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A PRELIMINARY ASSESSMENT OF THE ECOLOGICAL ROLE AND IMPORTANCE OF SQUID IN THE PELAGIC TROPHIC WEB OF THE NORTHWEST ATLANTIC OCEAN INCLUDING THE SARGASSO SEA

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SUMMARY

In the northwest Atlantic, two species of squids are commercially exploited: Northern shortfin squid Illex illecebrosus (Ommastrephidae) *which is an oceanic species and the longfin squid* Doryteuthis (Loligo) pealeii (Loliginidae) *which is a neritic species. The populations of both of these species are strongly influenced by the Gulf Stream, a powerful western boundary current system. Most squid species have life spans of a year or less and, as a consequence, their populations often display irregular annual fluctuations in abundance. As squids function as both predator and prey, they play an important role in the trophic web of pelagic ecosystems. Ommastrephidae are major contributors to the diets of large pelagic fishes in the central north Atlantic and all five tuna species (*Scombridae*) plus swordfish (*Xiphius gladius*) managed by ICCAT, have squid as an integral prey group in their diets. Squids are essentially "annual" species and are highly responsive to changes in their environment. Due to the importance of squid species in pelagic ecosystems, data on these species should be incorporated into ecosystem-based fisheries management (EBFM) models for tuna and tuna-like species.*

RÉSUMÉ

Dans l'Atlantique Nord-Ouest, deux espèces de calmars sont exploitées commercialement : l'encornet nordique Illex illecebrosus (Ommastrephidae) *qui est une espèce océanique et le calmar* totam Doryteuthis (Loligo) pealeii (Loliginidae) *qui est une espèce néritique. Les populations de ces deux espèces sont fortement influencées par le Gulf Stream, un système de courant puissant de frontière ouest. La plupart des espèces de calmars ont des durées de vie d'un an ou moins et, en conséquence, leurs populations présentent souvent des fluctuations annuelles irrégulières en abondance. Comme les calmars fonctionnent comme des prédateurs et des proies, ils jouent un rôle important dans le réseau trophique des écosystèmes pélagiques. Les* Ommastrephidae *sont d'importants contributeurs à l'alimentation des grands poissons pélagiques dans le centre Nord Atlantique et le calmar constitue pour toutes les cinq espèces de thons (*Scombridae*) plus l'espadon (*Xiphius gladius*) gérés par l'ICCAT un groupe de proies formant partie intégrante de leur alimentation. Les calmars sont essentiellement des espèces « annuelles » et sont très sensibles aux changements de leur environnement. En raison de l'importance des espèces de calmars dans les écosystèmes pélagiques, les données sur ces espèces devraient être incorporées dans des modèles de gestion des pêcheries fondés sur l'écosystème (EBFM) pour les thonidés et les espèces apparentées.*

RESUMEN

En el Atlántico noroccidental, dos especies de calamares son explotadas comercialmente: La pota, Illex illecebrosus *(*Ommastrephidae*) que es una especie oceánica y el calamar europeo* Doryteuthis (Loligo) pealeii *(*Loliginidae*) que es una especie nerítica. Las poblaciones de ambas especies están muy influenciadas por la corriente del Golfo, un potente sistema de corriente de límite occidental. La mayoría de las especies de calamares tienen una longevidad de un año o menos y, en consecuencia, sus poblaciones muestran a menudo fluctuaciones anuales irregulares en su abundancia. Dado que calamares son al mismo tiempo depredador y presa, desempeñan un papel importante en la red trófica de los ecosistemas pelágicos. Los* Ommastrephidae *son el principal componente de la dieta de grandes peces pelágicos en el Atlántico central norte, y las cinco especies de túnidos (*Scombridae*) más el espada* (Xiphius

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gladius*) gestionadas por ICCAT tienen a los calamares como un grupo de presas que forma parte de su dieta. Los calamares son especies esencialmente "anuales" y son altamente sensibles a los cambios en su entorno. Debido a la importancia de las especies de calamar en los ecosistemas pelágicos, los datos sobre estas especies deberían incorporarse en cualquier modelo de ordenación de pesquerías basado en el ecosistema (EBFM) para los túnidos y especies afines.*

KEYWORDS

Squid, pelagic ecosystem, trophic web, predator, prey, northwest Atlantic, Sargasso Sea, EBFM

