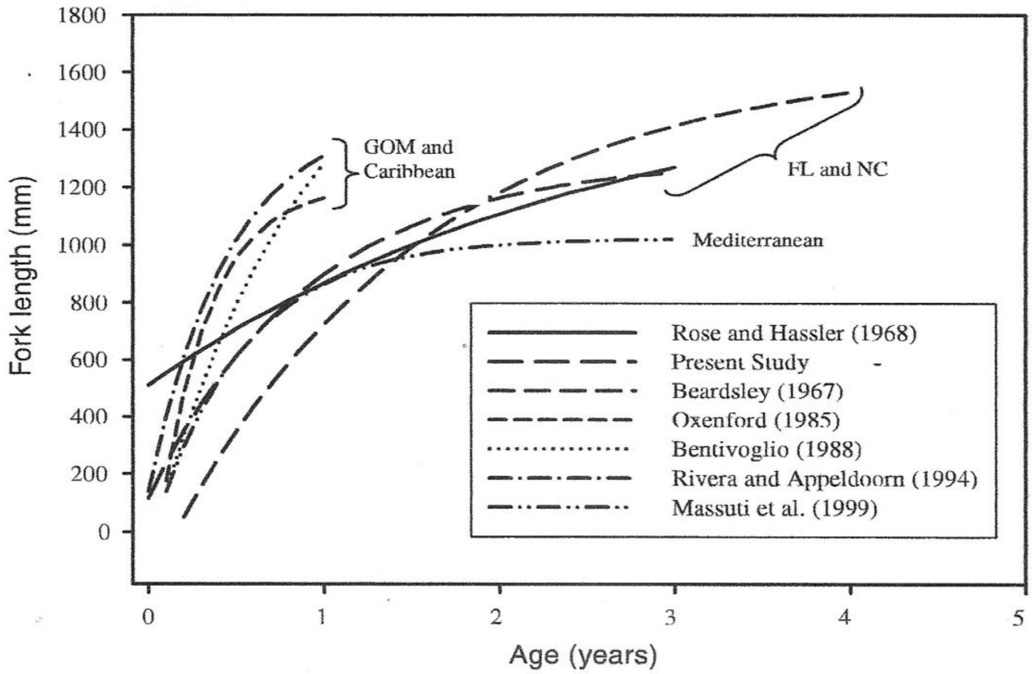


Figure 8 - Proposed stock structure with migration pathways of the dolphin, *Coryphaena hippurus*, in the western central Atlantic (from Oxenford and Hunte, 1986).



Calculated von Bertalanffy growth functions (VBGFs) for dolphinfish (*Coryphaena hippurus*) from various locations in the North Atlantic. GOM = Gulf of Mexico, FL = Florida, NC = North Carolina.

Figure 9 – A comparison of dolphinfish growth curves from different locations in the North Atlantic.

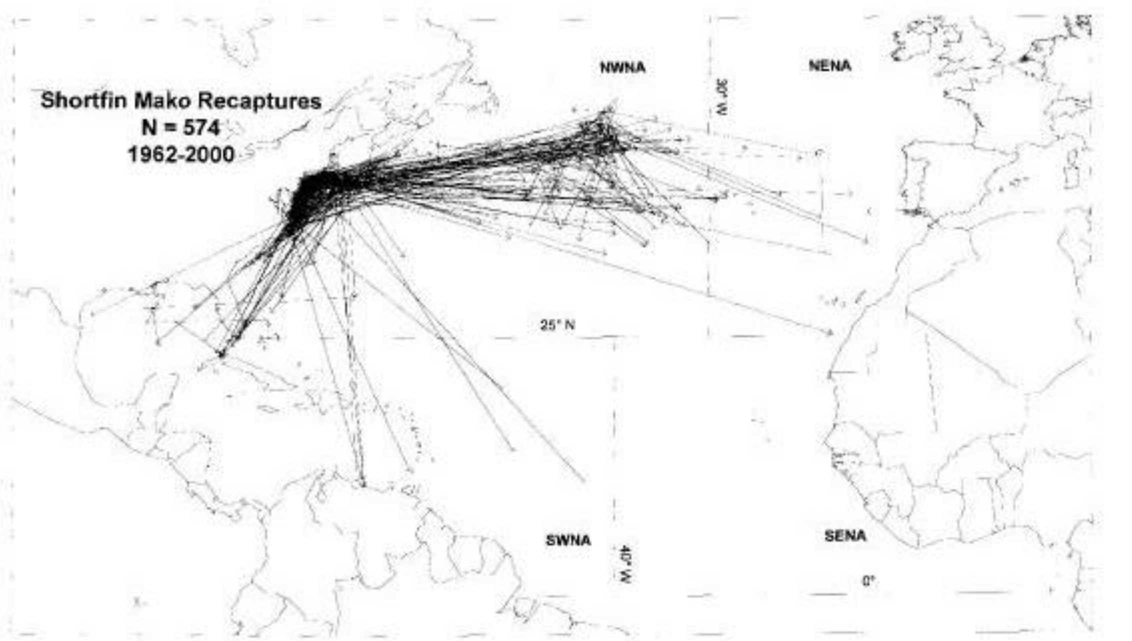


Figure 10 - Recapture distribution for the shortfin mako, *Isurus oxyrinchus*, from the CSTP (Cooperative Shark Tagging Program) from 1962 to 2000.

