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Comparative ecology of widely distributed pelagic fish species in the North Atlantic: implications for modelling climate and fisheries impacts

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Abstract:

This paper reviews the current knowledge on the ecology of widely distributed pelagic fish stocks in the North Atlantic basin with emphasis on their role in the food web and the factors determining their relationship with the environment. We consider herring (*Clupea harengus*), mackerel (*Scomber scombrus*), capelin (*Mallotus villosus*), blue whiting (*Micromesistius poutassou*), and horse mackerel (*Trachurus trachurus*), which have distributions extending

beyond the continental shelf and predominantly occur on both sides of the North Atlantic. We also include albacore (*Thunnus alalunga*), bluefin tuna (*Thunnus thynnus*), swordfish (*Xiphias gladius*), and blue marlin (*Makaira nigricans*), which, by contrast, show large-scale migrations at the basin scale. We focus on the links between life history processes and the environment, horizontal and vertical distribution, spatial structure and trophic role. Many of these species carry out extensive migrations from spawning grounds to nursery and feeding areas. Large oceanographic features such as the North Atlantic subpolar gyre play an important role in determining spatial distributions and driving variations in stock size. Given the large biomasses of especially the smaller species considered here, these stocks can exert significant top-down pressures on the food web and are important in supporting higher trophic levels. The review reveals commonalities and differences between the ecology of widely distributed pelagic fish in the NE and NW Atlantic basins, identifies knowledge gaps and modelling needs that the EURO-BASIN project attempts to address.

Highlights

► Comparative review of current knowledge on the ecology of widely distributed pelagic fish stocks in the North Atlantic basin. ► Emphasis on food web role and factors determining spatio-temporal distributions and changes. ► Overview of modelling approaches.

Keywords : Pelagic fish ecology ; North Atlantic ; Environmental drivers

1 Introduction

The North Atlantic Ocean basins are home to some of the largest populations of commercially exploited stocks as well as broadly distributed fish species (Figure 1). On the NE Atlantic side, Atlantic herring (*Clupea harengus*), mackerel (*Scomber scombrus*), blue whiting (*Micromesistius poutassou*), horse mackerel (*Trachurus trachurus*), capelin (*Mallotus villosus*), cod (*Gadus morhua*) and saithe (*Pollachius virens*) are among the most highly exploited abundant fish species. All but horse mackerel are also found in the NW Atlantic although blue whiting is predominantly a NE Atlantic species, with only a small, unexploited western population (Bailey, 1982). Total landings from the NW Atlantic are only 23% on average of those from the NE Atlantic (Figure 1). Conversely, Atlantic menhaden (*Brevoortia tyrannus*) is absent from the NE Atlantic. Most species migrate north to south and off the continental shelf, providing a link between distant areas and inshore and offshore production. Bluefin tuna (*Thunnus thynnus*), albacore (*Thunnus alalunga*), swordfish (*Xiphias gladius*) and blue marlin (*Makaira nigricans*) inhabit both shelf and open-sea parts of most of the North Atlantic basin, some carrying out large north-south and sometimes transatlantic migrations (i.e., bluefin tuna, albacore). We will concentrate on pelagic species that occur in the NE Atlantic and therefore exclude Atlantic menhaden from this review. Since saithe and cod are primarily linked to the continental shelves, we exclude them as well although they may occur pelagically.

A key characteristic of commercially important pelagic fish stocks in the North Atlantic is that they undertake extensive seasonal migrations (Arnold, 1981; Harden Jones, 1968, 1981; Leggett, 1977; Nøttestad et al., 1999). The migrations are tailored to the local current regime and the seasonal timing of ecosystem processes. The environmental conditions vary considerably across the North Atlantic and this consequently has a great impact on the spatial distribution and life history strategies of pelagic fishes.

Evidence for the interaction between fishing and climate impacts on population life history parameters (growth, maturation, recruitment), migration, spatial distributions, and food web complexity and stability has been found for a range of species (Hjerman et al., 2004). Population changes of abundant or widely distributed pelagic species will in turn impact the dynamics of lower trophic levels.

Large-scale physical oceanographic processes in the North Atlantic basin are key to understanding climate impacts. A brief summary of these processes is provided here (Figure

2). The North Atlantic Oscillation (NAO) index, a metric related to the strength of the westerly winds, has been the most popular climatic correlate for a wide selection of ecological variables on both sides of the North Atlantic. Another metric of the physical state of the North Atlantic is the Atlantic Multidecadal Oscillation (AMO) which is based on sea surface temperature (SST) field.

NAO related atmospheric forcing mechanisms drive the dynamics of the North Atlantic subpolar gyre (Eden and Willebrand, 2001). This large counter-clockwise rotating body of subarctic water is produced by convection in the northwestern basins (Labrador and Irminger Sea) and protrudes into the eastern basins at deeper layers. The North Atlantic Current (NAC), aligned with the sub-arctic front, defines the boundary between the subpolar and subtropical gyre. Changes in the extent of the subpolar gyre regulate the relative contributions of western NAC water and more saline eastern water from the Bay of Biscay region, to the mixing region west of the British Isles. This in turn determines the hydrography of the poleward flowing Atlantic water. The characteristics of this poleward flowing Atlantic water impact ecosystems all the way from the western European margin in the south to the Barents Sea in the north (Holliday et al., 2008). Regional atmospheric forcing also shifts the fronts between the Atlantic water and the sub-arctic water masses in the Nordic Seas (Blindheim et al., 2000), which are the main foraging regions for the pelagic species reviewed here. The southward flowing Arctic waters and the Atlantic waters from the Irminger Sea join in the West Greenland Current, and together determine the marine climate in the Labrador Sea (Hátún et al., 2007). Hence this flow regime influences the characteristics of the Labrador Current which in turn contributes to the subpolar gyre. Furthermore, the Labrador Current carries large amounts of freshwater originating partly from the West Greenland Current, and partly from the Canadian Archipelago (Myers, 2005). This freshwater transport plays a critical role in several ecosystems along the North American shelves. The outlined natural variability rides on top of a secular increasing temperature trend, likely related to anthropogenic global warming (IPCC, 2007).

Considered together and from a North Atlantic basin-wide perspective, the abiotic factors affecting abundance and spatial distributions of large highly migratory predators and their prey species are poorly known and constitute a major source of uncertainty for management (ICCAT, 2008; Fromentin, 2009; ICES, 2009). Consequently hampering our understanding of the top down influences of pelagic fish stocks on lower trophic levels. The objectives of this study were to perform a comparative review of the distribution, life history and predator-prey relationships of small, medium and large pelagic fishes in the North Atlantic and to identify knowledge gaps. We attempt to answer the following questions.

1) What are the commonalities and differences in distribution and life history of pelagics species across the North Atlantic?
2) What are the commonalities and differences in their trophic roles?
3) What models exist for evaluating environmental and fisheries impacts on the structure and functioning of North Atlantic ecosystems?

2 Distribution and life history of small and medium sized pelagic fish species in the North Atlantic

In this section we review environmental and biological factors shaping spatial patterns (spawning distributions, migration patterns), temporal patterns (spawning, migration timing), and life history parameters (hatching rates, maturity and fecundity, growth, survival) in the NE and NW Atlantic. The documented factors are summarised in table 1. Overlapping feeding areas are depicted in figure 3.

2.1 Herring

2.1.1 Geographic distribution

Atlantic herring inhabits most temperate waters of the North Atlantic. In the NW Atlantic, herring are found from Cape Hatteras in North Carolina (USA) to southern Labrador (Canada). Their distribution in the NE Atlantic extends from the Bay of Biscay, Celtic Sea and Southern North Sea in the south to Iceland and the Northern Norwegian and Barents Sea in the North. Herring is a population rich species (Sinclair and Iles, 1981; Iles and Sinclair, 1982) with numerous major and minor spawning components in each stock throughout the North Atlantic (Blaxter and Hunter, 1982; Payne 2010; Harma et al, 2012). Currently, the largest of the 20+ recognized herring stocks is the Norwegian spring-spawning herring (NSSH) with an estimated spawning stock biomass (SSB) of about 8 million tonnes in 2011 (ICES, 2011b). Other herring stocks of significance (SSB >1 million tonnes), both past and present, include those of the North Sea and Georges Bank in the Gulf of Maine, although their present levels are well below historical highs (Overholtz et al., 2004; TRAC, 2009).

2.1.2 Spawning habitats and migrations

Herring spawning is restricted to the central regions of their distribution. Along the North

American coast most spawning occurs from Cape Cod to northern Newfoundland, while off Europe/Scandinavia spawners are observed from the English Channel to southern Norway (Alheit and Hagen, 1997). Physical oceanographic features affect the distribution or retention of larvae (Sinclair and Isles, 1981; Grimm, 1982; Heath and MacLachlan, 1986; Petitgas et al., 2010). Atlantic herring deposit demersal adhesive eggs in areas with strong currents. The eggs adhere to the sea floor on a variety of substrates ranging from boulders, rocks, and gravel, to sand, shell fragments, and macrophytes. The eggs remain attached to the bottom throughout the incubation period.

Herring undertake annual migrations from their spawning grounds to summer feeding and over-wintering areas, but the extent varies between stocks. One of the main differences between NSSH and other NE Atlantic stocks is their oceanic feeding migration and that they sometimes overwinter off the shelf, i.e. outside the North Sea. For NSSH the feeding migration distances increase with body size and temperature seems to play a role in determining their distribution (Østvedt, 1965; Nøttestad et al., 2007). Younger fish do not undertake long migrations, and spend their adolescence along the Norwegian coast or in the Barents Sea (Holst and Slotte, 1998). The large amounts of food resources available due to this extended distribution are thought to be important in maintaining the large NSSH stock size. Another important feature is that juvenile herring inhabit the Norwegian coast and the Barents Sea reducing competition for prey with adult herring. In other stocks there is often horizontal overlap between adult and juvenile fish, though it is not uncommon to see a vertical separation (Power et al., 2012).

In the NW Atlantic, several herring stocks undertake distant inter-annual migrations, often exceeding 1500 km before returning to their spawning habitat. Hence, these stocks influence several ecosystems along the continental shelf of North America. Georges Bank and the Gulf of Maine herring move south annually to the offshore waters of the Mid-Atlantic States for overwintering (Kanwit and Libby, 2009). The southwest Nova Scotia spawning component has been found to migrate to one of two overwintering areas in the coastal waters of Nova Scotia and south of Cape Cod in the USA (Stobo and Fowler, 2009). In general, northern stocks tend to move south for overwintering to avoid the extremely cold winter waters (Wheeler and Winters, 1984; Chadwick et al., 1993). Inter-stock mixing of adult herring is known to occur during the feeding and over-wintering migrations. Juvenile herring do not undertake as extensive migrations as older fish and tend to be distributed throughout the coastal and near-shore waters of the stock in which they were larvae. There are several highly productive nursery areas where young herring aggregate as well as some mixing of juvenile fish from different stocks occurs near stock boundaries. For example, juvenile herring from several spawning components are known to co-exist at the mouth of the Bay of Fundy. Similarly, Baltic Sea juveniles mix with North Sea juveniles in the Kattegat-Skagerrak region (ICES, 2011a).

On both sides of the North Atlantic the annual migrations of some herring stocks have changed spatially and temporally (Dragesund et al., 1997; Holst et al., 2002; Huse et al., 2010). There have also been reports of contraction of spawning and larval distributions associated with declining stock abundance and the loss of spawning components within a stock, as well as expansion in distribution during increasing abundance and the colonisation of new (or former) spawning grounds (Melvin and Stephenson, 2007).

The NSSH stock shows all these features. Variations in the southern extent of spawning areas are believed to be due to the experience and condition of individuals making up the population, and the latitude of the overwintering area (Slotte, 1999). Large herring positioned south in the overwintering area will spawn further south than small herring overwintering far north. The overwintering grounds in the 1950s and 1960s were east of Iceland, and the feeding areas were mainly north and east of Iceland. Spawning was on the shelf to the west of the Norwegian coast, although the southern boundary for spawning moved north as biomass decreased (Dragesund et al., 1997). After the stock collapsed at the end of the 1960s, the NSSH stayed close to the Norwegian coast both during overwintering and the feeding period. When the stock abundance again increased in the late 1980s, the overwintering area was in fjords in Northern Norway and the feeding area was throughout the Norwegian Sea. During the 1990s overwintering took place primarily in the Vestfjord system, but it has gradually shifted northwards to open sea areas outside Tromsø. The changes in overwintering area are typically initiated when particularly abundant cohorts enter the spawning stock (Huse et al., 2010). This is likely linked to absence of social learning between the old and young cohorts when the younger fish are too numerous (McQuinn, 1997; Corten, 2002; Huse et al., 2002). Migration patterns of herring in the North Sea, Irish Sea and around Iceland have also changed over time in response to changes in population abundance and environmental conditions (Maravelias, 1997; Corten, 2002; Oskarsson et al., 2009).

