SCRS/2014/120

A PRELIMINARY FOOD WEB OF THE PELAGIC ENVIRONMENT OF THE SARGASSO SEA WITH A FOCUS ON THE FISH SPECIES OF INTEREST TO ICCAT

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SUMMARY

This paper provides information on the pelagic habitat of the Sargasso Sea and the feeding ecology and diet of a total of 15 different fish predators whose distributions include the Sargasso Sea. These species are divided into four groups that broadly correspond with ICCAT species groupings: Group 1 – Principal tuna species including yellowfin tuna, albacore tuna, bigeye tuna, bluefin tuna and skipjack tuna, Group 2 – Swordfish and billfishes including blue marlin, white marlin and sailfish, Group 3 – Small tunas including wahoo, blackfin tuna, Little tunny (Atlantic black skipjack tuna) and dolphinfish, and Group 4 – Pelagic sharks including shortfin mako and blue shark. Values from stable isotope analysis of nitrogen in tissue samples as well as stomach contents analysis are used to estimate trophic position (TP) for each species listed above and a preliminary pelagic food web of the Sargasso Sea is proposed. All of these species have TP values equal to or greater than 4.0 with the exception of skipjack tuna (3.8). Large swordfish are the top-ranked predator (TP = 5.1) followed by white marlin (4.9). Small swordfish and two other species - blue marlin and bigeye tuna - follow with the same TP (4.8). Large ommastrephid squid have a TP of 4.7 ranking them at a similar trophic level to other large fish predators. Squids are shown to be an important element of this food web in the role of both predator and prey. The significance of Sargassum in relation to the feeding habits and ecology of these predators is discussed as is the importance of Sargassum habitat for some prey species, e.g. flyingfishes.

KEYWORDS

Sargasso Sea, food web, pelagic habitat, tunas, swordfish, billfishes, sharks, feeding ecology, diet, stable isotopes

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Study commissioned by Sargasso Sea Alliance, led by the Government of Bermuda

Introduction

The Sargasso Sea has a unique pelagic ecosystem based upon floating brown algae of the genus *Sargassum.* This ecosystem provides essential habitat for key life history stages of a wide variety of species and hosts a highly diverse community of associated organisms. The Sargasso Sea is a distinctive area of open ocean situated within the North Atlantic Subtropical Gyre, bounded on all sides by the clockwise flow of major ocean currents (Trott et al, 2011). The Gulf Stream and North Atlantic Drift form the western and northern boundaries, while the Canary Current forms the eastern boundary and the North Equatorial Current and Antilles Current form the southern boundary (Fig. 1). The Gulf Stream is perhaps the most influential current as it transports quantities of *Sargassum* northward from areas such as the Gulf of Mexico (Laffoley *et al*., 2011). The formation of rings and eddies along the eastern margin of the Gulf Stream helps to concentrate *Sargassum* and carry it into the Sargasso Sea. The Subtropical Convergence Zone where warm and cold water masses meet, occurs between 20° and 30°N in the western portion of the Sargasso Sea, and it is here that distinct thermal fronts occur in the upper 150 m of the ocean from fall through spring. *Sargassum* accumulates in this area, along with other organisms, so the fronts are important feeding areas for predatory pelagic fishes and migratory marine mammals in the Sargasso Sea (Laffoley *et al*., 2011). The Sargasso Sea Alliance (SSA), in seeking to better understand and conserve this complex pelagic ecosystem, has defined a large portion of the Sargasso Sea as its study area. The proposed study area (approximately 4,163,499 km^2) extends from 22^o–38^oN and from 76^o–43^oW, and is centered on 30^oN and 60^oW (Fig. 1).

The Sargasso Sea plays an important role in the ecology and life history of a variety of pelagic fish species, many of which are large apex predators and form the basis of significant fisheries in the Atlantic Ocean. Many of these species are highly migratory and are managed by the International Commission for the Conservation of Atlantic Tunas (ICCAT). The species presented in this paper are divided into four groups that broadly correspond with ICCAT species groupings: Group 1 – Principal tuna species including yellowfin tuna (*Thunnus albacares*), albacore tuna (*Thunnus alalunga),* bigeye tuna (*Thunnus obesus*) , bluefin tuna (*Thunnus thynnus*) and skipjack tuna *(Katsuwonus pelamis),* Group 2 – Swordfish (*Xiphius gladius*) and billfishes including blue marlin (*Makaira nigricans*), white marlin (*Tetrapterus albidus*) and sailfish (*Istiophorus albicans*), Group 3 – Small tunas including wahoo (*Acanthocybium solandri*), blackfin tuna (*Thunnus atlanticus*), Little tunny (Atlantic black skipjack tuna) (*Euthynnus alletteratus*) and dolphinfish (*Coryphaena hippurus*), and Group 4 – Pelagic sharks including shortfin mako (*Isurus oxyrinchus*) and blue shark (*Prionace glauca*). The habitat, migration and movement patterns of all of the above species in relation to the Sargasso Sea are discussed in Luckhurst (2014).

The five tuna species in Group 1 and swordfish are of major commercial importance in the North Atlantic while the three species of billfishes have significant recreational importance. The four species in the Small tunas group play an important role in the pelagic food web at a level below the apex predators. The two species of pelagic sharks (shortfin mako, blue shark), which can comprise a significant element of longline catches (www.iccat.int) are also important predators in this ecosystem. The focus of this paper is to describe the food habits and feeding ecology of the 15 species listed above (eight of them from the family Scombridae) and to include these species in a proposed pelagic food web of the Sargasso Sea. Trophic levels have been assigned in relation to stable isotope values from tissue samples and stomach contents analysis.

The pelagic habitat of the Sargasso Sea

Studies of the bathymetric structure of pelagic communities in the world's oceans have revealed a pattern of vertical zonation that is often clearly seen in the tropics and subtropics. Light penetration, water temperature, and water mass structure define vertical zonation (Allan and Cross, 2006). For the purposes of this study, the vertical zonation outlined by Angel (2011) for the Sargasso Sea will be followed. The zones are: 1) the epipelagic [surface to ~200m] 2) the mesopelagic [200-700m] subdivided into shallow [200-400m] and deep [400-700m] 3) the bathypelagic [700-2500m] 4) the abyssopelagic [2500-6000m] 5) the hadal [>6000m] and 6) the benthopelagic [within a 100m of the seabed]. As the maximum depth in the Sargasso Sea is less than 6,000 m, there is no hadal zone (Angel, 2011). A generalized diagram of the vertical zonation of the pelagic habitat (Fig. 2) provides a useful reference when describing the vertical habitats used in the feeding ecology of the fish species included in this report. In general, the biomass of pelagic communities declines by an order of magnitude from the epipelagic to around a depth of 1000m (Angel, 2011). As the availability of food resources decreases markedly with depth, the biomass of communities at a depth of 4000m is another order of magnitude lower than that found at 1000m (Angel, 2011).

The epipelagic zone

The epipelagic zone is normally defined as the upper 200m of the ocean beyond the continental shelf (Fig. 2) in all the world's oceans (Helfman et al., 1997). The epipelagic zone is euphotic, and temperatures fluctuate diurnally and seasonally. It is usually shallower (approx. 50m deep) in turbid nearshore waters but increases in depth offshore in clear oceanic waters like the Sargasso Sea (Allan and Cross, 2006). The majority of large, apex predators e.g. tunas, billfishes, pelagic sharks, spend most of their time in this zone where most of their prey species are found. Some species, e.g. bigeye tuna and swordfish, have special physiological adaptations which allow them to feed in deeper water and take advantage of other prey populations.

The epipelagic zone is subject to major changes in the species composition of the zone as a result of diurnal vertical migration. The most abundant group of mesozooplankton is the Copepoda which dominate the plankton populations throughout the water column. However, during nocturnal hours, the species composition of the plankton changes markedly with many larger species, including fish, decapod crustaceans, euphausiids and large copepods migrating from deeper depths into the epipelagic zone (Angel, 2011). This phenomenon of diurnal vertical migration is thought to occur because of the greater availability of food resources near the surface in the epipelagic zone and the reduced risk of predation in the dark. The downward migration at dawn is to escape the increased exposure to visual predation during daylight (Angel, 2011). Sampling throughout a range of depths during early summer just north of the Sargasso Sea determined that migrations by the mesozooplankton were restricted to the upper 700m while migrations by the large micronekton, e.g several species of lanternfishes (Myctophidae) and decapod crustaceans extended down to a maximum of 1000m at around 40°N (Angel, 2011).