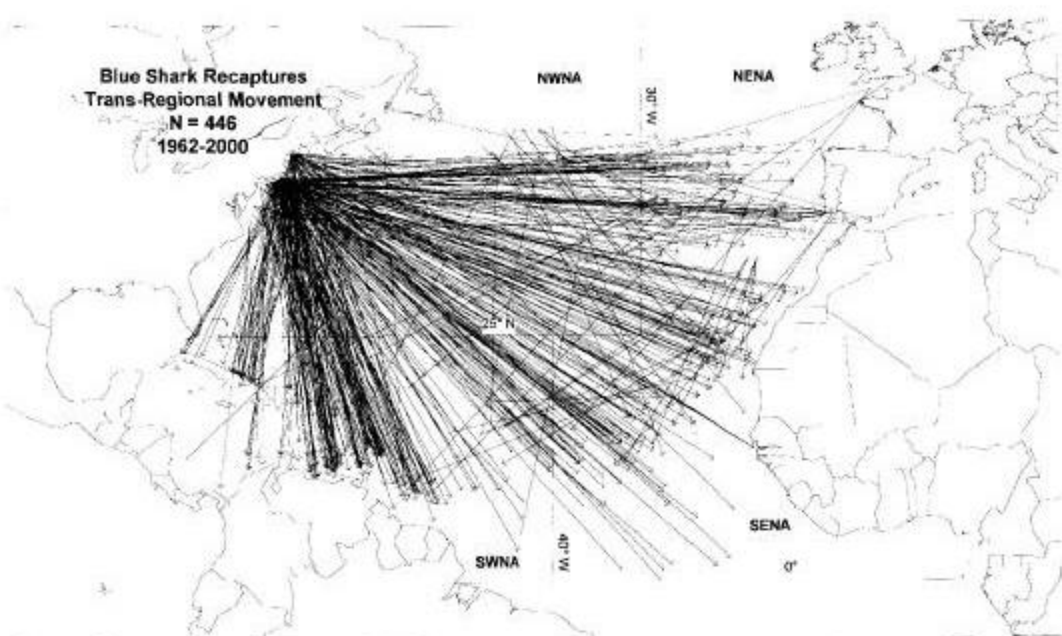


Figure 11 - Recapture distribution for trans-regional movements of the blue-shark, *Prionace glauca*, from the CSTP (1962-2000).

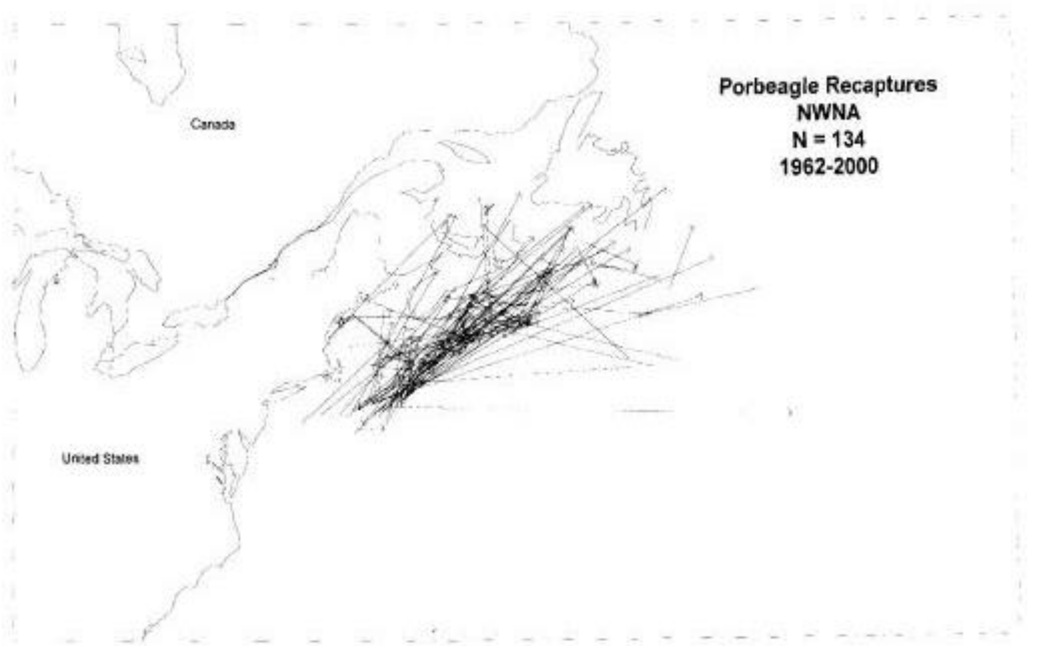


Figure 12 - Recapture distribution in the NW Atlantic for the porbeagle shark, *Lamna nasus*, from the CSTP (1962-2000).