Introduction

Squids are found in most oceanic regions of the world and occupy a wide range of habitats from shallow tropical seas to the deep ocean. Ecologically, they play a very important role as both predators and prey in these various habitats. There is a diversity of body morphology between near-shore and oceanic squid and their success in the ocean is largely related to their ability to fill a variety of ecological niches (Jackson and O'Dor 2007). In many pelagic ecosystems, the large ommastrephid squids (e.g. *Ommastrephes*, *Dosidicus*) are considered to be formidable predators and play a pivotal role in trophic webs. These large, fast-swimming squids that inhabit the epipelagic zone often function as the ecological equivalents to teleost apex predators such as tunas, swordfish and billfishes (Luckhurst 2015). A rapid life history is one feature that distinguishes all squid species from the majority of large teleost fishes. Most squid species have life spans less than a year with only a few species living beyond a year and tropical squids generally have life spans no greater than 200 days (Jackson 2004). The majority of squid species grow throughout their lifetime and attain a maximum body size very shortly before senescence and, as a result, the asymptotic phase of growth, which is a dominant feature of the life history of most teleost fishes, is absent or very short in many cephalopods (Moltschaniwskyj 2004). The brief lifespan of squids contrasts sharply with the majority of large teleost predators that have life cycles spanning many years (e.g. Bluefin tuna, 24+ years, ICCAT 2010). As a consequence of this short life span, squid have been referred to as living 'life in the fast lane' (Jackson and O'Dor 2001). There are several elements of their biology that enable this fast life style: 1) rapid, efficient digestion and a protein-based metabolism that converts food into growth rather than storage, 2) continual recruitment of new muscle (hyperplasia) fibres throughout growth and 3) efficient utilization of oxygen. These features enable the rapid, continual non-asymptotic growth and short life spans that are common to most squids (Jackson and O'Dor 2001).

Squid populations can be described as displaying irregular or spasmodic abundance fluctuations, as opposed to steady or cyclical patterns. Because generations are essentially non-overlapping, modelling of population dynamics is based largely on predicting recruitment success (Caddy 1983; Pierce *et al.* 2007). Squids are thought to be especially sensitive to environmental influences and these factors are expected to have a strong effect on spawning and hatching success and subsequent growth and survival of early life stages (Pierce *et al.* 2007).

In order to better understand the dynamics of pelagic ecosystems, it is necessary to define the role of key components in the system and the impact of environmental factors on that ecosystem.

The traditional pelagic trophic web model, with its many ecosystem interactions, is a conceptual pyramid (Maury and Lehodey 2005). It has large pelagic fishes as its apex and these fishes prey on an increasingly diverse and complex group of organisms at lower trophic levels. The pyramid is supported by primary production (phytoplankton) at the base (Maury and Lehodey 2005). Cephalopods play a pivotal role in most marine pelagic trophic webs because they link the massive biomass of micronekton (particularly myctophid fishes in the mesopelagic zone) to many of the apex predators such as tunas, swordfish and pelagic sharks. Given their role as both prey and predators and the high trophic flux passing through squids, it is essential to gain a better understanding of the key role they play in pelagic ecosystems (Maury and Lehodey 2005).

However, in spite of their importance in pelagic ecosystems, an in-depth knowledge of squid biology is generally lacking. This is due partly to their ability to avoid capture by most conventional marine sampling techniques (e.g. being fast swimmers, they can avoid trawl nets). Identification of squid species in trophic web studies is made more difficult due to their relatively fast digestion in predator stomachs. Often only the chitinous beaks remain in stomachs but this allows the identification of various squid to species level (Menard *et al.* 2007). The use of stable isotope analysis to identify squid presence in the tissues of their predators (Ruiz-Cooley.and Markaida 2007) and to assign trophic levels in pelagic food webs (Logan and Lutcavage 2013) have helped resolve a number of issues in squid trophic ecology.

The lack of detailed biological information has hindered defining their ecological role in many ocean ecosystems. New technologies, including those able to track squid movements with PSAT tags (Gilly *et al.* 2006; Gilly 2007) have demonstrated that the ommastrephid squid *Dosidicus gigas* can migrate at least 200 km in one week and time-at-depth data showed a consistent pattern of daytime hours spent at depths of about 300 m, whereas night time hours were spent in much shallower depths (<150 m) (Gilly 2007). Payne and O'Dor (2007) determined that *D. gigas* can migrate much greater distances over several months (see Trophic ecology below). The rhythmic episodes of diving activity were prominent during both day and night at both deep and shallow depths (Gilly 2007). This diving activity is believed to be related to foraging activity in at least two ways: 1) squid appear to forage (i.e. rhythmic diving) at night both in the shallow zone and at depth and 2) they may also make deep night-time dives to recover from thermal stress encountered while foraging in warm surface waters (Gilly 2007).