In the NW Atlantic changes in the migration patterns over the past couple of decades have been observed in the Southwest Nova Scotia spawning component (Kanwit and Libby, 2009) and in spring and autumn spawners in the southern Gulf of St. Lawrence (Chadwick, 1993).

This may be due to decreased abundance and/or warmer water. For some herring populations it has been suggested that annual migrations are guided by inter-cohort social learning (Corten, 1999, 2002; McQuinn, 1997; Fernö et al., 1998; Slotte, 1999; Huse et al. 2002) while others argue that imprinting at a young age is the driving mechanism (Isles et al., 1985). Alternative mechanisms are a genetically controlled sense of direction developed during their larval phase (Iles and Stochasky, 1985), habitat pheromones (Kieffer and Colgan, 1992), or larval imprinting (Brophy et al., 2006; Horrall, 1981). Feeding migration seems to be driven by a combination of predictive and reactive mechanisms (Fernö et al., 1998). The herring seem to use some kind of memory to actively seek areas used in previous years. If environmental changes lead to reduced quality in the traditional feeding areas, the herring will stay faithful to these areas for some time.

The horizontal and vertical diel distribution of Atlantic herring is dynamic, and differs for larvae, juvenile, and adults (Huse and Toresen, 1996; Huse et al., 2012; Utne et al., 2012b). Most herring, regardless of size and time of the year, undertake some degree of diel migration moving up in the water column at night and down during the day (Heath et al., 1988; Misund et al., 1997; Huse et al., 2012). However, in recent years herring in the western Atlantic seem to have changed their vertical distribution. Fishermen and scientists have reported that herring are staying closer to bottom than usual during certain periods of the year. In several areas fish were not coming off bottom and inaccessible to purse seine gear (Power et al., 2011).

2.1.3 Life history

Herring stocks exhibit temporal and geographic differences in life-history traits. Populations are described as spring, winter, summer, or autumn spawners, although more than one type can occur in a stock. Spring and summer spawners are more prevalent in northern waters, autumn and winter spawners in the south, and a mixture in central regions (Melvin et al., 2009). In the Gulf of St Lawrence the two types use the same spawning habitat, although spring spawners generally spawn in more shallow inshore waters. Hatching time takes from 8-14 days and depends on water temperature.

Herring mature between ages 2 and 6, with the majority maturing at 3-4 years. Northern stocks, like NSSH and Newfoundland herring, become mature later at ages of 3–6 years and have a maximum life span of over 20 years. Stocks at the southern extent of their range have shorter maximum life-span of 12-14 years, especially in recent years, and mature younger.

Gulf of Maine herring reach maturity at 23-25 cm aged 2-4 years, while those off the east coast of Newfoundland take 3-6 years to reach a similar size and mature (Melvin and Stephenson, 2009; Wheeler et al., 2009). Variations in age at maturity are believed to reflect variations in body growth, stock abundance, and environmental change (Melvin and Stephenson, 2007). Length specific fecundity has been reported for most populations (e.g., Zijlstra, 1973; Kelly and Stevenson, 1985; Óskarsson et al., 2002). The reproductive strategy of a spawning population also has an influence on how fecund the fish will become (van Damme, 2009). In general autumn spawners produce smaller and more numerous eggs than winter/spring spawners. Stock density and environmental factors, which affect feeding and body condition, may also affect fecundity (Flinkman et al., 1998).

Generally, populations in colder water grow more slowly and live longer than those in warmer water (Brunel and Dickey-Collas, 2010). Individuals of strong year classes tend to be smaller when maturity is reached (Toresen, 1990; Melvin and Stephenson, 2007). The reduced growth rate of large cohorts is less pronounced once they become adults. For the NSSH growth rate is thought to depend on their distribution. If young NSSH migrate into the Norwegian fjords, reduced growth rate is caused by density dependence, while if they move into the Barents Sea it occurs because of lower temperatures. Evidence of density dependent herring growth are also found in the Icelandic summer-spawning herring (Óskarsson, 2008), while density dependent growth is not observed in the Celtic Sea (Molloy, 1984). In the NW Atlantic, density-dependent growth also occurs in stocks from Georges Bank (Melvin and Stephenson, 2007), Gulf of Maine (Anthony and Fogarty, 1985), southwest Nova Scotia (Sinclair et al., 1982) and possibly the east coast of Newfoundland (Moores and Winters, 1984). Length- and weight-at-age in many stocks have shown decadal declines, which have been hypothesized to be environmentally driven (Wheeler et al., 2009; Power et al., 2010; Brunel and Dickey-Collas, 2010).

Recruitment in herring stocks as in most fis stocks has been linked to the classical recruitment hypothesis as outlined by Houde (2008). Larval survival and subsequent year class strength in NSSH is enhanced by early hatching time (Husebø et al., 2009), reduced cannibalism (Dalpadado et at., 2000), rapid displacement of larvae to the Barents Sea nursery area (Vikebø et al., 2010), and higher temperature in the Barents Sea (Toresen and Østvedt, 2000). In the Western Atlantic, declines in predator abundance and environmental conditions, decreased fishing effort, and increased spawning biomass have generated strong year classes (Overholtz et al., 2004; Melvin et al., 2009; Wheeler et al., 2009). Temperature changes may also have influenced the relative reproductive successes of the different spawning strategies (Melvin et al., 2009).

Recruitment patterns can be local, regional, or sometimes synchronous on an oceanic scale, suggesting wide scale climatic influence. It is not uncommon for herring stocks to have several years of poor (i.e., below average) recruitment to be followed by 1 or 2 years of strong recruitment when optimum conditions are met: however, systematic directional changes have also been observed in some stocks (Payne et al. 2009). For example, Gulf of St. Lawrence spring spawners have had more than a decade of below average recruitment while the fall spawners have had average or above recruitment for the same period (LeBlanc et al., 2010). Instances of large year classes and thus high recruitment success have also been reported in the NE Atlantic herring stocks (Óskarsson and Taggart, 2010; Toresen and Østvedt, 2010). In the NW Atlantic, regional and broad synchronous recruitment pattern have been reported in Scotia-Fundy herring by Óskarsson, (2005), Georges Bank by Melvin et al. (1996), in the Gulf of St Lawrence by Leblanc et al (2010) and off the east coast of Newfoundland by Wheeler et al. (2010).

2.2 Mackerel

2.2.1 Geographic distribution

Mackerel are widespread in the NE Atlantic, from Morocco to Norway, with observations the Mediterranean Sea, Skagerrak, Kattegat and westernmost Baltic Sea. Periodically in the summer mackerel can also be found in coastal areas around Iceland (Astthorsson et al., 2012). In the NW Atlantic mackerel is found from the Gulf of Maine to the Gulf of St Lawrence. The Atlantic mackerel have traditionally been divided into five spawning components, two in the west and three in the east. However, the population structures on either side of the Atlantic are possibly better described as dynamic clines, rather than as connected entities (Jansen et al., 2013, Jansen and Gislason, 2013).

2.2.2 Spawning habitats and migrations

NEAM spawn along the shelf break from Spanish and Portuguese waters in March to the west of Scotland and in the North Sea in June. The highest spawning intensity is off Ireland (ICES, 2010c), in the same area as blue whiting but later in the year. Previously, spawning in the North Sea likely supported a large part of the NEAM stock; this changed after the collapse in the late 1960s-70s (Jansen et al., 2012b, Jansen, 2013).

Spawning activity of NEAM has progressively moved north during the period 1977- 2010 with a shift of 39 km for every degree Celcius of warming (Hughes et al., submitted). In warm years, mackerel in the North Sea spawn earlier than in cold years (Jansen and Gislason, 2011). As for the southern and western spawning components, there is substantial interannual variation but no simple relationship with water temperature seems to exist (Punzon and Villamor, 2009).

Stocks on both sides of the Atlantic perform extensive annual migrations between spawning and feeding grounds. In the NE Atlantic the post-spawning migration disperses the mackerel into adjacent shelf waters and northwards, where feeding takes place (Uriarte and Lucio, 1996; Belikov et al., 1998; Uriarte et al., 2001). While NEAM also migrate into open waters in the Nordic Seas to feed during summer, there is no evidence of such off-shelf feeding in NWAM. In late summer and early autumn the pre-spawning migration begins. This migration includes shorter or longer pauses, which sometimes are referred to as overwintering, and ultimately ends at the spawning areas. A deeper understanding of the main drivers of the highly dynamic mackerel distribution patterns remains elusive.

Free floating eggs of NEAM mackerel occur deeper early in the spawning season when there is little thermal stratification (Röpke, 1989; Coombs et al., 2001). As stratification develops, eggs become progressively more restricted to the surface layers (Coombs et al., 2001). In spawning areas along coasts of the USA and Canada as well as the North Sea and Kattegat/Skagerrak, stratification is already developed when spawning occurs. In these systems high abundances of eggs are found above the thermocline (Nilsonn, 1914; Sette, 1943; Myrberget, 1965; Iversen, 1977; Ware and Lambert, 1985). Transport of eggs and larvae to known nursery areas has been examined employing individual-based models. These studies suggest that passive transport in the short egg/larval phase is insufficient to bring larvae to the known nursery grounds (Bartsch and Coombs, 2004; Bartsch et al., 2004; Bartsch, 2005). Hence it seems that active migration of juveniles is required to reach the nursery grounds.

Environmental conditions impact post- and pre-spawning migration patterns and the spatial distribution of adult NEAM and NWAM. In warm years an eastward post spawning migration occurs earlier from the North Sea spawning area (Jansen and Gislason, 2011). Mackerel feeding distribution in the Nordic Seas (up to 76 °N North of Norway in the north-east, beyond Iceland in the west) is positively correlated with temperature, which is influenced by the Atlantic inflow, indicating warmer temperature preferences compared to herring and blue whiting (Utne et al., 2012b). Thus warming of the Nordic Seas has enlarged the potential habitat for NEAM. The northwestwards expansion during spawning and summer feeding migrations is confirmed by catch and survey data from recent years, although the observed change could also be a consequence of changes in food availability and increased stock size. The pre-spawning migration from the northern feeding grounds occur through the northern North Sea and the areas to the west of Scotland (Walsh et al., 1995; Reid et al., 1997) where over-wintering occurs.

Fisheries data show that the changes in the timing of the pre-spawning migration of the westernspawning component of the NEAM have been dramatic over the last 30 years. The migration passed through the west of Scotland area in September 1975. By the late 1990s it passed through this area in January/February. This appears to have remained fairly consistent up to 2005 (Walsh and Martin, 1986; Reid, et al., 2003; 2006), but subsequently changed. In 2006-2007 the migration was later (ICES, 2007), while commercial catch and survey data from 2008-2010 suggested that either the stock initiated the southwestern migration earlier, or that the pre-spawning migration took a more westerly route. Temperature clearly plays a role in the modification of the pre-spawning migration. The distribution and timing of the fisheries that follow the mackerel are correlated with sea-surface temperature (Jansen et al., 2012a). Local shoals appear to be constrained by temperature before the onset of migration towards the wintering and spawning areas (Reid et al., 2001b) with temperature also influencing migration path and speed (Walsh et al., 1995; Reid et al., 1997). Similar to herring, body size also affects migration patterns, with larger individuals migrating farthest (Holst and Iversen, 1992; Nøttestad et al., 1999). Furthermore, at the eastern end of the feeding migration large mackerel arrive earlier and leave later than small mackerel (Jansen and Gislason, 2011).