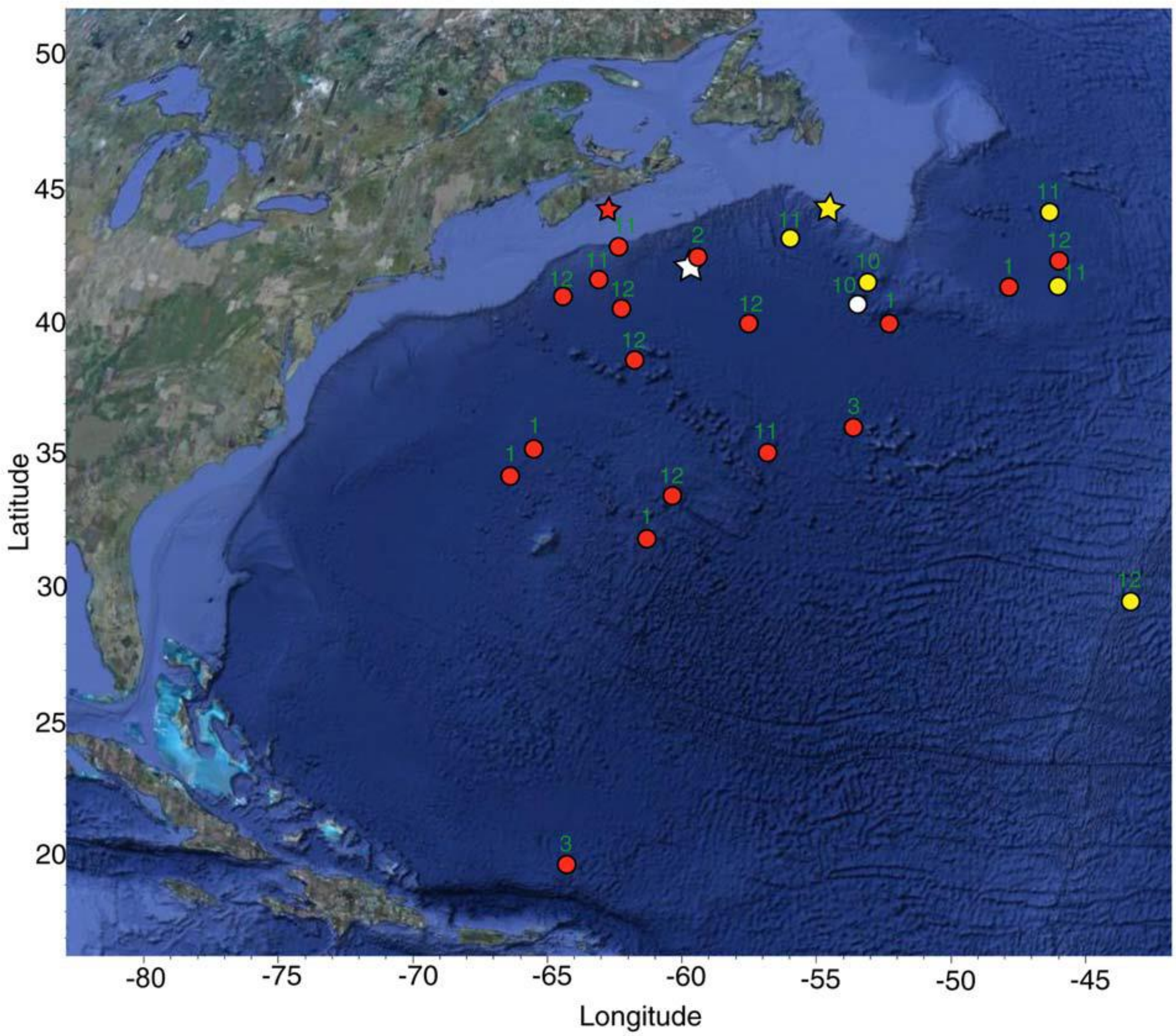


Figure 13 - Blue shark tagging locations (stars) and pop-up locations (dots) for 23 blue sharks tagged off the eastern coast of Canada. Pop-up symbols are coloured to match the corresponding tagging symbol. Month of pop-up indicated by number.