Northwest Atlantic

The bulk of the global squid catch comprises species from two families, the Ommastrephidae and Loliginidae (Arkhipkin *et al.* 2015). Five species from the Ommastrephidae dominate in terms of biomass and four of these—*Todarodes pacificus*, *Nototodarus sloanii*, *Illex argentinus*, and *I. illecebrosus*—inhabit high velocity western boundary current systems of the Pacific and Atlantic Oceans. The fifth species, *D. gigas*, inhabits the low-velocity eastern boundary current systems of the eastern Pacific which are characterized by coastal upwelling (Arkhipkin *et al.* 2015).

In the North Atlantic, the northwest region (defined here as 20-50° N. lat., from 45° W. long. to the eastern seaboard) includes the coastal, shelf and oceanic waters off the east coasts of Canada and the USA and includes the Sargasso Sea. The continental shelf broadens in a northward direction and lies primarily within the jurisdiction of these two countries, except that the Flemish Cap and parts of the Grand Banks are located in international waters. A large portion of the Sargasso Sea lies in an area beyond national jurisdiction (ABNJ). Regional oceanographic conditions are mainly driven by the cold, relatively fresh Labrador Current which flows southwestward and a warmer, saltier western boundary current, the Gulf Stream, which flows northeastward (Arkhipkin *et al.* 2015). The Gulf Stream forms a powerful western boundary current with meandering systems that generate warm and cold-core rings. These rings can provide "rapid transport" systems for planktonic squid eggs and larvae. Most of the theory and data on the interactions between squid populations and physical oceanography have been focused on the stocks inhabiting western-boundary current systems. The ommastrephid life cycle in these western boundary systems is generally well described (O'Dor and Dawe 1998). The squid have a one-year life span and spawn in low-latitude warm water. The planktonic eggs and larvae develop in this environment and are subject to transport by ocean currents. When the juvenile squid have grown into the nektonic phase, they migrate in the direction of the prevailing flow (Gulf Stream flows NE) into cooler, higher latitude waters **(Figure 1).** Here the primary production is generally higher and food is more abundant. This promotes faster growth leading to larger maximum sizes and hence, fecundity is maximized (O'Dor and Coelho 1993).

In the northwest Atlantic, two species of squids are subject to commercial exploitation in the region: Northern shortfin squid *I. illecebrosus* (Ommastrephidae) which is an oceanic species that is fished in USA, Canadian and international waters and the longfin squid *Doryteuthis (Loligo) pealeii* (Loliginidae) which is a neritic species that is fished on the USA shelf (Arkhipkin *et al.* 2015). Both species have been exploited since the late 1800s, originally mostly as bait, but fishing pressure increased rapidly in the region and was highest during the 1970s when large factory trawlers from Japan, the former USSR, and Western Europe targeted both species for food (Arkhipkin *et al.* 2015). There were large scale fluctuations in the landings of Northern shortfin squid in the US trawl fishery from 1982 to 2012 (range 2,000 – 26,000 mt) (**Figure 2)**, and it appears as if these fluctuations were due to changes in fishing effort (Arkhipkin *et al.* 2015) as well as possibly being related to recruitment success/failure. In terms of economic importance, a portion of the landings by the USA fleet are sold domestically as bait, but the majority is exported as food. Ex-vessel price is highly influenced by the global squid market (Arkhipkin *et al.* 2015) and the average price of Northern shortfin squid nearly doubled during the development of the domestic fishery, from $511/t in 1982 to $1,013/t in 1991 **(Figure 2)**.