The mesopelagic zone

The boundary between the epipelagic and the mesopelagic zones is marked by a shift in the species composition by day and an increase in the average size of the mesozooplankton. The shallow mesopelagic zone (200-400m) tends to be dominated by gelatinous organisms such as Siphonophora and Chaetognatha (Angel, 2011). The fishes within this zone frequently have silvery sides and rows of light organs (photophores) along their lateral and ventral surfaces. The hatchet-fishes (Sternoptychidae) of the genus *Argyropelecus*, which frequent this zone exemplify this coloration pattern (Fishbase, 2014). These fishes, which are plankton-feeders, are abundant at depths of 400-600m (Angel, 2011). Squids of the family Histioteuthidae, which are common in the mesopelagic zone of the Sargasso Sea, also have photophores on the underside of their bodies. Species of this family comprise an important prey group for both tunas and swordfish in the Sargasso Sea (Logan and Lutcavage, 2013).

The zone from 400-700m (deep mesopelagic) has a shift in species composition and an extension in the size ranges of the species composing the assemblage (Angel, 2011). The fishes in this zone generally exhibit darker colours than those found in shallower depths. The most abundant fish at these depths is the bristlemouth *Cyclothone braueri* (Gonostomatidae) and, in fact, this species dominated catches both above and below 1,000 m depth in the Sargasso Sea (Sutton et al, 2010). It is a small, semi- translucent species with photophores arranged along its ventral surface. It is not a strong swimmer, feeds mainly on small copepods and is considered to be non-migratory. This species and siphonophores are the possible source of a non-migratory deep scattering layer (DSL) detected in the Sargasso Sea (Conte et al, 1986). Given its abundance in the water column, *Cyclothone* must constitute a major food source for predators inhabiting these depths.

Another abundant group of pelagic fishes in the mesopelagic zone, the myctophids are extremely important in pelagic assemblages with their distribution extending well into the bathypelagic zone. Most lanternfish species migrate up into the epipelagic zone at night to feed (Roe and Badcock, 1984a). They in turn provide food for many larger predators including tunas. Shoals of myctophids are largely responsible for many of the migratory DSLs detected in the world's oceans.

The bathypelagic zone

This zone is perpetually dark and, as a result, intraspecific communication is either by bioluminescent displays or by chemical signals (pheromones). The majority of species which inhabit this zone are non-migratory with only a few of the large species, which inhabit the top of this zone by day, migrating upward at night (Angel, 2011). The species inhabiting this zone generally have a different appearance to those species from shallower depths and they have reduced metabolic rates as food is consistently in short supply.

Significance of *Sargassum* to pelagic fishes

The overall importance of *Sargassum* to fish species was recognized in the USA by the South Atlantic Fishery Management Council (2002) and the National Marine Fisheries Service (2003) when it was designated as essential fish habitat. More recently, ICCAT has also recognized the importance of *Sargassum* as fish habitat and has requested that Contracting Parties assess the ecological status of *Sargassum* as habitat for tunas, billfishes and sharks. In addition, ICCAT has requested that countries "report on activities that may affect the abundance of *Sargassum"* (ICCAT, 2005, 2011). Finally, in the most recent recognition of the importance of *Sargassum*, ICCAT has requested that the Standing Committee on Research and Statistics (SCRS) examine the available data and information concerning the Sargasso Sea and its ecological importance to tuna and tuna-like species and ecologically associated species (ICCAT, 2012).

With respect to feeding ecology, Ruderhausen et al (2010) examined the diets of four pelagic predators, namely, yellowfin tuna, dolphinfish, blue marlin and wahoo in the North Atlantic. They classified prey into three groups: 1) prey associated with floating *Sargassum* 2) Flying fish (Exocoetidae) - associated with *Sargassum* during spawning and 3) schooling prey, primarily *Auxis* spp. (Scombridae) and cephalopods. The dominant prey of yellowfin tuna (>50cm FL) were flying fish, as well as scombrids and cephalopods. Dolphinfish fed mostly on prey associated with floating structure, mainly *Sargassum*, and flying fish. Blue marlin and wahoo preyed predominantly on scombrids. These findings indicate that flyingfish were a significant component of the diet of these pelagic predators (Ruderhausen et al.,2010). *Sargassum* is a critical habitat component of reproduction in flying fish as *Sargassum* mats are used as a spawning substrate. The spawned eggs, which have long filament extensions, become entangled in the seaweed and may develop with less predation on the eggs in the seaweed matrix (Oxenford et al., 1995). This association of flying fish with *Sargassum* indicates its significance as habitat for a principal prey group of pelagic predators. This represents an important trophic link between the Sargasso Sea and the diets of pelagic predators.

In more general ecological terms, Coston-Clements et al (1991) found the early life history stages (primarily juveniles) of a number of pelagic predators associated with pelagic *Sargassum* in the North Atlantic. These included dolphinfish, wahoo, swordfish, blue marlin, white marlin and sailfish. Luckhurst et al (2006) found clear evidence of blue marlin spawning in the Sargasso Sea (in Bermuda waters) and also documented the first occurrence of a young juvenile blue marlin (42 days old) at Bermuda's northerly latitude (32° N). The nature of the association of juvenile pelagic predators with *Sargassum* is not always evident but is most probably related to feeding and shelter.

In another demonstration of the importance of *Sargassum* habitat, Casazza and Ross (2008) found significantly more fishes (n = 18,799) representing at least 80 species, were collected from samples containing *Sargassum*, than from samples collected from open water habitat (60 species, 2,706 individuals). Sampling took place in the Gulf Stream off North Carolina. The majority (96%) of fishes collected in both habitats were juveniles. Underwater video observations of schooling behaviors of dolphinfish and jacks (Carangidae) under *Sargassum* may suggest feeding in proximity to floating mats. 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 and found a total of 36 species from 17 families. Over 95% of the species collected were in early life history stages confirming the importance of pelagic *Sargassum* as nursery habitat for some species. The trophic ecology of *Sargassum*-associated fishes in the Gulf of Mexico was also studied using stable isotopes (Rooker et al, 2006).

Feeding habits of pelagic predators

Group 1 – Principal Tunas

Yellowfin tuna (*Thunnus albacares*)

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 (ICCAT, 2010a). The broad food spectrum of the yellowfin tuna's diet provides evidence of its generalist eating habits in the oceanic pelagic environment where there are low concentrations of prey organisms. In the North Atlantic, the principal prey of yellowfin tuna (>50cm FL) were flying fish, as well as scombrids and cephalopods (Ruderhausen et al, 2010).

Albacore tuna (*Thunnus alalunga)*

Albacore are apex predators and they opportunistically feed on schooling stocks of sardine, anchovy, mackerel and squid. In the northeast Atlantic, albacore diet is mainly composed of fish, primarily *Trachurus trachurus* (Scombridae) and, to a lesser extent, crustaceans (ICCAT, 2010b). Only mature albacore are capable of diving to the mesopelagic zone to feed but they are not as well adapted physiologically to deep diving as bigeye tuna (Maury and Lehodey, 2005)**.** The diet of albacore tuna from the driftnet fishery in the northeast Atlantic indicated an almost complete absence of myctophids and other mesopelagic fishes and crustaceans from the diet (Hassani et al, 1997) suggesting that feeding was confined to the epipelagic zone.

Bigeye tuna (*Thunnus obesus*)

Bigeye tuna are also opportunistic predators. Bigeye feed on oceanic, mesopelagic fishes (migratory and non-migratory), cephalopods (mainly squid) and euphausiids. As a consequence, its diet is less affected by latitude or distance from the coast than that of other tuna species (ICCAT, 2010c) because the prey groups in the mesopelagic zone remain similar over large sections of the ocean. Bigeye tuna conduct regular migrations to depths in excess of 500m during daylight hours to forage on organisms in the DSL（Maury and Lehodey, 2005). As feeding appears to be the motivation for vertical migrations for predators such as bigeye, it must be assumed that prey concentrations are higher at depth during daylight than in the epipelagic zone（Maury and Lehodey, 2005).