In the NW Atlantic, the 7°C isotherm was long seen as forming a temperature barrier to the northern advance of mackerel along the US east coast (Goode, 1884; Sette, 1950; Bigelow and Schroeder, 1953). Captive mackerel increase their swimming speed in water below 7 °C and this has been interpreted as a behavioural response to low temperature (Olla et al., 1975; 1976). However, field observations have shown that mackerel from the southern component of the NWAM avoid waters below 5 °C, most individuals being found in waters above 6 °C. Furthermore, the spring distribution seems to be more northern and in-shore in warmer years (Overholtz et al., 1991). However, in 1990 mackerel from the northern component migrated into Cabot Strait where the water temperature was approx. 4 °C in order to reach their spawning grounds (D'Amours and Castonguay, 1992). These authors argued that this demonstrated how thermal preferences can become subordinate to reproductive requirements, a point supported by the fact that this stock always enters the Cabot Strait around the same date (Anon., 1896; Castonguay and Gilbert, 1995).

On a smaller scale, local distribution also can be affected by temperature. For example, local mackerel abundance has been observed to coincide with wind-induced warming of coastal water on a time-scale of days in a coastal area in Northern Canada (Castonguay et al., 1992).

2.2.3 Life history

Mackerel reach maturity at the age of 2-3 years and can grow to over 60 cm length and 20 years in age (Lockwood, 1988). We know of no studies linking variation in fecundity or reproductive potential to environmental factors.

The growth rate increases from hatching until young mackerel measure 40-100 mm, by which time they grow at up to 2.5 mm day^{-1} under optimal conditions (Ware and Lambert, 1985; Bartsch, 2002). Larval growth and development is faster at higher temperatures (Mendiola et al., 2007; Robert et al., 2009). Growth rate, especially in smaller fish, is density- dependent. The mean length of age-1 fish is negatively correlated with stock biomass in NEAM (Agnalt, 1989; Dawson, 1991) and NWAM (MacKay, 1973; Overholtz, 1989; Neja, 1995; Ringuette et al., 2002). Adult growth rates may vary spatially, although observed patterns are confounded by size-dependent migration in which large fish leave spawning and feeding areas earlier (Dawson, 1986; Eltink, 1987; Nøttestad et al., 1999; Villamor et al., 2004; Jansen and Gislason, 2011).

In the NW Atlantic, recruitment from the northern spawning area of NWAM depends on the production of the nauplii of copepod species that make up the larval diet (Robert et al., 2007; Castonguay et al., 2008). Recruitment of NEA mackerel has been surprisingly stable for the last three decades when compared to other pelagic species, such as blue whiting and herring, and a significant part of the variability has been explained by an index of wind induced turbulence (Borja et al., 2002).

2.3 Capelin

2.3.1 Geographic distribution

Capelin is a cold-water species inhabiting arctic and subarctic waters in the North Atlantic and North Pacific. In the North Atlantic, several stocks are found in the Barents Sea, around Iceland, and in the Newfoundland and Labrador waters (Vilhjálmsson, 1994).

2.3.2 Spawning habitats and migrations

Capelin are demersal spawners that deposit their eggs on fine gravel (Vilhjálmsson, 1994). Spawning locations are determined by temperature (Nakashima and Wheeler, 2002) or by bottom substrate with temperature as a secondary factor (Carscadden et al., 1989). The larvae drift to nursery grounds whose locations vary according to changes in the coastal currents. Icelandic capelin larvae drift mainly to the northwest and northeast Icelandic shelf and to a varying extent to the East Greenland plateau (Vilhjálmsson, 1994). The effect of this variation on larval survival is unknown. For northwest Atlantic capelin, the extent of larval drift from the coast to the shelf may (Taggart and Leggett, 1987) or may not (Dalley et al., 2002) have an important role for recruitment.

Before 2001, the Icelandic capelin migrated north to the Iceland Sea (to at least 72°N) for summer feeding (Vilhjálmsson, 2002), while since then summer feeding is believed to have taken place further west on the Greenland plateau (Pálsson et al., 2008). Similar patterns have been observed for juveniles, implying displacement of the distribution to the west and south. Both of these changes were linked to likely increased temperature in the Iceland Sea during this period possibly because of observations of increased inflow of warm Atlantic water into Icelandic waters. Barents Sea capelin also undertake extensive feeding migrations northwards into the Barents Sea and the position of the feeding areas varies with hydrographic conditions such that in warmer years the distribution of capelin extends further north- and eastwards (Gjøsæter, 1998). The distribution is thus broader in warmer years (Orlova et al., 2010). The NW Atlantic capelin stocks undertake similar extensive feeding migrations. In the early 1990s the stocks had a generally more southerly distribution in both the west (Scotian Shelf) and the east (Flemish Cap; Carscadden et al., 2001). These changes were linked to colder seawater as a consequence of a positive NAO. However, these changes persisted after the temperature returned to 'normal' again, which might have been caused by changes in prey quality in offshore feeding areas (DFO, 2011).

Sea ice formation probably affects the capelin feeding distribution. During summer capelin often feed near the receding ice edges, which are areas rich in phytoplankton and subsequently zooplankton (Gjøsæter, 1998).

Capelin undertake diel vertical migrations following their prey, aggregating at greater depths during the day (Mowbray, 2002). In the NW Atlantic diel vertical migration is apparently length dependent where small capelin (<12 cm) migrate between 0 and 100 m together with smaller zooplankton preys (copepods) and large capelin (>12 cm) down to 300 m together with large zooplankton prey (amphipods and euphausiids; Davoren et al., 2008). The feeding preferences of Barents Sea and Icelandic capelin suggest similar diel migrations in the NE Atlantic.

2.3.3 Life history

Spawning mainly occurs in March-April in the Barents Sea and around Iceland and in May-July in the NW Atlantic stocks (Vilhjálmsson, 1994; Nakashima and Wheeler, 2002). Barents Sea and Icelandic capelin are deep-water spawners while most of the capelin populations in the NW Atlantic are principally beach spawners although some spawning occurs in adjacent deeper waters.

Capelin first reaches maturity at age 2-4 (majority 3 yrs). Only a small proportion survives spawning, and few females spawn a second time (Carscadden and Vilhjálmsson, 2002). Maximum length is 20 cm with males larger than females. Variability in growth affects age-at-maturity of the Icelandic capelin (2 to 4 yrs; Vilhjálmsson, 1994).

Age- and length-specific fecundity of the capelin stocks is highest for NW Atlantic beach-spawners and lowest for the Barents Sea bottom spawners and Icelandic stocks (Jóhannsdóttir and Vilhjálmsson, 1999). Fecundity is density-dependent in Barents Sea capelin (Tereshchenko, 2002). We know of no study linking variations in fecundity or reproductive potential to environmental factors.

The growth rate of Barents Sea capelin is positively related to zooplankton abundance (Gjøsæter et al., 2002) and temperature, and varies with location, probably driven by spatial patterns of temperature and/or food availability (Gjøsæter, 1998). The fat content of Barents Sea capelin has been related to the NAO (North Atlantic Oscillation) and stock size (Orlova et al., 2010). The mean weight-at-age of Icelandic capelin is higher during warmer periods, which are characterized by higher zooplankton abundance (Astthorsson and Gislason, 1998).

Being short-lived, capelin population dynamics are driven by recruitment, which can lead to large and rapid changes in stock biomass. Despite the importance of recruitment, the causes of its variability are poorly understood. Although stock and 0-group size are related for Icelandic capelin, no stock-recruitment (age 1) relationship has been found. This points towards the importance of environmental and/or ecological factors during the first winter for determining recruitment success (Jóhannsdóttir and Vilhjálmsson, 1999). In contrast, acoustic surveys showed that the abundances of age 1 and age 2 fish one year later (i.e. a single cohort) were strongly related (Vilhjálmsson, 2002). Recruitment in Newfoundland capelin was found to be positively related to the frequency of onshore winds during larval emergence (Carscadden et al., 2000). Capelin recruitment in the Barents Sea depends on herring and cod predation, and is positively correlated to temperature (Hjermann et al., 2010).

2.4 Blue whiting

2.4.1 Geographic distribution

The major biomass of blue whiting inhabits the eastern half of the North Atlantic basin and exhibits a broad distribution in this region. Smaller stocks of this species exist in the NW Atlantic and Mediterranean Sea (Bailey, 1982). The NW Atlantic stocks are not commercially exploited with little known about their spatial and temporal dynamics. For this reason, we focus exclusively on the NE Atlantic populations where information is more readily available. The NE Atlantic latitudinal distribution ranges from the Iberian Peninsula and the Mediterranean in the south to the Barents Sea in the north while they range longitudinally from the North Sea to the mid-Atlantic ridge.

2.4.2 Spawning habitats and migrations

Blue whiting spawn in spring along the eastern margin of the North Atlantic basin in the water column at around 500-700 m. The majority of spawning takes place between Porcupine Bank in the south and the Hebridean shelf in the north, although significant spawning aggregations have also been observed (intermittently) across the Rockall Trough, on Rockall Bank and Hatton Bank (Hátún et al., 2009b). Larvae as an indicator of spawning have also been observed along the continental shelf-edge in the Bay of Biscay (Arbault and Lacroix-Boutin, 1969), around the Iberian Peninsula (Ibaibarriaga et al., 2007) as well as off the coast of Norway and Iceland (Bailey, 1982). Numerical particle tracking studies focused on the drift of eggs have examined the potential for separation into northern (Hebridean shelf and Norwegian Sea) and southern (Porcupine Bank and Bay of Biscay) stocks (Svendsen et al., 1996; Bartsch and Coombs, 1997; Skogen et al., 1999). Environmental barriers to gene flow within the centre of the range have been identified, with the suggestion of up to four stock components (Was et al., 2008).

The spatial distribution of the spawning populations has been shown to be influenced by the dynamics of the subpolar gyre (Hátún et al., 2009b). Spawning appears to take place preferentially between the 9 and 10 ºC isotherms, the locations of which are influenced by the dynamics of the subpolar gyre. In years when the gyre is weak and the Rockall Plateau and trough are flooded with warm, saline water from the south, spawning is more widespread, extending in the north towards the Hebridean shelf and possibly also expanding onto Rockall Bank. Conversely, in years when the gyre is strong, colder, fresher gyre-water pushes the isotherms southwards and eastwards, resulting in spawning limited to the Porcupine Bank. These conclusions appear to be relatively robust, and are confirmed by historic observations of blue whiting larvae, acoustic survey data and fisheries catch statistics. However, it is not clear how they relate to the dynamics of the putative northerly and southerly populations, particularly as observations of the spawning distribution south of Porcupine Bank are very limited.

The eggs, larvae and juveniles drift both northwards and southwards after spawning, depending on where they were released in relation to the ―separation line‖ (Bartsch and Coombs, 1997; Skogen et al., 1999). Observational studies have also confirmed a significant impact of environmental variables upon larval dispersal and retention in the Porcupine Bank area (Kloppmann et al., 2001). Unfortunately, there are no modern studies that cover the period of strong year-classes associated with changes in the sub-polar gyre after 1995: it is therefore not known what these oceanographic changes have meant for larval dispersal and recruitment. Studies covering more recent years are therefore required to understand the implications of the observed recruitment changes.

It is believed that the major nursery grounds are along the Norwegian coast (possibly in fjords), to the south west of Iceland, and along the continental shelf-edge south of Porcupine Bank (Bailey, 1982). More recent work has highlighted the presence of small immature blue whiting in the Barents Sea: their abundance in this region however, appears to be modulated by both population dynamics and hydrographic conditions, and it is not clear whether this is a regularly inhabited nursery ground (Heino et al., 2008). There are also nursery grounds in the south. In the Bay of Biscay and Celtic Sea in early winter, 0-group blue whiting have been found primarily along the shelf edge, with no relationship between spatial location and bottom temperature or salinity (Persohn et al., 2009).

The post-spawning adults (from the northerly population) return northwards to the feeding grounds in the Nordic Seas. The route taken by this post-spawning migration has been shown to be influenced by the dynamics of the subpolar gyre (Hátún et al., 2009a). In years where the gyre is weak and has retreated westwards, the migration route passes to the west of the Faroe Islands, whereas in years when the gyre is strong, the route passes through the Faroe-

Shetland Channel. It is thought that this migration reflects, at least partially, the differences in the spawning distribution also induced by the gyre (i.e. a more westerly spawning distribution when gyre is weak (Hátún et al., 2009b)) and therefore the starting point for this particular migration.