The second dominant species in the northwest Atlantic, the Longfin squid is very frequently found in predator diets and is also a highly-valued commercial resource (Staudinger *et al.* 2007). As a consequence, it is important to assess whether fishers are competing with predators for similar squid resources in the northwest Atlantic. Length-frequency distributions were obtained from the diets of 31 predators taken in the region and were compared to the length-distributions of squid harvested by the commercial fishing industry to evaluate the degree of overlap between squid user groups. The analysis indicated significant differences (Kolmogorov Smirnov test, $D = 0.69$, $p < 0.001$) between the lengths of squid consumed by predators and those harvested by the fishery (Predator mode = 4 cm, median = 7 cm; Fishery mode = 12 cm, median = 16 cm) (Staudinger et al, 2007). These data indicate that predators are targeting smaller squid in comparison to the commercial fishing industry. However, many of the predator stocks which were included in these analyses have experienced severe age-truncation over recent decades due to heavy fishing pressure and therefore, data on the largest individuals are scarce (Staudinger *et al.* 2007).

Oceanography and Environmental factors

Dawe *et al.* (2000), using a 73-year time series of catch and meteorological data, illustrated that the recruitment of *I. illecebrosus* was strongly influenced by environmental variability. Abundance was positively related to: 1) the negative phase of the North Atlantic Oscillation (NAO), 2) high water temperature, and 3) southward shifts in the Gulf Stream and the boundary between shelf and offshore slope water. An increase in the meanders in the Gulf Stream was also associated with increased abundance. In a further analysis of ocean climate effects on the relative abundance of the squids *I. illecebrosus* and *Doryteuthis (Loligo) pealeii* in the northwest Atlantic, Dawe *et al.* (2007) suggested that the efficiency of downstream dispersal of *I. illecebrosus* by the Gulf Stream and the survivorship of young stages was affected by variation in the latitudinal position of the shelf/slope front **(Figure 1**). In contrast, the abundance of the *Doryteuthis (Loligo) pealeii* population was favored by higher inshore water temperatures (Dawe *et al.* 2007) which helped to explain the documented range expansion of *Doryteuthis (Loligo) pealeii* in the year 2000. The documentation of the influence of environmental factors on squid populations, such as those described above, are essential elements to be incorporated in any EBFM models.

The natural ability of squid stocks to recover from low biomass levels following a period of unfavorable environmental conditions might make them less susceptible to a long-term reduction in population size due to overfishing (Rodhouse, 2013). However, if heavy fishing pressure happened to coincide with poor environmental conditions it might create a critical tipping point for a population. The biological characteristics of squid raise interesting questions about the response of populations to future climate change and it could be argued that in some situations "opportunism in a changing environment might enable populations to expand" (Rodhouse, 2013).

Trophic Ecology

Squids are important prey for large numbers of vertebrate predators including many fish species, toothed whales, pinnipeds, and seabirds (Cherel *et al.* 2007; Jereb and Roper 2010). Squid are also predators themselves that make long migrations over their life cycle and are responsible for the spatial transfer of substantial biomass in an ecosystem (Arkhipkin 2013). Payne and O'Dor (2007) estimated that individuals of two different squid species, *L. opalescens* and *D. gigas* could undertake migrations on the order of 500 km and 2500 km, respectively, during the last three months of their lives, independent of currents. It is clear that these squids can make extensive migrations to find areas of high production for feeding and then return to natal spawning grounds.

In a study of the stomach contents of large pelagic fishes sampled by longlining in the central North Atlantic in 2001-02 (Lutcavage and Luckhurst 2002), prey biomass consisted mainly of cephalopods and teleost fishes (Logan *et al.* 2007). The remaining stomach contents were composed mostly of crustacean prey, including decapod larvae and hyperiid amphipods. In many instances, cephalopods dominated the prey biomass of apex predators. The greatest overall prey biomass was comprised of Ommastrephidae. Other families of squids (Gonatidae, Chiroteuthidae and Histioteuthidae) also accounted for high proportions of cephalopod prey biomass (Logan *et al.* 2007) particularly in swordfish (*Xiphius gladius*). These stomach content results are similar to historical findings which demonstrated major contributions of Ommastrephidae to the diets of large pelagic fishes in the central north Atlantic (Matthews *et al.* 1977). Bowman et al (2000) also found that squid played a prominent role in the trophic ecology of the northwest Atlantic based on an extensive sampling of stomach contents. Based on depth ranges defined using pop-up satellite archival tags (PSAT), Atlantic tuna and billfish forage from the surface to at least 900 m depth (Luckhurst 2015) presumably feeding on cephalopod and teleost prey. Stomach contents from deep-diving pelagic predators, such as bigeye tuna (*Thunnus obesus*) and swordfish, contained the greatest diversity and proportional biomass of cephalopods (Logan *et al.* 2007).