Bluefin tuna (*Thunnus thynnus*)

In common with the preceding tuna species, 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 the western Atlantic, juveniles feed on a relatively small range of prey species including crustaceans, fish and cephalopods (Logan et al, 2011) while adults feed mostly on fish e.g. herring, anchovy, sand lance, sardine, sprat, bluefish and mackerel (ICCAT, 2010d). Juveniles also remain in relatively shallow water (< 50 m) and do not undertake deep dives for feeding (Galuardi and Lutcavage, 2012). Bluefin stomach contents are normally dominated by one or two prey-species, e.g. Atlantic herring and sand lance in the western Atlantic (Logan et al, 2011; 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 fish prey (those greater than 40 cm FL) are normally only consumed by giant bluefin (> 230cm FL) (ICCAT, 2010d).

Skipjack tuna (Katsuwonus pelamis)

Skipjack tuna is an opportunistic predator as well and its diet varies seasonally and by geographic location. The principal prey groups are fish, cephalopods and crustaceans (ICCAT, 2010e). As skipjack are active predators, which normally seek out schools of prey, there may be a predominance of a few species in stomach contents at a given time. Off the Brazilian coast, the main components of the skipjack's diet were two fish species, *Maurolicus muelleri* (Sternoptychidae) and *Engraulis anchoita* (Engraulidae) which made up about 60% of stomach contents by volume and a euphausiid *Euphausia similis* (ICCAT, 2010e). Skipjack foraging is largely confined to the surface mixed layer (epipelagic zone) where the schools of prey groups are found（Maury and Lehodey, 2005). Cannibalism is known to occur among skipjack tuna but its occurrence is considered incidental.

Group 2 – Swordfish and billfishes

Swordfish (Xiphius gladius)

Swordfish diet composition studies in the North Atlantic and elsewhere indicate that swordfish change their feeding habits at a very early age, moving from a diet based on copepods to one based mainly on fish. Adult swordfish usually remain in the surface mixed layer at night where they are typically caught by longliners. During the day, they descend to deeper waters (mesopelagic and upper bathypelagic) to feed on mesopelagic fish and squid (ICCAT, 2010f). The PSAT (Pop-up satellite archival tag) track of a swordfish moving across the Sargasso Sea, illustrated routine diurnal vertical migrations from the epipelagic zone to depths of 700m, with a maximum depth of 850 m being attained (Luckhurst, 2007).

The adult diet varies considerably with habitats and seasons with fish dominating the diet in some locations whereas cephalopods 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%.

Blue marlin (*Makaira nigricans*)

Blue marlin are apex predators that normally feed near the surface but they are known to make forays into deeper water to feed than other billfish species. They opportunistically prey on schools of flying fishes (Exocoetidae), small tunas (scombrids), 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, frigate mackerel (*Auxis*), and mesopelagic fishes (ICCAT, 2010g). Other prey items include scombrid fishes (including bigeye tuna weighting up to 50 kg), snake mackerels (Alepisauridae) 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).

White marlin (*Tetrapterus albidus*)

In common with blue marlin, white marlin are opportunistic 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 fish 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 *Dactylopterus volitans* (ICCAT, 2013). Other prey items included moon fishes, puffer fishes, pomfret fishes, snake mackerels, and deep water red prawns. The variety and constant presence of prey items in stomach contents have led to the suggestion that because of the high active metabolic rate of billfishes, they are forced to feed almost constantly to meet their energy needs (ICCAT, 2013).

Sailfish (*Istiophorus albicans*)

Adult sailfish feed opportunistically on schools of small tunas, jacks (Carangidae), halfbeaks (*Hemiramphus spp.)* and cephalopods. Adult sailfish in the Straits of Florida and adjacent waters feed on Little tunny, *Euthynnus aletteratus*, halfbeaks, cutlassfish (*Trichurus lepturus*), rudderfish, *Strongylura notatus*, jacks (*Caranx spp.)* and cephalopods (ICCAT, 2010h). In the tropical North Atlantic, about 75% of the diet was composed of fish prey and the rest was cephalopods. Among prey fish species, the most important families were Bramidae and Gempylidae.

Group 3 – Small tunas

Wahoo (*Acanthocybium solandri*)

Wahoo are fast, voracious predators that feed primarily on fishes. Along the southeastern coast of the US, it has been observed that the most productive fishing areas for wahoo are often in the vicinity of *Sargassum* mats (Manooch, 1984). Wahoo are known to prey upon scombrids, flyingfishes (exocoetids), clupeids, scads and other pelagic fishes and squids (Collette and Nauen, 1983). In Bermuda, Little tunny and flyingfishes are common fish prey (Luckhurst, pers. obs.; Oxenford et al, 2003). The groups of key importance to the diet are similar among locations and comprise fast swimming pelagic families 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). It appears that wahoo do not feed on small prey items probably because they lack gill rakers (Collette and Nauen, 1983) and there is no apparent relationship between predator and prey size (Manooch and Hogarth, 1983) since wahoo can bite large prey into pieces with their razor-sharp teeth.

Blackfin tuna (*Thunnus atlanticus*)

Blackfin are not primarily piscivorous but feed mainly 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). 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).

Little tunny (*Euthynnus alletteratus*)

Little tunny is an opportunistic predator and feeds 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 (99%) as the functional prey group (Bowman et al, 2000). Little Tunny are preyed upon by large yellowfin tuna and billfishes (Collette and Nauen 1983) as well as by wahoo (Oxenford et al, 2003).

Dolphinfish (*Coryphaena hippurus*)

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 (Oxenford, 1999), but this is probably incidental ingestion. Dolphinfish feed primarily during the day, as they rely upon their vision (as well as their lateral line system) to detect prey (Oxenford, 1999). Feeding behavior of dolphinfish varies greatly – sometimes they are voracious predators that pursue and capture fast-swimming prey such as flying fish and mackerels (Oxenford and Hunte, 1999) while at other times they simply nibble on small crustaceans found in floating *Sargassum* mats (Manooch, 1984). Predators of dolphinfish include large tunas – yellowfin, albacore; billfishes – blue marlin, white marlin, sailfish, swordfish and pelagic sharks (Oxenford, 1999). The diets of these predators indicate that dolphinfish, particularly juveniles, are an important prey item.

Group 4 – Pelagic sharks

Shortfin mako (*Isurus oxyrinchus*)

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. 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%).

Blue shark (Prionace glauca)

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). Regional and seasonal differences in diet were reported in the western North Atlantic (Kohler *et a*, 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 the northeast Atlantic, Henderson et al (2001) reported finding the same major prey groups (i.e. fish and cephalopods) as in other studies, but also included seabirds and crustaceans.

Predator – prey relationships

Table 1 summarizes the data on the principal prey groups taken by the tunas and billfishes presented in this paper with an emphasis on those groups that are a part of the Sargasso Sea ecosystem. With respect to the five species of tuna, it can be seen that several families of epipelagic teleosts, viz. exocoetids, scombrids and clupeids are important prey groups whereas mesopelagic families, viz. Gonostomatidae and Myctophidae dominate the diet of bigeye tuna (Table 1). All tuna species have squid as an integral prey group in their diets (Table 1). The results from a recent study in the central North Atlantic confirm that ommastrephid squids are the most ubiquitous prey group across large pelagic fish predator species (Logan et al, 2013).

All three species of istiophorid billfishes prey on epipelagic families but also on mesopelagic families which they apparently feed on during periodic, short-duration dives during daylight hours (Goodyear et al., 2006). In contrast, swordfish feed almost exclusively on mesopelagic teleosts and squids during their diurnal migrations to deep water. The one prey group which is common to all of these pelagic predators is squid (Logan et al, 2013). which comprise an important dietary element for all of these species (Table 1).