Blue whiting perform diel vertical migrations (Johnsen and Godø, 2007). During summer feeding in the Norwegian Sea the diel migration is about 65 m between a median day depth of 325 m and a median night depth of 260m (Huse et al., 2012). The adults from the northerly population feed in the Nordic Seas during summer (Utne et al., 2012b), with large aggregations being found near the entrance to the Barents Sea while those from the southerly population are found on Bay of Biscay the shelf edge in late spring. Little is known about the overwintering behaviour of the fish, or pre-spawning migrations.

2.4.3 Life history

Spawning starts in January-February in the southern part of the blue withing distribution and gets progressively later with increasing latitude. The peak season is in March and April, corresponding to the productive period at the main sites around Porcupine Bank and the Irish and Scottish west coasts. Spawning typically starts at 2-4 years, when the fish are between 19 and 24 cm in length (ICES, 2007).

Larvae occur mostly in the upper 60 m of the water column (Coombs et al., 1981). Several studies have examined the linkages between the environment and larval growth rates. Increased larval growth has been linked to the intrusion of warm, saline tongues of water along the continental shelf edge (Bailey and Heath, 2001) and larval condition to turbulence and wind mixing events (Hillgruber, 2000; Kloppmann et al., 2002). However, again there are no published post-1995 studies that examined the impacts of the changes that occurred during this time. In the Bay of Biscay, 0-group size in late autumn is negatively related to density but unrelated to mean summer water temperatures, suggesting density-dependent juvenile growth in this area (Persohn, 2009). Adults captured in the southern part of the range have faster growth rates as larvae and juveniles than those from the northern part (Brophy and King, 2007).

The population dynamics of blue whiting has been dominated in recent years by large swings in recruitment. Recruitment of the Northern population increased suddently from 1995 to 2004 to four to ten times that of the previous decade before suddenly returning to levels comparable to, or even below, pre-1995 levels (Payne et al., 2012). By contrast, the putative southern population showed low recruitment between 2001 and 2005 (Persohn et al., 2009). The sudden increase in northern population recruitment from 1995 onwards occurred synchronously with large changes in the physical and biological environment in the North Atlantic. The sub-polar gyre collapsed and retreated rapidly westwards during this time, allowing the influx of warmer, more saline water from the south into the area to the west of Ireland and Scotland, together with large changes in the phytoplankton and zooplankton communities (Hátún et al., 2005; 2009a). The temporal co-occurence between these phenomena has led several authors to propose a causal linkage (Hátún et al., 2009b; Payne et al., 2012): however, the termination of a string of strong year-classes from 2005 onwards is not fully explained by the dynamics of the sub-polar gyre, and there is no significant correlation between the state of the gyre and year–class strength (Payne et al., 2012). Furthermore, the mechanisms driving a potential linkage between the sub-polar gyre and the recruitment remain unclear, with two candidate mechanisms being identified. One hypothesis suggests that large mackerel stocks in the same region may potentially exert a high (and controlling) predation upon pre-recruit blue whiting: changes in the spatial and temporal overlap between the two species, possibly modulated by the dynamics of the sub-polar gyre, can therefore influence the survival rates of blue whiting and thus recruitment. Alternatively, gyre-driven variations in the physical and biological environment may change the amount, type, and availability of food for larvae and juveniles, impacting growth and availability. It is not currently possible to distinguish between these two hypotheses (Payne et al., 2012).

2.5 Horse mackerel

2.5.1 Geographic distribution

Horse mackerel is only found in the NE Atlantic, from the southern Norwegian coast to Mauritania and across the whole Mediterranean Sea, overlapping widely with mackerel and blue whiting. Three horse mackerel stocks are currently identified, one in the southern North Sea, one stretching from the Norwegian Sea to the Cantabrian Sea (Western stock) and the third along the Atlantic coast of the Iberian peninsula (Southern stock) (ICES, 2010a).

2.5.2 Spawning habitats and migrations

Spawning takes place in the water column on the shelf edge and adjacent continental shelf. After hatching eggs drift to the nursery grounds. In a simulation study with a hydrodynamic model for the southern North Sea, Peck et al. (2009) found that horse mackerel larvae had a short drift phase (9-10 days) and a small drift distance though it varied between years. The short period is due to high temperatures during the summer leading to rapid development of the embryo.

Horse mackerel migrate between spawning, feeding and overwintering grounds (Abaunza et al., 2003). Migrations of adults from the spawning grounds in the Bay of Biscay and Celtic Sea to the feeding grounds in the Norwegian Sea might be related to the transport of Atlantic water into the North Sea (Iversen et al., 2002). It is plausible that horse mackerel also follow these productive waters to the Norwegian Sea and further north (Iversen et al., 2002) in a similar fashion to mackerel (Langøy et al., 2012); their migration might be assisted in years of high northerly advection of waters along the western edge of the European shelf (Reid et al., 2001). As with herring and mackerel, the migration pattern of horse mackerel is also size dependent.

Migration of horse mackerel from the feeding grounds in the Norwegian Sea to areas further south and from the southern North Sea into the Eastern English Channel is thought to be triggered by temperatures falling below 10 °C (see review in Abaunza et al., 2003).

Vertical distribution of horse mackerel eggs and larvae shows the increased movement of early life stages towards the surface (Coombs et al., 1979; Southward and Barrett, 1983; Coombs et al., 1996). In the Celtic Sea and Bay of Biscay eggs and larvae occur predominantly above the thermocline, situated at around 80m depth. When the seasonal thermocline develops there is a progressive reduction in the mean depth of both eggs and larvae. Adult horse mackerel can occupy a large range of depths in the water column, with a strong demersal behaviour during daylight hours (Lloris and Moreno, 1995).

2.5.3 Life history

Horse mackerel is a batch spawner with an extended spawning season (up to 8 months) that varies between regions and years (Abaunza et al., 2003). The highest incidence of spawning is from May to July at the shelf-edge and over adjacent shelf region on the Celtic platform and Biscay (Eaton, 1989; Franco et al., 1993). In the southern Bay of Biscay eggs and larvae have been found year-round (d'Elbée et al., 2009; Franco et al., 2009).

Fecundity in horse mackerel is length- and area dependent with lowest fecundity in the North Sea (Abaunza et al., 2008). Size at first maturity increases with latitude in a similar manner as length (Abaunza et al., 2008). We know of no studies linking variation in fecundity or reproductive potential directly to environmental factors.

Maximum body length is between 40 and 50 cm (Abaunza et al., 2003), maximum age 40 years and females reach maturity between 2 and 4 years (Abaunza et al., 2003). Variability in individual growth of horse mackerel is thought to depend on food availability and cohort strength (Abaunza et al., 2003) showing increased length-at-age with latitude, which for the western stock is interpreted as size-dependent migration (Abaunza et al., 2008). Growth varies seasonally; it is more rapid between August and December (Macer, 1977).

Horse mackerel can produce extremely strong year classes, with the well-documented 1982 yearclass providing the bulk of catches for over ten years (De Oliveira et al., 2010). A second large, though not as extreme, year class appeared in 2002. However, little is known about the factors controlling recruitment. Santos et al. (2001) found a negative relationship between upwelling events and horse mackerel recruitment in Portuguese waters which could be caused by increased offshore larvae transport and consequent mortality. In complete contrast, Lavín et al. (2007) concluded that years with cooler coastal SST (an indication of upwelling and less stormy weather) during spring and summer supported strong recruitment.

2.6 Knowledge gaps

Our review highlighted the wealth of currently available knowledge on the distribution and life history of small pelagics in the North Atlantic but also allowed us to identify important knowledge gaps (Table 1).

Herring is probably the most studied species among those considered, which is not surprising given its commercial importance. However, some aspects of its biology still need further studies, such as the reasons for the frequent observed changes in migration patterns and the impacts of the oceanographic environment on recruitment success.

Temperature has been shown to have a great effect on mackerel distribution and phenology in some parts of the life cycle. However, it has been difficult to find simple causal relationships with any specific parameter, (e.g. prey availability, spawning conditions, temperature etc.). Clearly, more research is needed relating migration and production to variation in environment, regime shifts/large scale circulation patterns and stock size. It is likely that variation of the subpolar gyre, which has been shown to affect the northeastern pelagic food web (Hátún et al., 2009a), also affects mackerel migrations and subsequently recruitment. Clarifying the role of stock structure is fundamental for understanding the dynamics of mackerel stocks and for evaluating how they have and will respond to changes in the environment and the fisheries. Finally, doubt has beeen cast on historical and current estimates of NE Atlantic mackerel stock size (ICES, 2012; Simmonds et al., 2010). This issue needs to be addressed adequately to ensure research results concerning stock dynamics are reliable.

As capelin is a short-lived species, adult stock sizes reflect the recruitment success of only one to two year classes. The factors causing these recruitment variations are, however, poorly known and require further study. Climate change is likely to affect the distribution and life history of the capelin stocks but answers to questions such as how and what will be the consequences are uncertain.

The stock structure of blue whiting is currently strongly debated. A number of older published studies exist but unfortunately, there are no modern studies that cover the period of strong year-classes associated with changes in the sub-polar gyre after 1995: it is therefore not known what these oceanographic changes have meant for larval dispersion and (meta-) population dynamics in general. Further, few studies exist for the southern part or possibly southern population of blue whiting which would link recruitment, survival and growth to environmental factors. Clearly more work on the NE Atlantic blue whiting and in particular in its southern distribution area is required.

The impacts of environmental conditions on horse mackerel spatial patterns and life history parameters have been very poorly studied; much remains to be done.

3 Distribution and life history of large pelagic fish species in the North Atlantic

3.1 Albacore and bluefin tuna

3.1.1 Geographic distribution

Albacore is a highly migratory species with no evidence of any subpopulation structure within the north Atlantic basin (Arrizabalaga et al., 2004; Montes et al., 2012; Albaina et al., 2013). Albacore inhabit the epi- and mesopelagic layer with a general geographical distribution from the tropics to about 45°N roughly limited by a SST of 15-21°C (Sagarminaga and Arrizabalaga, 2010). Their high metabolic rates necessitate sufficient oxygen concentrations; the lower tolerance limit is around 3.7 mL L^{-1} (Graham et al., 1989) and below 1.23 mL L^{-1} oxygen concentrations become lethal (Sharp, 1978).

The geographic distribution of bluefin tuna is substantially wider than for albacore; it ranges from NW Africa to central/northern Norway in the east, including the Mediterranean Sea and formerly also the Black Sea. In the West Atlantic, the known latitudinal range is historically broader, extending from northern Argentina through the Caribbean to the north coast of Newfoundland (Mather et al., 1995; Rooker et al., 2007). Thermoregulation using a specialized vascular counter current heat exchange system called the –rete mirabile‖ allows bluefin tuna to extend their accessible habitat to colder waters. The range of surface temperatures experienced by bluefin tuna while in northern waters (e.g., near Iceland, North Sea, Norwegian Sea; Gulf of St. Lawrence, north coast of Newfoundland) during summer are ca. 3-20 °C (Mather et al., 1995; Tiews, 1978; MacKenzie and Myers, 2007; Galuardi et al., 2010). Historically, bluefin tuna inhabited the North Sea during spring and summer, exciting the system when temperatures fell below 12 °C (Tiews, 1978). There are presently two managed stocks of bluefin tuna in the north Atlantic, which are delimited by an east-west boundary through the north Atlantic at 45° W. The boundary was established before traditional and data-storage tagging studies revealed trans-Atlantic migrations in both NE and NW directions (Mather et al. 1995, Block et al. 2001, Block et al. 2005; Galuardi et al., 2010). The large-scale geographic distribution of bluefin tuna in the Atlantic has changed during the past 60 years. Some areas for example off northern Brazil, North Sea and Norwegian Sea which formerly supported fisheries no longer do with so occasional sightings occurring (Mather et al., 1995; MacKenzie and Myers, 2007; Fromentin, 2009; Worm and Tittensor, 2011). The reasons for these changes are not clear. In some of the eastern areas there have been major declines in the abundance of the key forage fish species. For example, both the NSSH and the North Sea herring populations collapsed in the 1960s and 1970s respectively. This reduction may be one mechanism contributing to an overall reduction in the range of bluefin tuna in the north Atlantic (Worm and Tittensor, 2011). Noteably, there isno apparent range reduction in the western Atlantic based on studies utilizing electronic tags (e.g., Galuardi et al., 2010) and recent aerial surveillance (Lutcavage et al., unpubl). Integration of information from catch trends, electronic tagging and life history modelling suggests that complex interactions between bluefin adult population size (density-dependent effects), exploitation, prey abundances and oceanographic conditions are at play for shaping bluefin spatial distribution and range (Schick et al., 2004; Schick and Lutcavage, 2009). In the Pacific bluefin tuna migrate to the west coast of North America from the eastern Pacific in years when prey abundance is high. However, in the NE Atlantic, the herring biomass in both areas formerly occupied seasonally by bluefin tuna has now recovered, yet the bluefin tuna have not reappeared. In contrast, in the western Atlantic, the spatial distribution patterns of adults and juveniles appear to be shifting northward and offshore (Golet et al., unpublished results), most likely in response to changes in availability of prey and physical forcing (Golet et al., 2007; 2011). Since 2009, individuals as small as 115 cm are occurring as far north as the Scotian shelf and Gulf of St. Lawrence, and in 2010 and 2011, giant bluefin were observed and caught in Canadian regions north of 55 °N, where they have not been previously reported.