Luckhurst (2015) presented data on the principal prey groups taken by tunas and billfishes in the northwest Atlantic with an emphasis on the Sargasso Sea ecosystem. With respect to the five principal species of tuna in the North Atlantic (bigeye tuna, yellowfin tuna *Thunnus albacares*, albacore tuna *T. alalunga*, bluefin tuna *T. thynnus* and skipjack tuna *Katsuwonus pelamis)*, several families of epipelagic teleosts (viz. exocoetids, scombrids and clupeids) are important prey groups (**Table 1**). However, mesopelagic families, e.g. Gonostomatidae and Myctophidae dominate the diet of bigeye tuna. However, all five tuna species have squid as an integral prey group in their diets (**Table 1**). Results from a recent trophic study in the central North Atlantic confirm that ommastrephid squids are the most ubiquitous prey group across large pelagic fish predator species (Logan and Lutcavage 2013).

All three species of istiophorid billfishes (blue marlin *Makaira nigricans*, white marlin *Tetrapterus albidus* and sailfish *Istiophorus albicans*), prey on epipelagic fish families but also on mesopelagic families which they apparently feed on during periodic, short-duration dives during daylight hours (Luckhurst 2015). 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 and Lutcavage 2013) which comprise an important dietary element for all of these apex predators (**Table 1**). Analysis of stomach contents of shortfin mako shark (*Isurus oxyrinchus*) and blue shark (*Prionace glauca***)** as well as mid-level predators such as wahoo (*Acanthocybium solandri*), dolphinfish (*Coryphaena hippurus*), blackfin tuna (*T. atlanticus*) and Little tunny (*Euthynnus alletteratus*) (**Table 2**) confirm the importance of squid in the pelagic trophic web of the Sargasso Sea (Luckhurst 2015).

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 similar 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) to those found in the eastern Pacific. Stable isotope analysis based on white muscle tissues provided TP estimates which ranged from 4.3 for dolphinfish to 5.1 for large swordfish (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. TP estimates increased significantly with size for swordfish and for white marlin, but not for any other species examined (Logan and Lutcavage 2013). It was observed that there was a high degree of overlap in isotope values although some sub-groupings did emerge. Albacore tuna, bigeye tuna, white marlin, blue marlin, ommastrephid squid, and small swordfish made up an intermediate TP group while 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). On the basis of this study and others, Luckhurst (2015) proposed a preliminary pelagic food web for the Sargasso Sea (**Figure 3**) in which squids figure prominently. The number of linkages (n = 16) of small squid as prey to higher trophic level predators is larger than for any other prey group (**Figure 3**). Squids can occupy a large range of trophic levels in marine trophic webs reflecting the large trophic width of this group. As has been demonstrated, squid species are an important prey group of apex predators and thus 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. However, the role of squids in pelagic ecosystems appears to be more constrained to a bottom-up impact on their predators (Coll *et al.* 2013).

Climate change

There are a number of predictions about the effect of global warming on marine populations and these include: 1) changes in species geographic distributions 2) increasing invasion of highly mobile species, especially where local populations of other species are declining and 3) extinction of local populations along range boundaries (Peci and Jackson 2007). With respect to squid populations, all of these features are likely to be observed over time. Squids, and cephalopods in general, have the intrinsic flexibility to adapt to climate change - their life history and physiological traits enable them to be opportunists in variable environments (Peci and Jackson 2007).

Furthermore, squid biomass may be affected by the carrying capacity of a changing ecosystem and if productivity decreases substantially, the rate of cannibalism within squid populations may increase.

As squids are essentially “annual” species and are highly responsive to changes in their environment, it should be possible to detect changes in the system in a relatively short time period (Peci and Jackson 2007). With adequate baseline data for a species and monitoring population levels with a systematic sampling regime, changes could be detected in a matter of a few years or generations. However, it will be difficult to distinguish between natural variability and other causes e.g. fishing mortality, to attribute population changes to climate change. In contrast, for long-lived apex predators, it could take many years to establish cause and effect on their life-histories, populations and abundance.

Although individual life spans are short, the squid could migrate and spawn in new areas with appropriate conditions and expand the species range. The ability of squids to migrate, combined with rapid growth and high reproductive output, gives this group a significant capacity to adapt to changing environmental conditions, so increases in their biomass relative to longer-lived vertebrates with less adaptable life styles would not be unexpected (Payne and O’Dor 2007).