The two species of pelagic sharks included in this paper have epipelagic fishes (Scombridae, Clupeidae) as principal prey groups (Table 2) but larger shortfin mako will also feed on swordfish (Bowman et al, 2000). In contrast, blue sharks prey more on elasmobranchs. Both shark species also have squid as an important element of their diet (Table 2). At a level below the apex predators, wahoo are the most active pursuit predators preying on epipelagic families near the surface. In contrast, the prey groups of dolphinfish are more variable – sometimes they actively pursue flyingfish, presumably when they are seasonally abundant while at other times, they feed on small crustaceans and juvenile fishes associated with *Sargassum* mats (Table 2). Blackfin tuna are primarily crustacean feeders but will take juvenile fishes while Little tunny feed principally on schools of small clupeids.

Although anguillid eels are known to migrate into the Sargasso Sea to spawn, comprising a potential prey group for large, pelagic predators, there was no report of anguillid eels in stomach contents in a large dietary study of fishes and squids in the northwest Atlantic Ocean (Bowman et al, 2000).

Stable isotope analysis for diet and trophic level

Stable isotope analysis provides a powerful tool for estimating trophic positions in food webs (Post, 2002) and has been used to study the trophic ecology of large pelagic fishes and cephalopods in the world's oceans. There is a requirement that a direct comparison be made between diet and isotope data and estimates of the isotopic baseline are required to infer trophic structure (Olson and Watters, 2003). The isotopes of carbon and nitrogen have been found to be particularly useful as these isotope values reflect average assimilated diet over a range of timescales (Logan and Lutcavage, 2013). The proportion of stable isotopes of carbon (C13/C12) and nitrogen (N15/N14) are known and through a process called isotopic fractionation, the lighter isotope is excreted in greater proportion than the heavier isotope, leaving the animal enriched in the heavier isotopes relative to its food source (Olson and Watters, 2003). These isotope values are affected by growth rates and the metabolic turnover rate for a given tissue. For example, it has been estimated that complete isotopic turnover probably requires several months for tuna white muscle (Graham, 2008), during which time predators could migrate both vertically and horizontally to feed on prey associated with varied isotopic baselines. As a consequence, estimating trophic position (TP) using stable isotope values must be used with some caution

Cephalopod beaks, which accumulate in predator stomachs, reflect recent diet, even though they are slower to digest than mantle tissue. In comparison, isotope ratios derived from fish white muscle and liver tissues, reflect dietary information over timescales of weeks and months (Logan and Lutcavage, 2013). Carbon stable isotope ratios (13C/12C; d13C) increase moderately between diet and consumer and provide a chemical record of primary production sources e.g. type of phytoplankton, even at higher trophic levels. Nitrogen stable isotope ratio (15N/14N; d15N) increases are generally more amplified for fish and cephalopod muscle and can be used as a proxy for TP in a food web when combined with estimates of baseline isotope values and diet-tissue discrimination factors (Post, 2002).

Models of pelagic ecosystems appear to normally include five trophic levels, e.g. the model of the eastern tropical Pacific Ocean (Olson and Watters, 2003). The apex predators in this model (swordfish and bigeye tuna) were assigned the highest trophic position (TP = 5.2) followed by pelagic sharks (TP = 5.0). Large piscivores e.g. marlins, large tunas and wahoo were ranked with a TP of 4.5. All trophic positions in this model were based on nitrogen stable isotope values. In a study of the pelagic ecosystem of the central North Atlantic, including the Sargasso Sea, TP estimates of a range of large pelagic fish predators were similar (Logan and Lutcavage, 2013). Stable isotope analysis based on white muscle tissues provided TP estimates which ranged from 4.3 for dolphinfish to 5.1 for large swordfish (Table 3) (Logan and Lutcavage, 2013). Included in this range were large ommastrephid squids (TP = 4.7) placing them at a comparable trophic level to other large apex fish predators (Table 3). TP estimates increased significantly with size for swordfish and for white marlin, but not for any other species examined (Logan and Lutcavage, 2013). When examining the trophic structure of the cephalopods and large pelagic fishes in this study, it was observed that there was a high degree of overlap in isotope values although some sub-groupings did emerge. Dolphinfish and yellowfin tuna occupied the lowest TP amongst the pelagic fishes (Table 3) which appears to be consistent with their diets. Albacore tuna, bigeye tuna, white marlin, blue marlin, ommastrephid squid, and small swordfish made up an intermediate TP group (Table 3). Large swordfish (> 150 cm FL) had the highest TP (5.1) of all sampled species. This finding was confirmed by an examination of swordfish stomach contents during the study which found that they contained the largest prey, including a number of cephalopod species (Logan et al., 2013). Albacore tuna had the lowest carbon and nitrogen isotope values and also consumed the smallest prey, including a higher

proportion of crustaceans (Logan et al., 2013). The species with the largest vertical range for feeding in the water column, bigeye tuna and swordfish had higher N isotope values than the more epipelagic yellowfin tuna and dolphinfish, whose diets from the Sargasso Sea region contain fishes of several *Sargassum*-associated families, e.g. Exocoetidae, Diodontidae, Molidae, and Monacanthidae (Logan et al., 2013). This finding could account for slightly lower N isotope values for these pelagic predators.
Stable isotope analysis has been performed on four pelagic shark species in the northwest Atlantic including blue shark, shortfin mako, thresher shark (*Alopias vulpinus*) and basking shark (*Cetorhinus maximus*) (Estrada et al, 2003). Thresher sharks had the highest TP (4.5) while the values for shortfin mako and blue shark were slightly lower but more variable. The basking shark had the lowest TP (3.1) as would be expected for a plankton-feeder (Estrada et al, 2003). In a study of trophic groupings of pelagic predators and prey off eastern Australia, shortfin mako sharks had the highest TP amongst a group of "top predators" (Revill et al., 2009) which included co-occurring tunas and billfishes. As shortfin mako prey on swordfish in the NW Atlantic (Bowman et al., 2000), it is possible that they occupy a higher TP than indicated by Estrada et al. (2003) (Table 3).

Pelagic food web of the Sargasso Sea

The preliminary pelagic food web presented here (Fig. 3) is incomplete as toothed cetaceans and sea birds, two other important high-level trophic groups, have not been included as they were beyond the scope of the present study. They were, however, included in a more comprehensive pelagic food web of the eastern tropical Pacific (Olson and Watters, 2003). This proposed preliminary food web has been constructed using published values of TP for all of the pelagic predator species listed in this paper. The majority of the TPs are based on stable isotope values (Table 3) derived from a study conducted in the central North Atlantic, including the northern portion of the Sargasso Sea (Logan and Lutcavage, 2013). Values of TP from Fishbase.org have been included for comparison with the published values (Table 3). Despite the fact that the values in Fishbase.org are largely based on diet studies alone, the estimates of TP are similar to those derived from stable isotope analysis (Table 3). In the case of sharks, Estrada et al.(2003) found that there were no statistical differences between TP estimates derived from stable isotope analysis and those derived from stomach contents.

All of the pelagic fish predators in this study have a TP of 4.0 or greater with the exception of skipjack tuna (3.8). This ranks all of these species in the upper trophic levels of the food web. The highest ranked species and apex predator in this food web is large swordfish (TP = 5.1) (Fig. 3) followed by white marlin (4.9) and three species - blue marlin, bigeye tuna and small swordfish at a TP of 4.8. White marlin and blue marlin feed both at the surface, as evidenced by the importance of flying fishes in their diets, but also make short duration dives to the mesopelagic zone to feed on alternative prey groups there. Ranked just below this group of top predators are albacore tuna and large ommastrephid squid at 4.7 (Fig. 3). This TP indicates that

large ommastrephid squid are major predators in this pelagic ecosystem. However, with smaller squid (of several different families) ranked one full TP below at 3.7 (Logan and Lutcavage, 2013), squid are also a very important prey group for large pelagic predators (Fig.3). Logan et al. (2013) found that ommastrephid squids were the most ubiquitous prey group across top predator species in the central North Atlantic. Squids can occupy a large range of trophic levels in marine food webs reflecting large trophic width and, as some squid species are important prey of apex predators, they may be considered keystone species in pelagic ecosystems (Coll et al, 2013). Model results show that squids can have a large impact on other elements of marine food webs and top-down control from squids to their prey can be significant, although the role of squids in pelagic ecosystems appears to be more constrained to a bottom-up impact on their predators (Coll et al, 2013).
Shortfin mako shark, yellowfin tuna and sailfish are ranked at 4.5 (Fig. 3) with a progressive decrease down to adult bluefin tuna ranked at 4.2, the same level as blue shark. Stable isotope analysis has shown that juvenile bluefin feed at a significantly lower trophic position (3.2) than adults (Logan et al, 2011). This is lower than would be indicated by stomach contents analysis alone and this TP value of 3.2 is similar to those of suspension feeders suggesting that nektonic crustaceans and zooplankton may contribute significantly to the diet of juvenile bluefin (Logan et al, 2011).