3.1.2 Spawning habitats and migrations

Albacore spawning grounds have been found in waters offshore Venezuela, the Sargasso Sea (Le Gall, 1974; Nishikawa et al., 1985) and in the Gulf of Mexico (Richards, 1969; 1984). Juveniles seem to spend the winter in subtropical areas. In spring, one year old immatures (~ 40 cm) migrate to feeding grounds in the NE Atlantic, where they are caught by fisheries. They are found near the Azores at 38 ºN latitude in May and spread between southwest of Ireland and the Bay of Biscay 1-2 months later (Ortiz de Zárate and Cort, 1998). In late October albacore start migrating back to the mid Atlantic following a route south of Portugal, the Canary Islands and the Azores (Arrizabalaga, 2003). The feeding migration is linked to the seasonal SST warming and cooling, albacore tuna following a preferential SST window between 16 and 18 ºC (Sagarminaga and Arrizabalaga, 2010). This suggests that temperature is a strong environmental factor restricting the habitat of North Atlantic albacore juveniles. In fact, Dufour et al. (2010) showed that the latitude of the young albacore distribution in the offshore feeding area off the Bay of Biscay was correlated with the latitude of the 17 ºC isotherm, and that during warmer years albacore migrated earlier to the feeding grounds. Some albacore are also able to enter into the Bay of Biscay, which has significantly warmer waters (referred to as ―inner cluster‖ in Sagarminaga and Arrizabalaga, 2010). Mature adult albacore (>5 years, >90 cm) migrate to spawning grounds in spring or summer, swimming at depths of 50-150 m.

In contrast to albacore, bluefin tuna spawn in more enclosed areas such as the Mediterranean Sea and the northern Gulf of Mexico (Mather et al., 1995). There may be other spawning areas as well. Based on historic data, maturity ogive research and electronic tag results, the Bahamas, Caribbean Sea, and Gulf Stream margin have been hypothesized to be spawning areas for western bluefin tuna (Mather et al., 1995; Lutcavage et al., 1999; Goldstein et al., 2007; Galuardi et al., 2010). Skip spawning is also characteristic of this species with some recently matured bluefin tuna may skip spawning in some years (Rooker et al., 2007; Goldstein et al., 2007; Galuardi et al., 2010) an occurrence supported by life history modelling (Chapman et al., 2011). Finally, bluefin tuna have apparently spawned in the Black Sea (Mather et al., 1995; Zaitsev, 2003;MacKenzie and Mariani 2012) before their disappearance in the late 1980s (Karakulak et al., 2004). After spawning, adult bluefin generally migrate to foraging areas in the Bay of Biscay, Canary Islands areas, west of Ireland, North Sea, Norwegian Sea, south of Iceland, the Gulf of Maine, Scotian Shelf, Gulf of St. Lawrence, and north coast of Newfoundland (Avalon Peninsula). Some bluefin make trans-Atlantic transits to distant feeding grounds and back during a single season (Galuardi et al., 2010); larger individuals tend to make the longest migrations (Mather et al., 1995; MacKenzie and Myers, 2007; Galuardi et al., 2010). Changes in the timing of feeding migrations of bluefin tuna and albacore have been observed with spawners arriving progressively earlier in the Bay of Biscay over the last decades (Dufour et al. 2010) potentially evidence of the impact of climate warming on these species.

The vertical distribution of albacore has been observed directly by electronic tagging (Domokos et al., 2007; Childers et al., 2011) and acoustic telemetry (Laurs et al., 1980; Laurs and Lynn, 1991) or indirectly by the depth of longline hooks (Bard et al., 1999; Bertrand et al,. 2002). The depth distribution varies between the surface and 450 m depending on size and ambient temperature and the diurnal cycle. Juvenile albacore, during their feeding migration to the NE Atlantic (Goñi et al., 2009), seem to occupy surface waters, usually staying above the thermocline, while adult fish, whose swim bladder is fully developed, are more capable of exploiting deeper resources.

3.1.3 Life history

Environmental processes affecting growth, maturation, recruitment, and the timing of migrations are not well documented for albacore and bluefin tuna (see review in ICCAT 2010a,b). However, time series analyses showed that some large-scale climatic factors (e.g., NAO, temperature, precipitation) can explain some of the variation in long-term fluctuations in Mediterranean trap catches of bluefin adults during the 1800s-early 1900s, with time lags suggesting climatic-hydrographic effects on eggs, larvae and early juveniles (Ravier et al., 2004) even if the mechanisms remain obscure. In the case of albacore, recruitment seems also affected by large-scale environmental variability, but the mechanisms are not clearly identified (Arregi et al., 2006).

Compared to more tropical tunas such as yellowfin and skipjack tuna, albacore and bluefin have longer life spans, over 15 and 20 years respectively. Natural mortality is much higher for young than for adult fish. Age at first maturity is reached at 80 cm for albacore (5 yrs and 90 cm for 50% mature fish) and between 4 years (115 cm) and 6-8 years (190 cm or less) for east and west stocks respectively of Atlantic bluefin (Baglin, 1982; Medina et al., 2002; Heinisch et al., 2010). High fecundity is a characteristic of all tunas and tuna-like fishes, with females spawning several million eggs per year.

Albacore maximum length is 122 cm, with males growing larger than females (Santiago and Arrizabalaga, 2005). They show strongly seasonal growth, with higher growth rates in the summer feeding season in the Bay of Biscay and surrounding waters of the NE Atlantic. Growth is rapid in early life stages, and slows down with age. Adult albacore can grow to 40 kg (120 cm), while bluefin tuna can reach over 600 kg (>250 cm). Eastern and western bluefin tuna grow at similar rates (Restrepo et al., 2010), eat similar prey (Logan et al., 2011), share feeding grounds, and are likely to have similar life history profiles (Chapman et al., 2011). Recent studies confirm that east-west differences in size and age at maturity are much less than previously assumed, with some western fish maturing at 160 cm or less (Knapp et al, 2009). Availability of prey and migration distance have been shown to affect bluefin life history traits such as age of maturity and spawning frequency and migration distances (Chapman et al., 2011).

3.2 Swordfish and blue marlin

3.2.1 Geographic distribution

North Atlantic swordfish are considered a subtropical species, but they are also common in temperate waters (Fromentin and Fonteneau, 2001). Mejuto and Hoey (1991) based on reviewing the literature concluded that an appropriate model for swordfish distribution in the North Atlantic would be one of seasonal expansion and contraction around the equatorial region, with the largest individuals showing the greatest range - similar to bluefin tuna. There are relatively few records of movement between the NW and the NE Atlantic (Neilson et al., 2009) compared to blue marlins and bluefin tuna. Instead, there are relatively discrete north-south migratory pathways with individuals marked in Canadian waters typically spending winter months, presumably for spawning, in the Caribbean/Sargasso Seas (Neilson et al., 2009). Those authors also described a striking fidelity to foraging sites.

In contrast to swordfish, blue marlin are found in the Atlantic, Pacific and Indian oceans, with genetic evidence indicating that they form a single species across their range (Collette et al., 2006). Blue marlin occur in tropical to temperate waters, with the highest abundances in waters >25° C. This temperature association results in a broader latitudinal range for blue marlin in the western Atlantic versus the eastern Atlantic. Conventional tagging data shows that individuals cross the Atlantic and the equator, with one individual even exhibiting inter-ocean movement (Orbesen et al., 2008). No range changes have been found for blue marlin over the past half-century (Worm and Tittensor, 2011). Interannual variability in blue marlin distribution has been documented in the Pacific Ocean in response to El Nino Southern Oscillation events (Su et al., 2011) but not for the Atlantic. At finer spatial scales, interannual variability in recreational blue marlin catch has been associated with the presence of cyclonic eddies, with catches occurring in the frontal region of the eddy (Seki et al., 2002).

3.2.2 Spawning habitats and migrations

Spawning areas for swordfish are geographically extensive, with the main spawning areas being south of the Sargasso Sea and east of the Antillean Arc. The spawning period is latitude dependent, and spans the whole year. Reproductive activity has been associated with surface 23 – 26º C isotherms (Tåning, 1955; Mejuto and Hoey, 1991), or possibly isotherms below the surface (Mejuto and García, 1997). It has been suggested that these oceanographic features are similar on the spawning grounds in the NW Atlantic and in the South Atlantic (Mejuto and García, 1997). Recent genetic analyses have revealed separation of populations in the NW and South Atlantic, though there might be some mixing between NW and NE Altantic populations (Alvarado Bremer et al., 2005). It has been widely hypothesized that swordfish eggs and larvae in the Northwest Atlantic may be carried from the spawning grounds via the Gulf Stream system to adjacent areas (Arata, 1954; Tibbo and Lauzier, 1969). Oceanographic features such as independent eddies from the Gulf of Mexico (Markle, 1974) and filaments and trajectories from the Gulf Stream (Govoni et al., 2000) may be responsible for altering the pathways for larval transport. Swordfish retain their larval characteristics to a length of at least 188mm (Govoni et al., 2000), and passive transport has been assumed to some extent for larvae up to 115mm.

For blue marlin numerous spawning locations have been documented: larvae have been collected in the waters offshore of Brazil, the Outer Bahamas, the Mona Passage off the Dominican Republic, the Gulf of Mexico, and in the Straits of Florida (Richardson et al., 2009). However, spawning habitat does appear to be restricted by temperature. Blue marlin larvae are generally only collected in areas with surface temperatures >28° C, with higher densities between 28 and 30° (Rooker et al., 2012).

During times of the year when swordfish are actively foraging in more northerly latitudes, they show a distinct and predictable form of vertical migration. The behaviour seems to follow the movement of mesopelagic organisms in the deep scattering layer (Carey, 1990). At night, swordfish tend to remain in the mixed layer, where they can feed and recover from a thermal or oxygen debt acquired by day.

The vertical movement patterns of adult blue marlin are strongly tied to oxygen and temperature levels. Satellite tagging studies have shown that blue marlin are within the mixed layer about 85% of the time during the night and about 60% during the day. However they also make frequent short duration dives below the mixed layer; the minimum temperatures experienced during these dives are generally 17-18° C (Goodyear et al., 2008). In the eastern Atlantic, levels of dissolved oxygen are the primary factor limiting the dive depths, a factor that likely increases the susceptibility of blue marlin to bycatch in surface fishing gear in these regions (Prince et al., 2010).

3.2.3 Life history

Swordfish are among the largest of the teleosts, reaching a maximum weight in excess of 500 kg. Rouyer et al. (2010) found that catch rates of the larger, slower-growing and later- maturing species such as swordfish and blue marlin showed links with environmental conditions. These authors considered swordfish to be slow growing, but there is virtually no information on environmental influences on growth processes due to a paucity of age and other life history information.