Summary

An assessment of the contribution of cephalopods to global marine fisheries was made by Hunsicker *et al.* (2010), both as a commodity and in terms of a supportive ecosystem service, i.e. as food (prey) for other commercially exploited species. A variety of ecosystems, including continental shelves, major currents and upwelling zones and open oceans were evaluated.

In each ecosystem, data for the top 25 taxonomic groups contributing to fishery landings were analyzed. The contribution of cephalopods, in terms of their supportive service, is substantial in many marine systems. Across all the ecosystems studied, average estimates of commodity and supportive contributions by cephalopods to total fishery landings and revenue were 15% and 20%, respectively (Hunsicker *et al.* 2010). Generally, the contribution of cephalopods as a commodity was greatest in the coastal ecosystems, whereas their contribution as a supportive service was greatest in open ocean systems. In terms of landed values, the average price per ton of cephalopods was greater than or near the average price per ton of the predator species in many of the ecosystems.

The productivity of lower trophic-level species such as squid can been enhanced by the depletion of many apex predator populations by targeted fishing. Squid may be predators of juvenile stages of apex predator fish stocks, so fishing can induce depensatory juvenile mortality (Hunsicker and Essington 2008). Bioenergetics and population models demonstrated that longfin inshore squid (*Doryteuthis (Loligo) pealeii*) consume high quantities of prey on daily and seasonal time scales and may thus potentially exert a trophodynamic control on the recruitment success of commercially exploited fish species even if these species are only a minor prey item of squid (Hunsicker and Essington 2008). These findings suggest that the predation interactions of longfin inshore squid should be considered when managing and rebuilding fish stocks in the northwest Atlantic continental shelf ecosystem.

In conclusion, there are important relationships between squid fisheries and marine ecosystems and this is especially relevant in the context of ecosystem-based fishery management (EBFM). Squid fisheries themselves need to be managed with regard to their impact on the ecosystem but equally importantly, squid stocks should be considered as a key element in many ecosystems in the context of the management of other fisheries, particularly those pelagic fisheries for tunas and billfishes.

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Table 1. Pelagic fish predators – tunas (Scombridae) and billfishes (Istiophoridae) and principal prey groups in the North Atlantic. Squid not defined by family due to insufficient taxonomic detail (Table from Luckhurst 2015).

PREDATORS	Epipelagic teleosts	Mesopelagic teleosts	Cephalopods	Crustaceans	Other
Yellowfin tuna	Exocoetidae Scombridae		squid		
Albacore tuna	Clupeidae Engraulidae Scombridae		squid		
Bigeye tuna		Gonostomatidae Myctophidae	squid	euphausids	
Bluefin tuna	Clupeidae Engraulidae Ammodytidae		squid octopus	crabs	sponges
Skipjack tuna	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 teleost mesopredators and their principal prey groups in the North Atlantic. Squid not defined by family as insufficient taxonomic detail (Table from Luckhurst 2015).

SHARK	PREY				
PREDATORS	**Epipelagic teleosts**	**Mesopelagic teleosts**	**Cephalopods**	**Crustaceans**	**Other**
Shortfin mako	Pomatomidae Scombridae Clupeidae Xiphiidae		squid		
Blue shark	Scombridae Clupeidae		squid		elasmobranchs local demersal fishes
MESOPREDATORS					
Wahoo	Scombridae Exocoetidae Clupeidae		squid		
Blackfin tuna	juvenile teleosts		squid	larvae	
Little tunny	Clupeidae		squid	crabs shrimps	tunicates
Dolphinfish	Exocoetidae Scombridae		squid	crabs shrimps	