Mesopelagic fishes (TP = 3.4) are a major prey group for some of the apex predators in this food web (Fig. 3). The species which undertake diurnal vertical migrations to the mesopelagic zone to feed, i.e. swordfish and bigeye tuna, are also the highest ranked species in the food web (Fig. 3) and appear to have a larger array of prey groups upon which to feed. It is unknown but this may confer some trophic advantage over other top predators which are largely confined to the epipelagic zone, e.g. sailfish, wahoo, dolphinfish, blackfin tuna. A study of the diet of five large predatory mesopelagic fishes (species in the families Gempylidae and Lampidae) in the central North Pacific (around Hawaii) concluded that adult tunas and billfishes occupying a shared vertical habitat did not appear to compete for prey resources with these mesopelagic predators to any appreciable level (Choy et al, 2013). They suggested that this may be an example of successful partitioning of limited prey resources within an oligotrophic gyre ecosystem.

Summary

The trophic relationships of apex predators such as tunas, sharks, and billfishes in the central North Atlantic Ocean are not well understood (Logan and Lutcavage, 2013) despite the fact that important commercial fisheries have been operating in this region for decades (www.iccat.int). These top predators range widely across pelagic habitats (e.g. billfishes, Ortiz et al., 2003) and undergo temporal and ontogenetic feeding cycles. Those predators which spend most of their time in the epipelagic zone e.g. billfishes, yellowfin tuna, skipjack tuna, wahoo and dolphinfish, appear to be primarily diurnal sight-feeders. They usually pursue fast-swimming prey near the surface such as flying fishes, scombrids and squid. There is evidence that dolphinfish may also feed at night when the moon provides ample light (Oxenford, 1999). In comparison to this feeding pattern, species such as swordfish and bigeye tuna spend the nocturnal hours in the epipelagic zone (usually >80m depth) where some feeding occurs but they also dive during daylight hours to the mesopelagic zone to feed. These vertically migrating predators must have specific adaptations to localize prey organisms at depths which are only lighted by residual luminosity and the bioluminescence of meso- and bathy-pelagic organisms (Maury and Lehodey, 2005). There is frequently a relationship between size of predator and size of prey but because of the diversity of feeding habits amongst these predators and their opportunistic nature, it is often difficult to characterize such relationships in a meaningful way. In the case of bluefin tuna, there does not appear to be a clear relationship between prey length and predator size; both small and large bluefin feed on similar ranges of prey-size (ICCAT, 2010d).

Landings from directed fisheries, mainly longlining (e.g. tunas, swordfish) and as by-catch (e.g. billfishes) must impact the trophic structure in pelagic ecosystems by altering top-down and bottom-up flows (Logan and Lutcavage, 2013). In addition, another factor which has become increasingly important is climate variability (Alheit, 2009) which must also presumably impact trophic structure as changes in the distribution and composition of mid-trophic level prey groups may alter linkages with their predators (Polovina et al, 2009). The timing of feeding migrations by albacore and eastern bluefin tuna in the northeast Atlantic has shifted in recent decades and climate variability has been identified as the probable cause (Dufour et al, 2010). To predict impacts of these various influences on top predators, an understanding of the trophic structure must first be available in order to model the system, and multispecies trophic models of ecosystems depend on the accurate depiction of trophic links (Maury and Lehodey, 2005). The traditional method of assessing diet is the analysis of stomach contents which provides "a snapshot in time" but which has the limitation that some dietary elements may be missing. The advantage of using stable isotopes is that they integrate biochemical "signatures" of all assimilated prey components into the animal's tissues. The use of stable isotope analysis has allowed significant advances in understanding trophic linkages. However, the estimates derived from this analysis must be used with caution as they are sensitive to a variety of factors, including the assumption of constrained movements within the timescales of tissue turnover (Logan and Lutcavage, 2013). For example, diets and estimates of TP based on stable isotopes for albacore varied between the northeast Atlantic and the Mediterranean on a seasonal and inter-annual basis (Goni et al, 2011).

The importance of *Sargassum* to feeding in pelagic predators such as dolphinfish is well documented (Oxenford, 1999) as is the significant association of wahoo with *Sargassum* windrows during feeding (Manooch, 1984; Oxenford et al, 2003). Mats of *Sargassum* typically act as shelter habitat for many prey species of pelagic predators and prey densities in association with *Sargassum* are generally much greater than in the open ocean (Casazza and Ross, 2008). Important prey groups like flyingfishes spawn on *Sargassum* mats and thus, the presence of these mats may well have an impact on spawning success for this forage group. This could in turn affect the biomass of this prey group which is available to top predators thus having a bottom-up effect on the food web. In terms of the importance of *Sargassum* habitat, Coston-Clements et al (1991) have documented the association of the juveniles of a number of pelagic predators discussed here with pelagic *Sargassum* in the North Atlantic. These species include dolphinfish, wahoo, swordfish, blue marlin, white marlin and sailfish. This pelagic habitat appears to be very important in the early life history stages of these predators for both feeding and shelter. The Sargasso Sea is also a known spawning ground for blue marlin (Luckhurst et al, 2006) with *Sargassum* able to provide habitat for young juveniles. Wahoo spawn during the summer months in Bermuda waters (Luckhurst, pers. obs.) and juveniles may take advantage of *Sargassum* mats in their early development stages for shelter and food.

In the context of this paper, the CLIOTOP (CLimate Impacts on Oceanic TOp Predators) program is highly relevant. It is designed to investigate the processes linking top predators with their environment, their responses to environmental and anthropogenic forcings and the impact of management measures on the ecosystem (Maury and Lehodey, 2005)**.** Specifically, the program aims to evaluate the impact of fishing and climate variability on marine ecosystems inhabited by oceanic top predators by analyzing and comparing long-term data sets, ocean/atmosphere and biogeochemical analyses and by conducting experiments. Modeling is an important tool for exploring the ecological consequences of fishing and improving our knowledge of how climate variability influences the structure and function of ecosystems. The use of models and extensive simulations to deduce and understand the dynamics of the ecosystem(s) and the component populations, should lead to a higher level of realism and predictive ability (Maury and Lehodey, 2005)**.** There is clearly a need to delineate the key trophic pathways linking primary production to the upper trophic levels through forage groups such as flyingfishes, and to understand how the sources of primary production and trophic pathways change in different productivity regimes (e.g. Sargasso Sea) and ecosystems (Maury and Lehodey, 2005)**.** The trophic model of the pelagic eastern tropical Pacific region (Olson and Watters, 2003) provides a useful comparison to the preliminary trophic web proposed here (Fig. 3). Both trophic webs have cephalopods (mainly squid) as a significant component of their respective ecosystems, both as predators and prey, and an enhanced understanding of this trophic group is essential to developing more realistic and predictive models of pelagic ecosystems (Olson and Young, 2007).

References

Alheit, J., 2009. Consequences of regime shifts for marine food webs. Int. J. Earth Sci. 98: 261–268.

Allen, L.G. and J.N. Cross. 2006. Chapter 12 – Surface Waters, p.320-341. In: The Ecology of Marine Fishes: California and Adjacent Waters. Allen, L.G., D.J. Pondella and M.H. Horn (eds.). University of California Press, Berkeley, 670 pp.

Angel, M.V. 2011. The Pelagic Ocean Assemblages of the Sargasso Sea Around Bermuda. Sargasso Sea Alliance Science Report Series, No 1, 25 pp.

Bowman, R.E, C.E. Stillwell, W.L. Michaels and M.D. Grosslein. 2000. Food of northwest Atlantic fishes and two common species of squid. NOAA Tech. Memo. NMFS-NE-155, 149 p.