Blue marlin exhibit substantial sexual dimorphism in size; females reach a maximum weight of >500 kg and males reach ≈160 kg (Wilson et al., 1991). The maximum longevity of blue marlin is uncertain as larger fish are difficult to age (Drew et al., 2006). However, in tagging studies blue marlin have been recaptured 12 years after release (Orbesen et al., 2008). For blue marlin substantial seasonal variation occurs in the sex ratio within specific regions, probably reflecting behavioural and habitat differences. In the Pacific, spawning has been estimated to occur every 2.4 days over a 4-5 month season (Sun et al., 2009). A similar season of extended repeat spawning also occurs in the Straits of Florida (Richardson et al., 2009). The average blue marlin batch fecundity in the Pacific is estimated at 7 million eggs.

The growth of the early life stages of blue marlin is extremely rapid with egg development times of approximately one day. Large variations in larval growth have been found between regions (Sponaugle et al., 2005). These differences were unrelated to water temperature, and it was speculated that they could have been driven by differences in larval prey field between regions or maternal effects if the size-structure of the spawning fish differed between regions. Larval mortality rates of blue marlin are very high and have been estimated at 30% per day (Richardson et al., 2009).

3.3 Knowledge gaps

Little is currently known about environmental or biological factors impacting life history traits of albacore, bluefin, swordfish and blue marlin in the North Atlantic (Table 1). Dedicated data analysis and modelling studies to elucidate the roles of environmental conditions and fishing in shaping population dynamics, spatial distributions and migrations are needed for all four species. These species also have in common that their spawning grounds are only partially or unprecisely known.

4 Diet and predators of small and medium sized pelagic fish species in the North Atlantic

In this section, we review the available knowledge of the diet (prey) of each species, as well as their predators. We strive as much as possible to elucidate regional differences.

4.1 Herring

4.1.1 Prey

Adult herring are opportunistic and feed on a variety of zooplankton and the larval stages of fish and invertebrates depending upon the location. However, throughout their range their primary food are copepods, such as *Calanus* and *Pseudocalanus* spp., and other small crustaceans (Scott and Scott, 1988; Prokopchuk and Sentyabov, 2006).

In the Norwegian Sea, *Calanus finmarchicus* is the dominant zooplankton species (Wiborg, 1955), making up 80 % of the annual zooplankton production and the primary adult herring prey (Gislason and Astthorsson, 2002; Dommasnes et al., 2004; Prokopchuk and Sentyabov, 2006). NSSH follow *C. finmarchicus* through the Norwegian Sea, resulting in a general clockwise migration pattern during the feeding period. The quantity of C. *finmarchicus* that contributes to the total herring diet varies from 0 – 99 % depending on the temporal and spatial distribution of herring.

Food composition of herring in the NW Atlantic varies in a similar way to the NE Atlantic, being dominated by one or two primary species, but including other organisms of appropriate size. The main prey of herring in Gulf of St Lawrence are also *Calanus* copepods, followed by capelin and euphausiids (Darbyson et al., 2003). It is not uncommon to find herring eggs in the stomachs of pre-spawning herring collected on spawning grounds in coastal and Southwest Nova Scotia (Gary Melvin, pers com.). The most important prey for herring collected on Georges Bank were chaetognaths, euphausiids, pteropods and copepods and in the Gulf of Maine it was euphausiids and copepods. In some areas herring have been found to feed on 0-group fish, including capelin, *Sebastes* spp. and herring themselves (Holst et al., 1997). Fish prey can even dominate the diet in some areas. Predation by juvenile NSSH in the Barents Sea is considered to impact year class strength of the local capelin stock, in addition to predation by 0-group cod and adult cod (Hjermann et al., 2010; Frank et al., 2011). On Georges Bank in the NW Atlantic, predation including that by herring, is believed to have contributed to the lack of a recovery of cod (Quinlan et al., 2000; Tsou and Collie, 2001; Murawski, 2010). In the North Sea where a more diverse group of prey organisms occur the principal herring prey are copepods (*Calanus finmarchicus* and *Temora longicaudata)*, however, euphausids and post-larval fishes (*Ammodytes* spp. and clupeoids) and fish eggs (*Pleuronectes platessa,* and pelagic fishes*)* contribute also to their diet (Last, 1989; Segers et al., 2007).

The summer of 2010 was anomalous with respect to weight-at-length, condition factor and fat content for a number of fish stocks on both sides of the north Atlantic (ICES, 2010b). Simultaneously, results from an international survey in the Nordic Seas in May indicated that zooplankton abundance had been declining, and in 2009-2010 it was at its lowest level since sampling started in 1997 (ICES, 2011d). Similar observations have also been reported for herring in the Gulf of Maine, Southwest Nova Scotia and the Gulf of St Lawrence where there is some evidence that the mean weight at age has been declining for several decades. Melvin and Martin (2012) found a significant relationship between mean monthly sea surface temperature, chlorophyll and herring body condition for specific months. They also noted that the decrease was not the same throughout the stock complex and varied among regions in the same stock. These observations could indicate a resource control on herring which would work via chlorophyll (plankton production), zooplankton through to fish growth on the western Atlantic. These observations evoke not only questions about trophic control but also about carrying capacity of the regional seas and gulfs.

4.1.2 Predators

Herring are eaten by many predators at every stage from eggs to adult, and they are a key link in the transfer of energy from one trophic level to another in many ecosystems of the

North Atlantic. Eggs are preyed upon by numerous species of ground fish, invertebrates, and pelagic species, including herring themselves. As larvae they are consumed by fish and planktonic invertebrates, and filter feeding mammals. Once herring metamorphose into juveniles they become important prey for a wide variety of marine and terrestrial organisms, including seabirds which depend upon these small fish to feed the recently hatched chicks. As they increase in size so does the size of the predators feeding on them, and even the largest herring have several species that depend upon them for a major portion of their food consumption. Large predators of herring include seals, toothed whales (e.g. killer whale *Orcinus orca*), minke whale (*Balaenoptera acutorostrata*), fin whale (*Balaenoptera physalus*), humpback whale (*Megaptera novaeangliae*) and dolphin species, tuna (see below) and tuna like species, seabirds and various demersal fish species (Sigurjónsson and Víkingsson, 1997; Overholtz and Link, 2007).

The total consumption of herring by predators is generally unknown and even when estimated it is usually only available for individual predator species or groups. Nevertheless, an estimate of total consumption of the Gulf of Maine-George Bank herring complex has been performed, and has shown that demersal fish species were the most effective predators, followed by marine mammals and large pelagic fish (Overholtz and Link, 2007). Changes in abundance of both prey and predators can cause major fluctuations in the estimate of total consumption (Overholtz et al., 2000).

In the Norwegian Sea the predation pressure on NSSH during the feeding season is considered low as the whales focus more on zooplankton or capelin. Saithe (*Pollachius virens*) is known to prey on herring during the spawning period and they are believed to follow herring into the Norwegian Sea, but the extent of this is difficult to evaluate since there are very few samples of saithe from this area. In other areas of the north Atlantic, where herring aggregate for feeding, spawning, or overwintering, they are also followed by their predators (Parrish, 1993; Pitcher et. al., 1996; Read and Brownstein, 2003). It is not uncommon to observe whales, seals, seabirds, tuna, and a multitude of groundfish species feeding on herring spawning aggregations (Christensen, 1988; Purcell, 1990; Lindstrøm et al., 2000; Nøttestad, 2002; Overholtz et al. 2008). In some areas groundfish fisheries concentrate on herring spawning grounds to take advantage of their increased density and their eggs laying on the seafloor which attract demersal fish that feeds on them (Toresen, 1991; Livingston, 1993).

4.2 Mackerel

4.2.1 Prey

Early life stages of Atlantic mackerel are characterized by fast growth and early feeding on copepod nauplii followed by a switch to piscivorous feeding habits at about 7 mm (Mendiola, et al., 2007; Robert et al., 2008). Early stages of mackerel exhibit selective feeding with calanoid copepods being preferred over cyclopoid copepods (Ringuette et al., 2002; Robert et al., 2008). When the larvae are > 6 mm and the potential growth rates are still increasing (Bartsch, 2002), high energy rich fish larvae become a central prey item. Piscivorous and cannibalistic feeding has been noted in all studies analysing mackerel larval feeding habits (Lebour, 1920; Grave, 1981; Ware and Lambert, 1985; Hillgruber and Kloppmann, 2001; Robert et al., 2008) with the exception of Last (1980), but this might be due to misidentification (Hillgruber and Kloppmann, 2001). Cannibalism was observed to be more prevalent at higher temperatures and increased with age and size (Mendiola et al., 2007). Comprehensive lists of prey species found in mackerel larvae stomachs are provided by Hillgruber and Kloppmann (2001), Robert et al. (2008), Hillgruber et al. (1997) and in references therein.

Juvenile and adult Atlantic mackerel are opportunistic feeders that can ingest prey either by particulate or filter feeding. They feed on a wide variety of zooplankton and small fish. Feeding behaviour and diet vary seasonally, diurnally, spatially and with size. Prey preference is positively size selective. Larger fish larvae are preferred over smaller larvae (Pepin et al., 1987; Pepin et al., 1988; Langøy, et al 2006; 2012). In the laboratory, prey size preference has been shown to be independent of prey concentration (Pepin et al., 1987; 1988).

In the North Sea, the main zooplankton prey are copepods (mainly *C. finmarchicus*), euphausiids (mainly *Meganyctiphanes norvegica*) and hyperiids, while primary fish prey are sandeel, herring, sprat, and Norway pout. The most intensive period for mackerel feeding is April to August. Euphausiids are the main prey in winter and up to the beginning of spawning. Through spawning, summer and autumn, copepods and fish are also important parts of the diet (Mehl and Westgård, 1983; ICES, 1997).

Mackerel in addition to herring is one of the major consumers of zooplankton in the Norwegian Sea, in particular of the dominant *C. finmarchicus* (Prokopchuk and Sentyabov, 2006; Langøy et al., 2012). Euphausiids and *Themisto* spp. also make up a significant bulk of the total zooplankton biomass in the Norwegian Sea (Dalpadado, 2002; Melle et al., 2004) and are among the preferred prey of mackerel (Langøy et al., 2012). The sea snail *Limacina* *retroversa* may also contribute significantly to the diet in coastal Atlantic and Arctic water masses, even though more by weight than by numbers (Langøy et al., 2012). Mackerel has also been found to feed on adult capelin in frontal regions, illustrating their opportunistic and adaptive feeding behaviour (Nøttestad and Jacobsen, 2009). NWAM mackerel diet is dominated by copepods, decapods and fish larvae (Grégoire and Castonguay, 1989). Mackerel and herring are potential competitors in the Norwegian Sea both being opportunistic feeders with overlapping spatial distributions (Prokopchuk and Sentyabov, 2006). However, in some years (2004, 2006 and 2010) the degree of overlap in selection prey and distribution of these two species has appeared to vary (Nøttestad et al., 2010; Utne et al., 2012b; Langøy et al., 2012). This perceived change could be due to stronger competition during the feeding season forcing the herring to the cooler fringe areas with poorer feeding. Support for this hypothesis is that herring were observed to be in poorer condition in 2010 than in previous years.

4.2.2 Predators

A range of fish, mammal and bird predators have been reported to prey on mackerel (du Buit, 1996; Hunt and Furness, 1996; Overholtz et al., 2000; Olsen and Holst, 2001; Henderson and Dunne, 2002; Lewis et al., 2003; Savenkoff et al., 2005; Trenkel et al., 2005). Locally mackerel can be important for some predators, such as killer whales in the northeast Atlantic and Norwegian Sea during summer (Nøttestad et al., Submitted).

4.3 Capelin

4.3.1 Prey

Capelin is a planktivore with the main diet items being copepods, euphausiids and amphipods (see overview in Vilhjálmsson, 1994; Gjøsæter, 1998; Carscadden et al., 2001). Generally, the importance of copepods decreases with capelin size and that of euphausiids and amphipods increases. On the feeding grounds north of Iceland, euphausiids were estimated to constitute between 74-90% of the capelin diet (in weight), with corresponding estimates being somewhat lower for the Barents Sea (Vilhjálmsson, 1994). The importance of amphipods in the capelin diet is highest in the arctic waters where they are most abundant, for example in the northern Barents Sea (Gjøsæter, 1998) and the Labrador Sea (Carscadden et al., 2001). Capelin can impact euphausiid density, as shown by an inverse relationship between their respective abundance estimates (Gjøsæter et al., 2002). Hassel et al. (1991) observed that the biomass of euphausiids in the upper water column was much lower in areas where capelin was present compared to where capelin was absent.