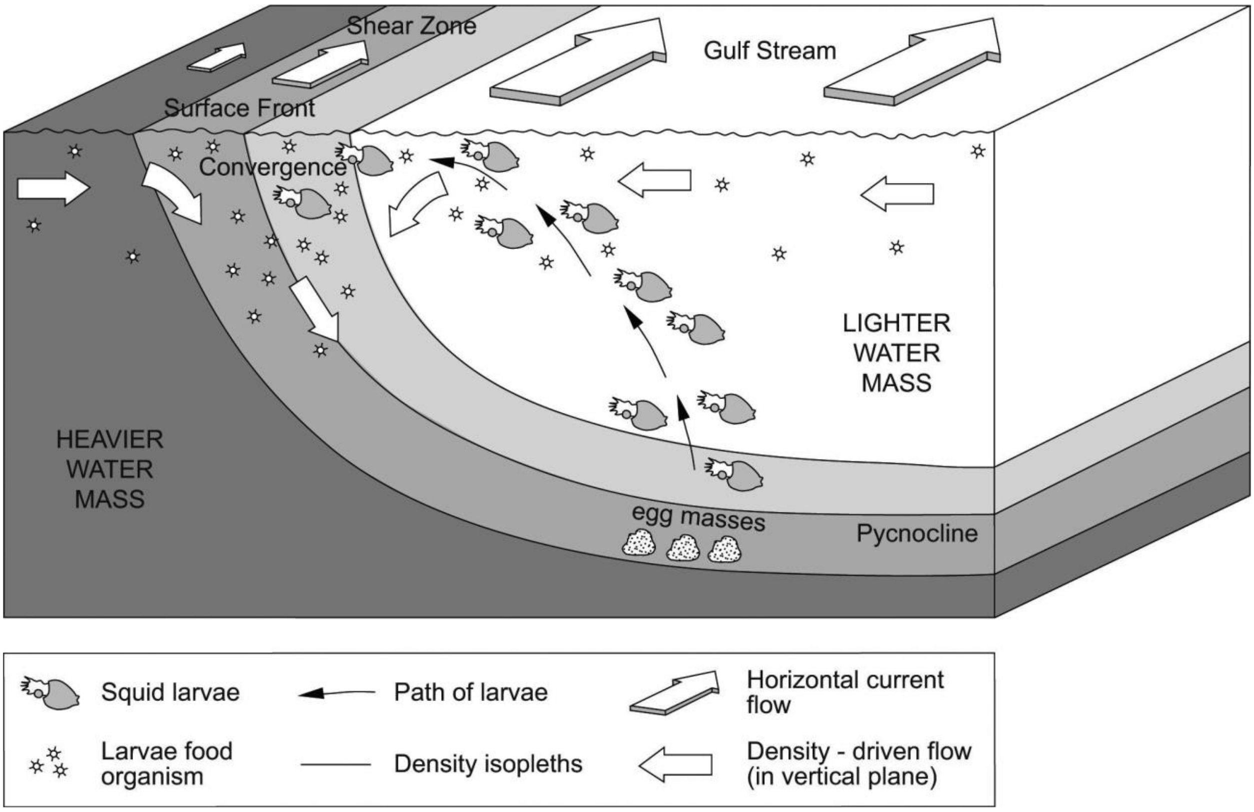

Figure 1. Schematic diagram showing the relationship between the early life cycle of an ommastrephid squid and the physical oceanographic processes at the convergent frontal zone between the waters of a western boundary current (e.g., the Gulf Stream) and adjacent shelf slope water (Bakun and Csirke 1998). Figure from Rodhouse (2008).