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.

Choy, C.A., E. Portner, M. Iwane and J.C. Drazen. 2013. Diets of five important predatory mesopelagic fishes of the central North Pacific. Mar. Ecol. Prog. Ser. 492: 169-184.

Coll, M., J. Navarro, R.J. Olson and V. Christensen. 2013. Assessing the trophic position and ecological role of squids in marine ecosystems by means of food-web models. Deep-Sea Research II 95: 21-36.

Collette, B. B. and C.E. Nauen. 1983. FAO species catalogue. Vol. 2. Scombrids of the World. FAO Fish Synop. 125, Vol. 2, 137 pp.

Conte, M.H., J.B. Bishop and R.H. Backus. 1986. Non-migratory, 12 – kHz, deep scattering layers of Sargasso Sea origin in warm-core rings. Deep Sea Research 33: 1869-1884.

Cortés, E. 1999. Standardized diet composition and trophic level of sharks. ICES J. Mar. Sci. 56:707-717.

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, pp. 24.

Dufour, F., H. Arrizabalaga, X. Irigoien and J. Santiago. 2010. Climate impacts on albacore and bluefin tunas migrations phenology and spatial distribution. In: CLIOTOP International Symposium Volume. Progress in Oceanography 86: 283-290.

Estrada,J.A., M. Lutcavage and S.R. Thorrold. 2005. Diet and trophic position of Atlantic Bluefin tuna (*Thunnus thynnus*) inferred from stable carbon and nitrogen istope analysis. Mar. Biol. 147: 37-45.

Fishbase, 2014. Gonostomatidae - *Cyclothone braueri.*

Galuardi, B and M. Lutcavage. 2012. Dispersal routes and habitat utilization of juvenile Atlantic bluefin tuna, *Thunnus thynnus*, tracked with mini-PSAT and archival tags. PLoS ONE 7(5): e37829. Doi: 10.1371.

Goni, N., J. Logan, H. Arrizabalaga, M. Jarry and M. Lutcavage. 2011. Variability of albacore (*Thunnus alalunga)* diet in the Northeast Atlantic and Mediterranean Sea. Mar. Biol. 158: 1057-1073.

Goodyear, C.P., J. Luo, E.D. Prince and J.E. Serafy. 2006. Temperature-depth habitat utilization of blue marlin monitored with PSAT tags in the context of simulation modeling of pelagic longline CPUE. Col.Vol. Sci. Pap. ICCAT 59: 224-237.

Graham, B.S., 2008. Trophic Dynamics and Movements of Tuna in the Tropical Pacific Ocean Inferred From Stable Isotope analyses, Ph.D. Thesis.University of Hawaii, Manoa, Hawaii, USA.

Hassani, S., L. Antoine and V. Ridoux. 1997. Diets of albacore, *Thunnus alalunga*, and dolphins, *Delphinus delphis* and *Stenella coerulaeoalba*, caught in the northeast Atlantic albacore drift-net fishery: a progress report. J. Northw. Atl. Fish. Sci. 22: 119-123.

Helfman, G.S., B.B. Collette, and D.E. Facey. 1997. The diversity of fishes, Blackwell Science, Inc. Malden, MA. 527 pp.

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.

ICCAT, 2005. Resolution 05-11 on pelagic *Sargassum*. Collected in Compendium Management Recommendations and Resolutions adopted by ICCAT for the Conservation of Atlantic tunas and tuna-like species, Madrid, ICCAT, 2011.

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. 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, 2011. Report of the Inter-sessional meeting of the SCRS Sub-Committee on Ecosystems. 5.4. Presentation by the Sargasso Sea Alliance, p. 10.

ICCAT, 2012. Resolution (12-12) by ICCAT on the Sargasso Sea.

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

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., H.S.J. Roe et al.. 2011. The protection and management of the Sargasso Sea: The golden floating rainforest of the Atlantic Ocean. Summary science and supporting evidence case. Sargasso Sea Alliance, pp. 71.

Logan, J.M., E. Rodriguez-Marin, N. Goni, S. Barreiro, H. Arrizabalaga, W. Golet and M.E. Lutcavage. 2011. Diet of young Atlantic bluefin tuna (*Thunnus thynnus*) in eastern and western Atlantic foraging grounds. Marine Biology 158: 73-85.

Logan, J.M. and M.E. Lutcavage. 2013. Assessment of trophic dynamics of cephalopods and large pelagic fishes in the central North Atlantic using stable isotope analysis. Deep-Sea Research II 95: 63-73.

Logan, J.M., R. Toppin, S. Smith, B. Galuardi, J. Porter and M. Lutcavage. 2013. Contribution of cephalopod prey to the diet of large pelagic fish predators in the central North Atlantic Ocean. Deep-Sea Research II 95:74-82.

Lordan, C., M.A. Collins, L.N. Key and E.D. Browne. 2001. The biology of the ommastrephid squid, *Todarodes sagittatus*, in the north-east Atlantic. J. Mar. Biol. Assoc. UK 81: 299-306.

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.

Luckhurst, B.E. 2014. Elements of the ecology and movement patterns of highly migratory fish species of interest to ICCAT in the Sargasso Sea. SCRS/2013/132, 23 p.

Manooch, III, C.S. and W.T. Hogarth. 1983. Stomach contents and giant trematodes from wahoo, *Acanthocybium solanderi*, collected along the south Atlantic and Gulf coasts of the United States. Bull. Mar. Sci. 33: 227-238.

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

Maury, O. and P. Lehodey (Eds.). 2005. CLimate Impacts on Oceanic TOp Predators (CLIOTOP). Science Plan and Implementation Strategy. GLOBEC Report No.18, ii, 42pp.

National Marine Fisheries Service (NMFS). 2003. "Fisheries of the Caribbean, Gulf of Mexico and South Atlantic; pelagic *Sargassum* habitat of the south Atlantic region (Final Rule)". Federal Register 68: 192 p. 57375, http://www.safmc.net/Portals/6/Library/FMP/*Sargassum*/SargFMPFinalrule.

Olson R.J. and G.M. Watters. 2003. A model of the pelagic ecosystem in the eastern tropical Pacific Ocean. Bulletin of the Inter-American Tropical Tuna Commission 22(3): 133-218.

Olson,R.J. and J.W. Young. 2007. The role of squid in open ocean ecosystems. Report of a GLOBEC-CLIOTOP /PFRP Workshop, November 2006, Hawaii. GLOBEC Report 24: 94 pp.

Ortiz, M., Prince, E.D., Serafy, J.E., Holts, D.B., Davy, K.B., Pepperell, J.G., Lowry, M.B., Holdsworth, J.C., 2003. Global overview of the major constituent-based billfish tagging programs and their results since 1954. Mar. Freshwater Res. 54 (4): 489-507.

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. and W.Hunte . 1999. Feeding habits of the dolphinfish (*Coryphaena hippurus*) in the eastern Caribbean. Scientia Marina 63: No. 3,4.

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., 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.

Parry, M.P. 2003. The trophic ecology of two ommastrephid squid species, *Ommastrephes bartrami* and *Sthenoteuthis oualaniensis*, in the north Pacific sub-tropical gyre. Ph.D. thesis, University of Hawaii, Manoa, Hawaii.

Polovina, J.J., M. Abecassis, E.A. Howell and P. Woodworth. 2009. Increases in the relative abundance of mid-trophic level fishes concurrent with declines in apex predators in the subtropical North Pacific, 1996-2006. Fish. Bull. 107: 523-531.

Post, D.M. 2002. Using stable isotopes to estimate trophic position: models, methods and assumptions. Ecology 83: 703-718.

Revill, A.T., J.W. Young and M. Lansdel, 2009. Stable isotopic evidence for trophic groupings and bio-regionalizationof predators and their prey in oceanic waters off eastern Australia. Mar. Biol. 156:1241-1253.

Roe, H.S.J. 1984. The diel migrations and distributions within a Mesopelagic community in the North East Atlantic. 2. Vertical migrations and feeding of Mysids and decapod crustacea. Progress in Oceanography 13: 269-318.