Competition for food with other pelagic species is probably low for Icelandic capelin as they dominate the feeding grounds. In contrast, in the Barents Sea capelin may compete with polar cod (*Boreogadus saida*) in the eastern and northeastern part of the Barents Sea (Ushakov and Prozorkevich, 2002), and with juvenile herring in the southern parts (Huse and Toresen, 1996). In the Gulf of St. Lawrence in the NW Atlantic, interspecific feeding, competion of larvae of capelin, smelt (*Osmerus mordax*) and herring was considered minimal as they occurred in distinct water masses and had mainly different sizes (Courtois and Dodson, 1986). No information was found concerning competition with the adult part for the capelin stocks in the NW Atlantic. However, it can be expected that the more southerly and easterly distribution of the stocks since the early 1990s, and thereby a less offshore distribution, might have lead to increased competition with species normally occupying the continental shelves, such as herring.

4.3.2 Predators

The large capelin stocks in the North Atlantic are important prey for a number of finfish, bird (Barrett et al., 2002; Carscadden et al., 2002), and marine mammal species (Carscadden et al., 2001; Dolgov, 2002). Gjøsæter (1989) considers capelin to play a key ecological role as an intermediary between zooplankton and higher tropic levels. Both cod and Greenland halibut (*Reinhardtius hippoglossoides*) feed heavily on capelin. The growth rates, somatic weight, and/or liver conditions of cod have been found to be positively related to biomass of capelin in the Barents Sea (Yaragina and Marshall, 2000), around Iceland (Vilhjálmsson, 2002) and in the NW Atlantic (Sherwood et al., 2007). Considering that capelin are an important forage species for many stocks, changes in their spatial distribution are likely to have significant consequences for their predators. For example, observed changes in capelin distribution, most likely caused by environmental factors, lead to them being less accessible to Greenland halibut (Dwyer et al., 2010), cod in the NW Atlantic (Rose and O'Driscoll, 2002), and mature cod in Icelandic waters in the 2000s (Marine Research Institute, 2010). Capelin larvae are also heavily predated on. As mentionned above, predation by juvenile herring in the Barents Sea is considered to affect the year class strength of capelin (Hamre, 1994; Gjøsæter and Bogstad, 1998; Huse and Toresen, 2000); no information is available for predation on capelin larvae in Icelandic waters. The overlap between predators and juvenile capelin is usually higher than that for pre-spawning mature individuals which have a more oceanic distribution (Vilhjálmsson, 1994; Gjøsæter, 1998; Carscadden et al., 2001).

4.4 Blue whiting

4.4.1 Prey

Blue whiting is a planktivorous species, with its dominant prey changing throughout lifetime. The diet of larval blue whiting consists predominately of *Calanus* spp, *Pseudocalanus* spp., *Arcatia* spp. and *Oithona* spp., with little or no phytoplankton or ichthyplankton (Conway, 1980). The diet of the juveniles and adults appears to be dominated by euphausiids together with *Calanus* spp.; small fish (Norway pout, pearlsides) also appear to be a part of the diet of the largest adults (Bailey, 1982; Bergstad, 1991; Dolgov et al., 2009). The abundance of all of these prey groups in the North Atlantic has been shown to have links to the sub-polar gyre (Hátún et al., 2009a) and therefore changes in the available prey for blue whiting can be expected as a consequence of environmental change.

As one of the major (by biomass) pelagic planktivorous species in the North Atlantic, it is almost inevitable that blue whiting competes with other species for resources. A recent study in the Barents Sea showed a high degree of dietary overlap between blue whiting and capelin, but also with herring and polar cod (Dolgov et al., 2009). It has recently been conjectured that the high abundance of pelagic fish in the Nordic Seas may be too large to be supported by the system‘s secondary (zooplankton) production (e.g. Payne et al 2012) although quantitative analyses capable of exploring this hypothesis in detail have yet to be carried out.

4.4.2 Predators

Important predators of the southern component of blue whiting are hake in the Bay of Biscay (Guichet, 1995; Mahé et al., 2005) and hake, saithe, megrim, cod and whiting in the Celtic Sea (Pinnegar et al., 2003), in particularly during the summer months (Trenkel et al., 2005). Hake, saithe, and squid are potential predators in the northern regions (Bailey, 1982). Juvenile blue whiting have been identified as the main prey species of mackerel around the Iberian coast during autumn (Cabral and Murta, 2002; Olaso et al., 2005). Mackerel is hypothesised to be a major, and possibly controlling predator on juvenile blue whiting throughout its range (Payne et al., 2012). Several whale species also feed on blue whiting in the Bay of Biscay (Spitz et al., 2011), as does bluefin tuna.

4.5 Horse mackerel

4.5.1 Prey

Horse mackerel is a planktivore, with the dominant prey being euphausiids and copepods, but also fish (Macer, 1977). Given its spatial overlap with other planktivores such as mackerel, blue whiting, and sardine, it is also likely to compete with these species for food, especially at an early age (Cabral and Murta, 2002).

In the eastern part of the North Sea (off Jutland) horse mackerel were found to forage predominantly on fish (Dahl and Kirkegaard, 1987), with 0-group whiting being the most important prey, followed by other gadoids and herring. A shift in prey preference with age has been found: smaller individuals (< 20-24 cm) preyed mostly on crustaceans, gobies and haddock, while larger specimens shifted towards herring. For the Bay of Biscay, Letaconnoux (1951) and Olaso et al. (1999) provided a description of the horse mackerel diet. These observations indicated possible seasonal differences: during spring they preyed mainly on crustaceans, while in the autumn larger individuals (> 30 cm) began to prey on fish (blue whiting, gobiids, anchovy), which represented 45% of the food volume in this size-range.

4.5.2 Predators

Horse mackerel is an important prey for cod, hake, megrim and whiting in the Celtic Sea, together with blue whiting (in summer) and mackerel (in winter) (Trenkel et al. 2005); it is also abundant in hake stomachs from the Bay of Biscay (Guichet, 1995;) and those of a number of piscivores fish in the Cantabrian Sea (Preciado et al., 2008). In the Celtic Sea hake diet was found to reflect horse mackerel availability (Pinnegar et al., 2003), similarly in the Cantabrian Sea (Preciado et al., 2008). Horse mackerel are also consumed by bleufin tuna (see below).

5 Diet and predators of large pelagic fish species in the North Atlantic

5.1 Albacore

5.1.1 Prey

Albacore is considered an opportunistic predator. In the Northeast Atlantic it has been reported to feed on fish, crustaceans and cephalopods with the most frequent and widespread prey being the euphausiid crustacean *Meganyctiphanes norvegica* (Aloncle and Delaporte, 1974; Ortiz de Zarate et al., 1987; Pusineri et al., 2005; Goñi et al. 2011). The most western investigations (up to 30ºW) were performed by Aloncle and Delaporte (1974) who found albacore fed mainly on amphipods (*Themisto gaudichaudii*), krill (*Meganyciphanes norvegica*) and the pelagic fish *Cubiceps gracilis* around the Azores islands. In the Bay of Biscay and surrounding areas, in addition to krill the sternoptychid fish *Maurolicus muellerii* as well as paralepidid fish represented an important part of albacore diet (Aloncle and Delaporte, 1974; Pusineri et al., 2005). However, as these species have become scarce in more recent years (Goñi et al., 2011), age-0 blue whiting has become a key prey, particularly along the shelf-break of the Bay of Biscay. Atlantic saury (*Scomberesox saurus*) have also been reported as an important prey for albacore in this zone in all studies to date. However, Atlantic saury is scarcer in the inner Bay of Biscay where sea surface temperature is higher (Aloncle and Delaporte, 1974). Anchovy is an important prey for albacore within the Bay of Biscay, mainly in the southern part (Ortiz de Zarate, 1987; Goñi et al., 2011), but is absent from the diet outside the bay. Average daily consumption of anchovy by albacore is around 10 individuals per day although after the recovery of the anchovy stock in 2010 as many as 103 individuals have been found in an individual stomach (N Goñi, pers. comm.).

The main spatial pattern in albacore diet is the difference between shelf-break areas and more oceanic areas with higher proportions of fish at the shelf break and more small crustaceans in oceanic waters (Goñi et al., 2011). In terms of feeding strategy, at the shelf-break albacore feed in the epipelagic layer during both daytime and night. In oceanic zones they feed in the epipelagic layer by night and dive into mesopelagic and/or bathypelagic layers to feed during the day (N Goñi pers comm.). These observations, together with the seasonal distribution of the fishing activity by surface gears (Sagarminaga and Arrizabalaga, 2010), suggest that the shelf-break areas are the main feeding areas for albacore in the NE Atlantic, whereas more oceanic areas would correspond to the last stages of the migration.

Current albacore diet studies concern mainly juveniles, which compose the majority of albacore catches by surface fleets in the NE Atlantic. Their feeding ecology in the NW Atlantic has not been studied to date.

5.1.2 Predators

Albacore is a top predator which probably has predators for juvenile stages.

5.2 Bluefin tuna

5.2.1 Prey

Bluefin tuna in the north Atlantic consume a variety of fish species, as well as crustaceans and squid. Common fish prey species include herring, mackerel, anchovy, sardine, sprat, silver hake, squid, and demersal fish and invertebrate species, particularly in shallow continental regions (Chase, 2002; Rooker et al., 2007; Logan et al., 2011). Bluefin tuna in the North Sea and the Norwegian Sea consume herring, mackerel, sprat, garfish and gadoids (Tiews, 1978; Mather et al., 1995). Adult bluefin tuna in the Gulf of Maine primarily eat herring, sandlance and mackerel (adults) (Crane, 1936; Chase, 2002; Estrada et al., 2005; Golet et al., 2007), while over a broad shelf area juvenile bluefin target sand lance (Chase, 2002; Golet et al., 2007; Logan et al., 2011). In the western Atlantic, stomach content analysis of long line caught bluefin and diving records from electronic tags show that in oceanic regions bluefin dive deeply and heavily target squids, with myctophids and other species identified to a lesser extent (Wilson et al, 1965; Logan et al., 2011). Stomach content studies of bluefin tuna captured south of Iceland in the late 1990s-early 2000s showed that diets in these waters were composed of an unidentified mixture of fish, crustacean and squid species (Olafsdottir and Ingimundardottir, 2000), although in 2011 they appeared to be targeting mackerel aggregations. The amount of prey consumed, and thus the predation impact that bluefin tuna formerly had in the North Sea has been estimated to be between 150-200,000 t of prey. Most (probably 75%) of this prey was herring (Tiews, 1978). This level of consumption occurred over a relatively short season because bluefin tuna were present in the North Sea for only 2-3 months per year (Tiews, 1978). The level of herring consumption by bluefin tuna in the 1950s was recently compared to consumption by all other predators (MacKenzie and Myers, 2007). The long-term mean consumption of herring by other predators was ca. 600,000 t during the mid-1960s-early 2000s (ICES, 2005). The bluefin consumption of herring could have been as high as 30% of that consumed by other predators, although in a much shorter period. This comparison suggests that predation by bluefin tuna on North Sea herring may have been quite substantial, and that bluefin tuna may therefore have been an important regulator of food web structure. The consumption of prey in the North Sea allowed bluefin tuna to increase their weights and condition factors before starting the return migration to southern waters in autumn (Tiews, 1978). Similar comparisons of predation impacts and condition have been conducted in the Gulf of Maine (Golet et al, 2007) and reveal relationships with prey availability, size, and energy status. In particular, significant associations between Atlantic bluefin tuna and

Atlantic herring schools were identified (Golet et al., 2011), although long-term shifts in Atlantic herring distributions did not follow the same trend as for Atlantic bluefin tuna.