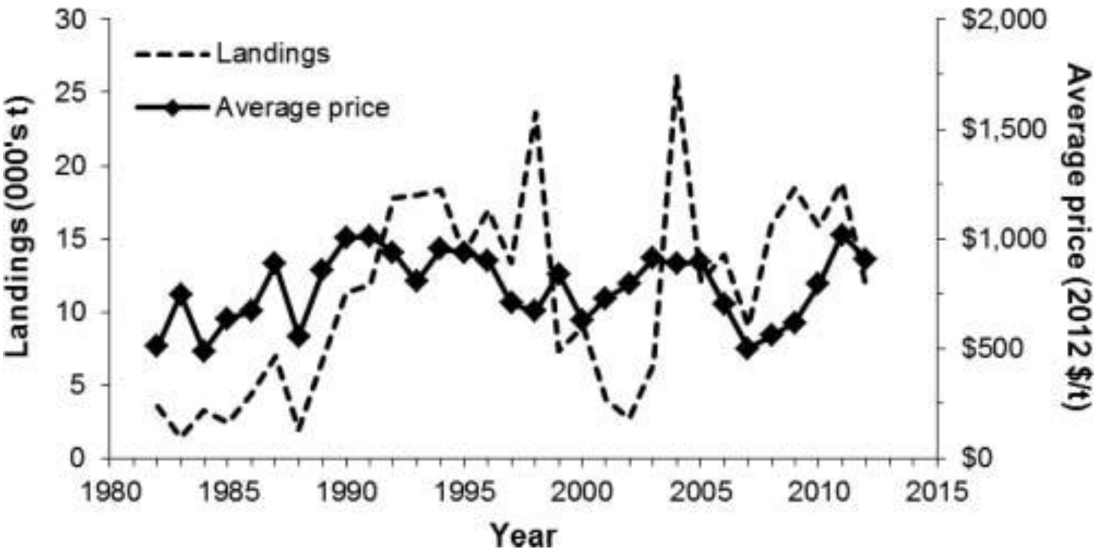

Figure 2. Landings (000's t) and average price (2012 $/t, adjusted for inflation using the Producer Price Index), of *Illex illecebrosus* in the USA directed fishery during 1982–2012 (from World squid fisheries - Arkhipkin, A.I. *et al.* 2015).

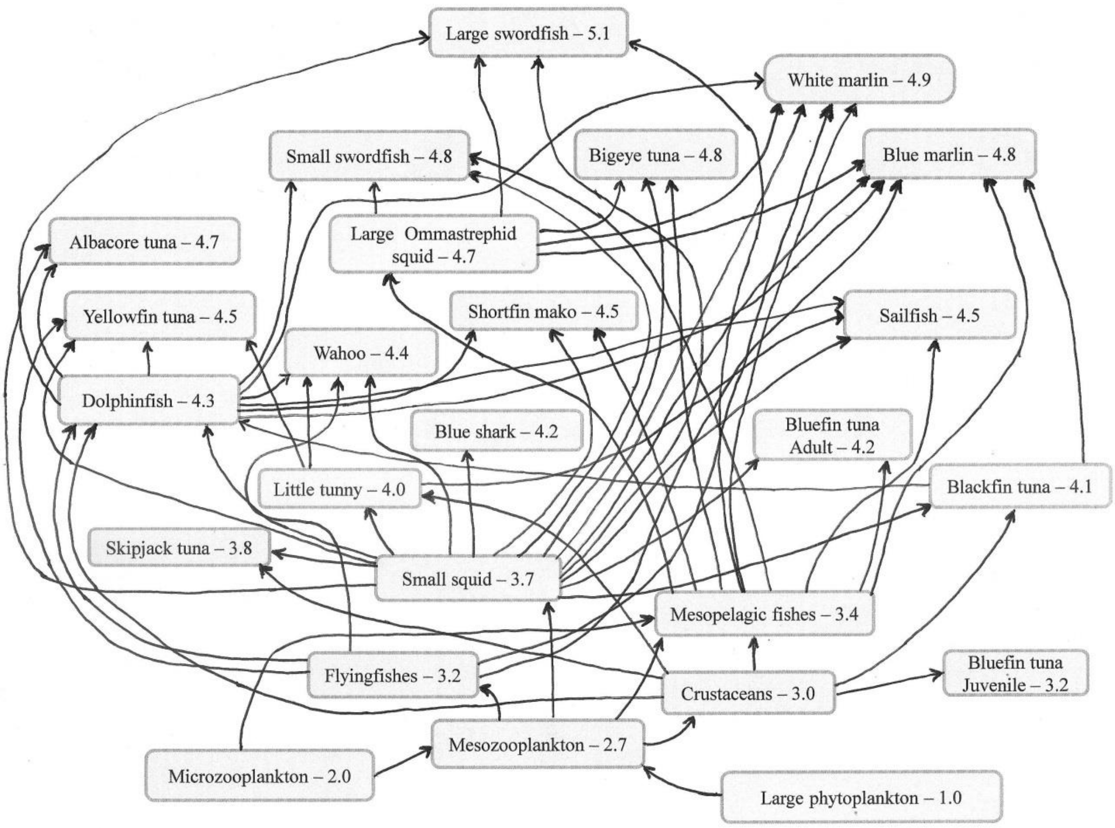

Figure 3. Preliminary pelagic food web of the Sargasso Sea. Trophic position (TP) is indicated in the respective species boxes. Many of the predators in this food web feed on small scombrids but this category is not included as a separate entity as it is comprised of a number of different species (Figure from Luckhurst 2015). Note large number of linkages of small squid (TP = 3.7) as prey for higher level predators and position of large ommastrephid squid (TP = 4.7) as predators.