Roe, H.S.J. and J. Badcock. 1984a. The diel migrations and distributions within a Mesopelagic community in the North East Atlantic. 5. Vertical migrations and the feeding of fish. Progress in Oceanography 13: 389-424.

Roe, H.S.J., P.T. James and M.H. Thurston. 1984b. The diel migrations and distributions within a Mesopelagic community in the North East Atlantic. 6. Medusae, ctenophores, amphipods and euphausiids. Progress in Oceanography 13: 425-460.

Rooker, J.R., J.P. Turner and S.A. Holt. 2006. Trophic ecology of Sargassum-associated fishes in the Gulf of Mexico determined from stable isotopes and fatty acids. Mar. Ecol. Prog. Ser. 313: 249-259.

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.

South Atlantic Fishery Management Council. 2002. Fishery management plan for pelagic *Sargassum* habitat of the south Atlantic region. South Carolina. 183 pp.

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.

Sutton, T.T., P.H. Weibe, L. Madin and A. Bucklin. 2010. Diversity and community structure of pelagic fishes to 5000 m depth in the Sargasso Sea. Deep Sea Research 57: 2220-2233.

Trott, T.M., S.A. McKenna, J.M. Pitt, A. Hemphill, F.W. Ming, P. Rouja, K.M. Gjerde, B. Causey and S.A. Earle. 2011. Efforts to enhance protection of the Sargasso Sea. Proc. Gulf Caribb. Fish. Inst. 63: 282-295.

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.

Table 1 - Pelagic fish predators (tunas and billfishes) and principal prey groups in the North Atlantic. Squid not defined by family as insufficient taxonomic detail available.

	PREY				
PREDATORS	**Epipelagic teleosts**	**Mesopelagic teleosts**	**Cephalopods**	**Crustaceans**	**Other**
Yellowfin	Exocoetidae Scombridae		squid		
Albacore	Clupeidae Engraulidae Scombridae		squid		
Bigeye		Gonostomatidae Myctophidae	squid	euphausids	
Bluefin	Clupeidae Engraulidae Ammodytidae		squid octopus	crabs	sponges
Skipjack	Clupeidae		squid	crabs	
Swordfish	Clupeidae	Gonostomatidae Myctophidae Gempylidae Sternoptychidae	squid		
Blue marlin	Exocoetidae Scombridae Coryphaenidae	Gempylidae	squid		
White marlin	Exocoetidae Scombridae Coryphaenidae	Bramidae Gempylidae	squid		
Sailfish	Scombridae Carangidae Hemiramphidae	Bramidae Gempylidae	squid	red prawns	

Table 2 - Pelagic sharks and Small-tuna category predators and their principal prey groups in the North Atlantic. Squid not defined by family as insufficient taxonomic detail.

		PREY			
PREDATORS	Epipelagic teleosts	Mesopelagic	Cephalopods	Crustaceans	Other
Shortfin mako	Pomatomidae Scombridae Clupeidae Xiphiidae		squid		
Blue shark	Scombridae Clupeidae		squid		elasmobranchs local demersal
OTHER PREDATORS					
Wahoo	Scombridae Exocoetidae Clupeidae		squid		
Blackfin tuna	juvenile teleosts		squid	mainly larvae	
Little tunny	Clupeidae		squid	small spp.	tunicates
Dolphinfish	Exocoetidae Scombridae		squid	crabs shrimps	

Table 3 - Estimation of trophic position (TP) of pelagic fish predators and cephalopods using nitrogen stable isotope (SI-N) values and diet studies.

Species	Trophic Position Mean ± 1 SD	TP source	Geographical region	Reference
Yellowfin	4.5 ± 0.3	SI-N	Central North Atlantic	Logan and Lutcavage, 2013
	4.3 ± 0.7	diet		Fishbase.org
Albacore	4.7 ± 0.3	SI-N	Central North Atlantic	Logan and Lutcavage, 2013
	4.3 ± 0.7	diet		Fishbase.org
Bigeye	4.8 ± 0.4	SI-N	Central North Atlantic	Logan and Lutcavage, 2013
	4.5 ± 0.8	diet		Fishbase.org
Bluefin	4.2	SI-N	NW Atlantic Ocean	Estrada et al, 2005
* juvenile	3.2*	SI-N	NW Atlantic Ocean	Estrada et al, 2005
	4.4 ± 0.8	diet		Fishbase.org
Skipjack	3.8 ± 0.6	diet		Fishbase.org
Swordfish (> 150 cm FL)	5.1 ± 0.3	SI-N	Central North Atlantic	Logan and Lutcavage, 2013
Swordfish	4.8 ± 0.3	SI-N	Central North Atlantic	Logan and Lutcavage, 2013
(=/< 150 cm FL)	4.5 ± 0.6	diet		Fishbase.org
Blue marlin	4.8 ± 0.3	SI-N	Central North Atlantic	Logan and Lutcavage, 2013
	4.5 ± 0.7	diet		Fishbase.org
White marlin	4.9 ± 0.6	SI-N	Central North Atlantic	Logan and Lutcavage, 2013
	4.5 ± 0.7	diet		Fishbase.org
Sailfish	4.5 ± 0.8	diet		Fishbase.org
Wahoo	4.4 ± 0.8	diet		Fishbase.org
Dolphinfish	4.3 ± 0.3	SI-N	Central North Atlantic	Logan and Lutcavage, 2013
	4.4 ± 0.8	diet		Fishbase.org
Blackfin tuna	3.3	SI-N	Gulf of Mexico	Rooker et al, 2004
	4.1 ± 0.7	diet		Fishbase.org
Little tunny	4	SI-N	Gulf of Mexico	Rooker et al, 2006
	4.5 ± 0.8	diet		Fishbase.org
Blue shark	4.1	diet	mean value	Cortés, 1999
	4.2 ± 0.7	diet		Fishbase.org

Shortfin mako	4.3	diet	mean value	Cortés, 1999
	4.5 ± 0.7	diet		Fishbase.org
Ommastrephid squid - large	4.7 ± 0.5	SI-N	Central North Atlantic	Logan and Lutcavage, 2013
Squid - small	3.7	SI-N	Central North Atlantic	Logan and Lutcavage, 2013

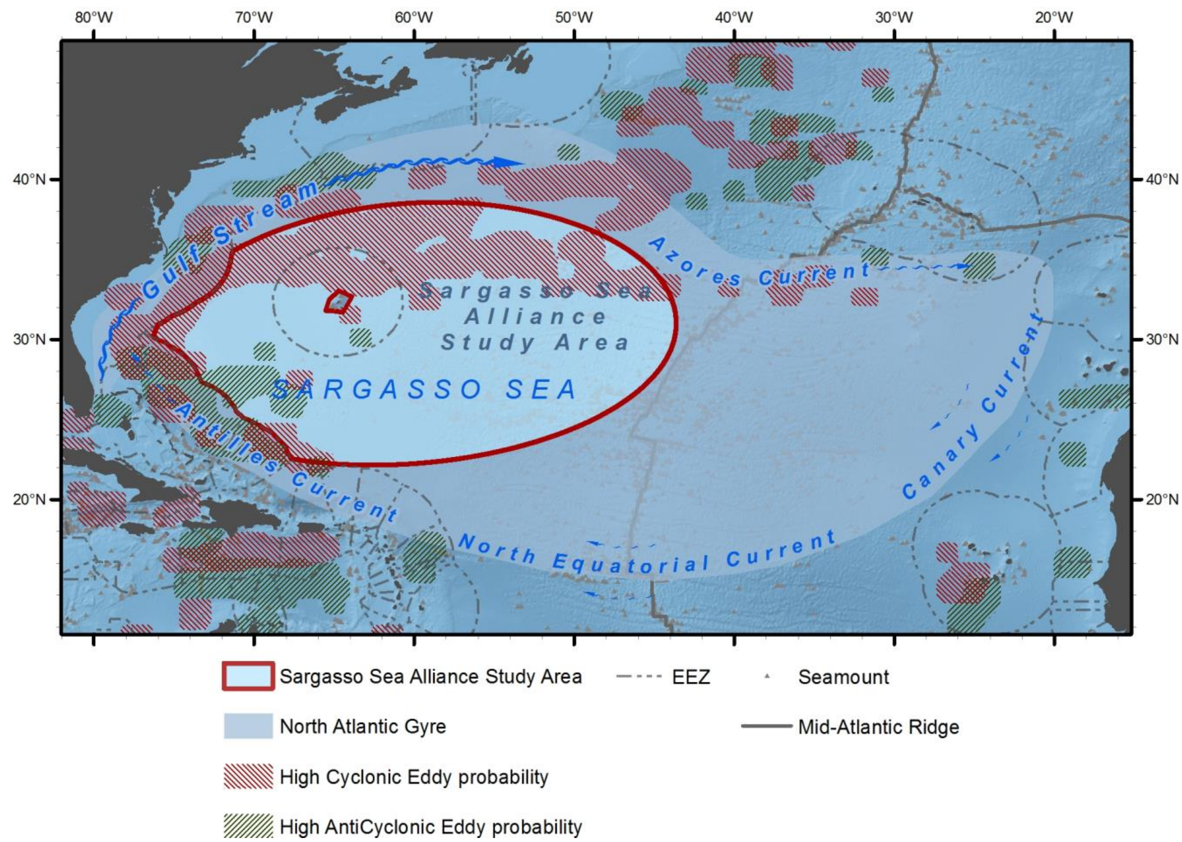

Figure 1 – Map of the Sargasso Sea Alliance Study Area, including the currents and some of the major features that influence boundary definition and location (from Laffoley *et al*.,2012).

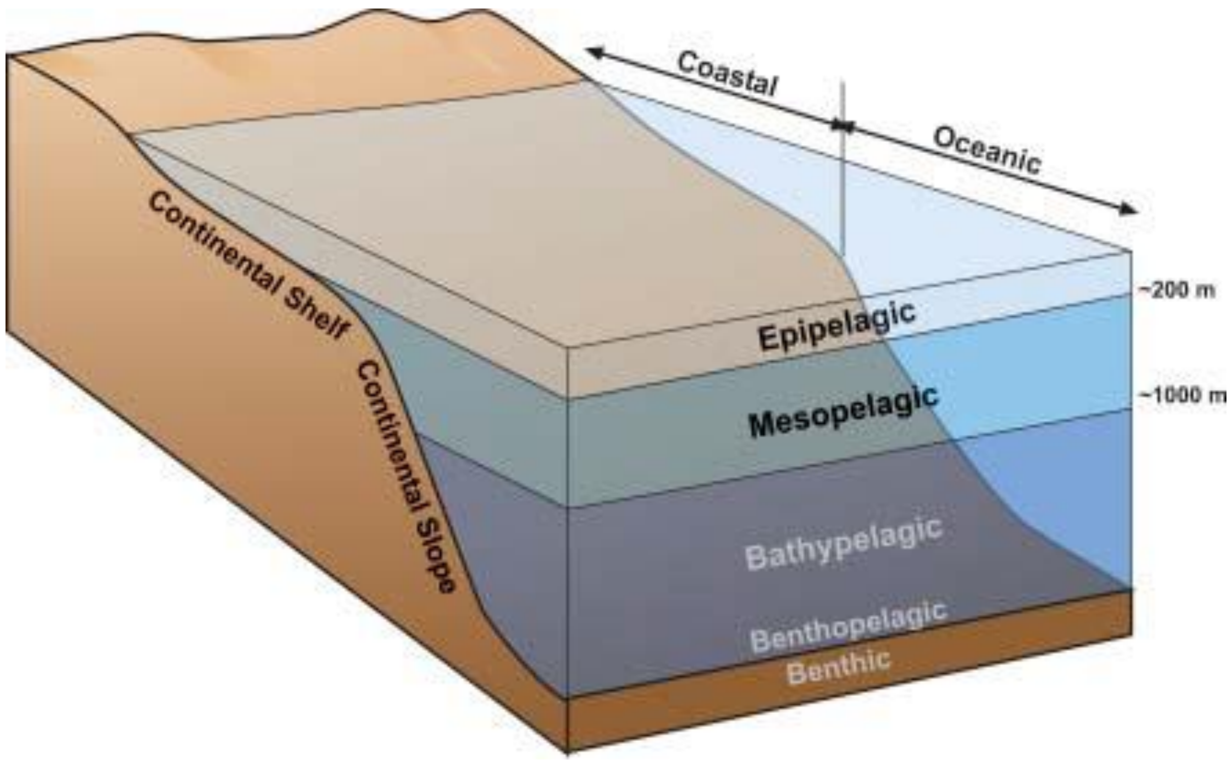

Fig. 2 - A general classification of pelagic habitats (after Allen and Cross, 2006). The mesopelagic zone in the Sargasso Sea is defined as 200-700m following Angel (2011). See text for details of zonation.

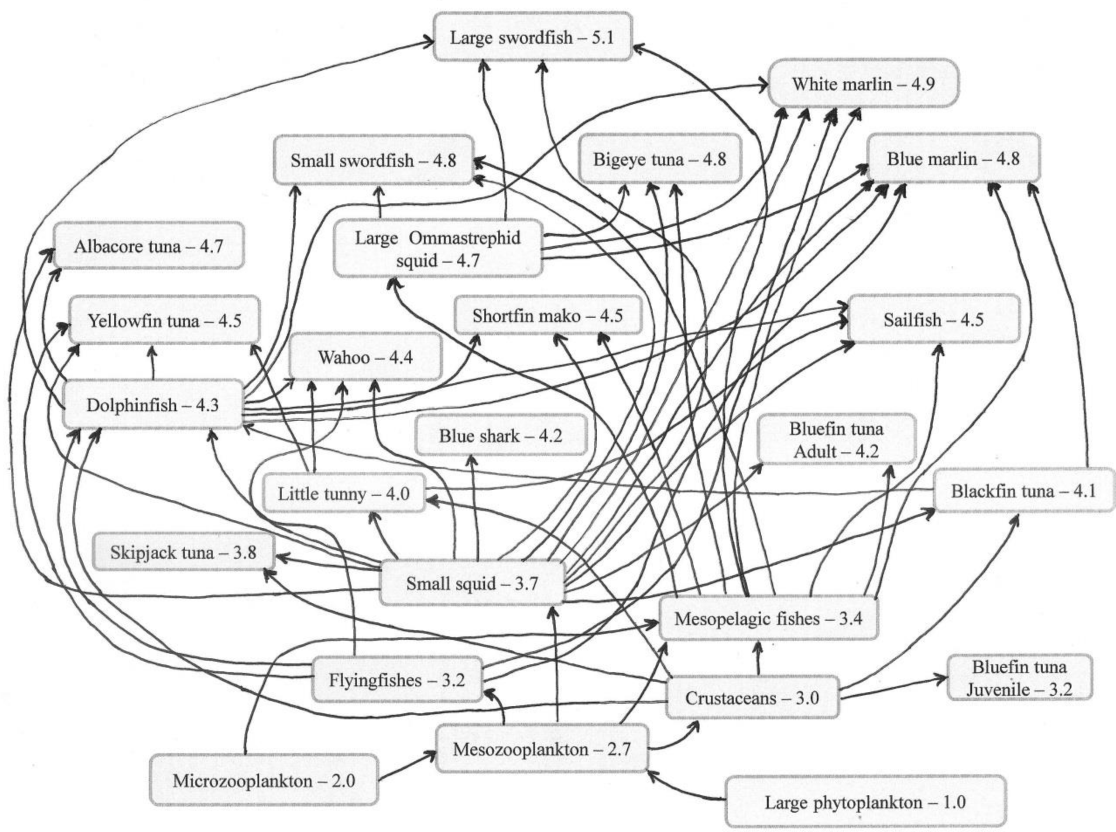

Fig. 3 – Preliminary pelagic food web of the Sargasso Sea. Trophic position (TP) is indicated in the respective species boxes. Many of the predators in this food web feed on small scombrids but this category is not included as a separate entity as it is comprised of a number of different species. Feeding information on mesopelagic fauna is taken from Roe (1984) and Roe et al. (1984b). The trophic position of crustaceans is an estimate based on generalized groups. Toothed cetaceans and seabirds are not included.