The published dietary studies are mainly based on adult bluefins. Juvenile (ages 1-4) prey also on fish but also other lower trophic levels as revealed by both stomach content and isotopic analyses (Sara and Sara, 2007, Logan et al., 2011). Juvenile bluefin in the Bay of Biscay preyed primarily on 0-group anchovy, blue whiting, horse mackerel with myctophids, krill, swimming crabs and squid being consumed seasonally. Sandlance were the dominant prey species of juveniles in the Mid Atlantic Bight (Eggleston and Bochenek, 1990; Logan et al., 2011). This pattern is evident both in periods when sand lance was abundant and relatively rare. Other species of prey such as Atlantic mackerel, herring, butterfish and longfin squid were consumed in lesser amounts. In contrast, in the Bay of Biscay, consumption of anchovy seems to co-vary with local abundance, as consumption declined when the biomass of anchovy declined, and the consumption of some alternative prey species (e.g., krill) increased. Comparison of the estimated trophic levels of prey consumed based on prey remains in stomachs and isotopic measurements of bluefin tuna liver and muscle showed that trophic levels were lower based on isotopic evidence.

Significant reduction in the condition of adult bluefin tuna in the Gulf of Maine has been linked to changes in the condition and availability of larger herring (Golet et al., 2007), possibly due to regional depletion, and bottom-up changes in trophic structure linked to oceanographic conditions (Golet et al., unpublished results). Prey switching is the norm for adult bluefin schools in the Gulf of Maine, where schools travel up to 75 km d^{-1} and may switch feeding from sandlance to herring or other small pelagic species (Lutcavage et al., 2000; Gutenkunst et al., 2007).

5.2.2 Predators

Bluefin tuna is a top predator but which has predators for juvenile stages.

5.3 Swordfish

5.3.1 Prey

Swordfish as with tunas maintain their eyes and the central nervous system above ambient temperature, as a result having a vision system with high temporal resolution which is an advantage for hunting species (Fritches et al, 2005). The dominant prey swordfish consume are fish and cephalopods with crustaceans being a secondary prey type (Chancollon et al., 2006). Lanternfish, including *Notoscopelus kroeyeri* and *Symbolophorus veranyi*, are abundant, but paralepidids, Atlantic pomfret (*Brama brama*), and squid (*Todarodes sagittatus*, *Ommastrephes bartramii*, and *Gonatus steenstrupi*) dominate the diet by mass. Swordfish also appear to show feeding plasticity both among different areas and among animals in the same area. In the NW Atlantic, swordfish prey include several families of mesopelagic fish (Paralepididae, Myctophidae) and squid (*Illex illecebrosus*) (Stillwell and Kohler, 1985).

5.3.2 Predators

Larval swordfish are eaten by surface dwelling fishes, including larger swordfish (Scott and Scott, 1988). Yabe et al. (1959) described predation of young swordfish by blue sharks (*Prionace glauca*). As adults, swordfish have few natural enemies, but shortfin mako (*Isurus oxyrinchus*) sharks are frequently associated with attacks on hooked or harpooned swordfish (Scott and Scott, 1988).

5.4 Blue marlin

5.4.1 Prey

Blue marlin are opportunistic feeders with substantial regional variation in their diets. For example the dominant prey items in blue marlin stomach contents were pomfret (*Brama brama*) and a squid (*Ornithoteuthis antillarum*) off Brazil (Junior et al., 2004), whereas skipjack (*Katsuwonus pelamis*) dominated in the western Pacific (Shimose et al., 2006), and frigate mackerel (*Auxis thazard*) in the Caribbean (Erdman, 2011). Analyses of food web structure consistently indicate that blue marlin is one of the top predators in pelagic ecosystems (Dambacher et al., 2010).

In contrast to the adults, larval blue marlin are highly selective feeders. In the Straits of Florida, about 90% of stomach contents of small (<5mm) larval blue marlin were either a specific genus of copepod (Farranula) or a cladoceran (Evadne). The onset of piscivory occurred at 5 mm with exclusive piscivory occurring at 12 mm. Remarkably, despite the low productivity in the Straits of Florida relative to more temperate areas, blue marlin larvae had a high feeding incidence of 98% (Llopiz and Cowen, 2008).

5.4.2 Predators

Blue marlin is a top predator which probably has predators for juvenile stages.

6 Discussion

Having reviewed the literature we can now come back to the questions formulated in the Introduction: What are the commonalities and differences in distribution and life history of pelagics species across the North Atlantic? What are the commonalities and differences in their trophic roles? What models exist for evaluating environmental and fishieries impacts on the structure and functioning of North Atlantic ecosystems?

6.1 Commonalities and differences in distribution and life history of pelagic species across the North Atlantic

A striking difference in the ecology of small pelagics between the NE and NW Atlantic is the extent of horizontal migrations. In the NE Atlantic these stocks perform extensive migrations and capitalize on large feeding grounds in the Nordic Seas and adjacent areas (Vilhjálmsson, 1994; Dragesund et al., 1997; Jakobsson and Østvedt, 1999; Nøttestad et al., 1999; Holst et al., 2002; Utne et al., 2012b). Comparable excursions into the adjacent Labrador Sea, for example, are not commonly seen on the western side of the Atlantic. There are clear differences in the temperature regime, which likely affects the profitability of foraging in the ocean basins. The Labrador Sea is downstream of the cold East Greenland current, whereas the Norwegian Sea on the other hand is downstream of the North Atlantic Current, which provides a great heat contribution to this area (Blindheim, 2004), making it a highly profitable feeding area for pelagic fish (Skjoldal, 2004). In particular the frontal areas in the western parts of the Norwegian Sea are used extensively as a feeding area during the summer (Dragesund et al., 1997; Vilhjalmsson, 1997; Jakobsson and Østvedt, 1999; Holst et al., 2002; Utne et al., 2012b). A recent review of ecosystem productivity found no apparent differences in aggregate productivity per area between ecosystems on the eastern and western Atlantic (Lucey et al., 2012). But a key difference between the east and west is that the areas of suitable habitat for pelagic fish are much more extensive in the NE Atlantic ecosystems compared to the ecosystems on the NW side and therefore support larger fisheries and fish stocks (Figure 1).

Our literature review of biological and ecological processes showed that the environment in a wider sense is a driving factor for all five small and medium size pelagic species (Table 1). In general, there are few documented differences between stocks of the same species on either side of the North Atlantic. Further, temperature impacts are a recurrent theme for all species. Environmental impacts determining larval survival and producing occasionally extremely large year classes have been observed for herring, capelin, blue whiting and horse mackerel, but not for mackerel to the same degree. However, there are differences in the knowledge level between species, which makes it difficult to draw a conclusion on this question. Furthermore, the degree to which recruitment variability is captured in the assessment data depends on the metholology applied and the quality of the input data. For mackerel there are some challenges with the available data that impact the quality of the assessment (Simmonds et al., 2010) and likely underestimates recruitment variation. Furthermore fishery-independent observations of mackerel stock size are only made every third year, which limits inferences about interannual variation in recruitment.

The four large pelagic species considered differ in their habitat requirements and tolerance as well as the extent of long distance migrations. Temperature and dissolved oxygen concentration control spatial distribution and accessibility to feeding grounds and are important factors for albacore spatial distribution (Table 1). Bluefin tuna spatial movements and distribution are environmentally, but also behaviourally, driven, with effects of population density possibly being important as well. Oceanographic conditions and in particular temperature plays a role for spawning habitat of blue marlin and the general horizontal and vertical distribution. For swordfish it is the Gulf Stream that influences larval dispersal and spatial distribution.

6.2 Communalities and differences in the trophic roles of pelagic species across the North Altantic

Based on the literature review, the trophic roles and controls of the studied pelagic species were determined (Table 1). In the trophic role classification, top-down effects of a species correspond to documented situations where abundance time-trends lead to detectable trends in the opposite directions in their preys, while for a bottom-up effect of a species similar time-trends in their predators have been found. If a pelagic species exerted both a top- down effect on its preys and a bottom-up effect on its predators this suggests an overall middle-out food web control. Next, for all pelagic species we summarised the published evidence for their population abundance to be controlled by prey availability, called resource controlled, or predation pressure, called predator controlled.

Due to its high abundance, broad distribution and position in the food web, herring is a key species in food webs throughout the North Atlantic. Herring are opportunistic zooplankton feeders focusing on the different dominant zooplankton species present. They also feed on ichthyoplankton and are cannibals (Holst, 1992). Mackerel larvae and juveniles are size- and species-selective feeders while adult mackerel are more opportunistic. Apart from disparate studies, the trophic role of blue whiting is poorly defined. However, mackerel, herring and blue whiting might be strong competitors in certain areas, such as the Norwegian Sea (Prokopchuk and Sentyabov, 2006; Langoy et al., 2012) where predation by these stocks appears to be responsible for the observed strong zooplankton reduction (Huse et al., 2012). In this area there are indications that herring has been resource controlled in recent years via impacts on length growth (Huse et al., 2012). In certain ecosystems and seasons, herring therefore exert a top-down effect on their prey, but in others they can exert a bottom-up effect on their predators (see tunas below). Mackerel could also exert a bottom-up effect on some of their predators (Nøttestad et al., Submitted). For blue whiting, extensive studies and stomach sampling programmes to examine both the predators and prey of this species would greatly improve our understanding of its dynamics, and its links to the environment and rest of the ecosystem. The currently available evidence points at a possible predation (on juveniles by mackerel, Payne et al., 2012) and competition control of the blue whiting population dynamics (e.g., by capelin, herring and polar cod, Dolgov et al., 2009). Capelin play an important role in local food webs, and both top-down and bottom-up effects have been observed (Skjoldal et al., 1992; Gjøsæter, 1998). They suffer predator control primarily via predation on their larvae. Finally, little is known about the food web role of horse mackerel in spite of it being a locally important prey.

All investigated large pelagic species are more or less opportunistic feeders but due to their different spatial and vertical distributions their diet overlap is small. For example, while albacore is a nocturnal epipelagic feeder, swordfish feed during day and night in mesopelagic layers and hence the two species have different prey species and a very low trophic niche overlap (Pusineri et., 2008). It is currently unknown to what extent albacore might exert local top-down pressure. Given the observed flexibility in observed diet it seems unlikely that albacore are resource controlled. The extensive migrations of bluefin tuna for foraging imply that the predation impact by bluefin tuna on their prey populations is dispersed and seasonal; its magnitudes are not yet well documented but are probably modest to substantial. In contrast, there is evidence for local resource control of bluefin body condition. The diet of swordfish does not include any of the abundant small pelagic species considered here. There is no evidence for any type of food web effect by swordfish. Similarly for blue marlin, for which there is no published evidence for any type of food web effect in the North Atlantic. This may be due to a lack of studies in this area. In the eastern tropical Pacific Ocean

Hunsicker et al. (2012) identified the potential for top-down control of sharks and billfishes on skipjack (*Katsuwonus pelanis*) and yellowfin tunas (*Thunnus albacares*).

6.3 Integrating pelagic species and environmental effects into models

A variety of approaches have been developed to model the impacts of fishing and environmental factors on the population dynamics and spatial distributions of abundant small and widely-distributed large pelagic fish species in the North Atlantic basins including capelin (Tjelmeland and Bogstad, 1998; Huse et al., 2004; Magnusson et al., 2005; Huse and Ellingsen, 2008), herring, mackerel and blue whiting (Utne and Huse, 2012). Below we will discuss some of these modelling approaches with particular relevance for the EURO-BASIN project in more detail.

A number of these models are considering food web relations explicitly. Recently different IBM models for fish and zooplankton were combined with the Norwegian Sea ecosystem model (NORWECOM) for lower trophic levels and nutrient cycling into the NORWECOM.E2E end to end model of the Norwegian Sea ecosystem (Hjøllo et al., 2012; Utne et al., 2012a). Within EURO-BASIN the NORWECOM.E2E will be further developed and expanded geographically to provide an integrated framework for modelling the spatial dynamics of some key stocks including NSSH, blue whiting and mackerel. These further model developments will take into account adaptive foraging behaviour of predators to spatial variations in prey abundance, resulting species interactions and have a closed lifecycle (Huse and Ellingsen, 2008).

The Spatial Ecosystem and Population Dynamics Model (SEAPODYM) which has been parameterised for albacore in the South Pacific (Lehodey et al., 2008; Senina et al., 2008) will be applied to the North Atlantic population. There is little evidence to suggest that the main biological characteristics of albacore (physiology and environmental preferences, lifespan, growth, spawning and feeding behaviour) vary significantly among oceans, and the South Pacific and the North Atlantic albacore stocks are very similar in terms of biological productivity when considering the levels of catch and catch rates. Therefore a first simulation will use the existing parameterisation achieved in the Pacific to test the robustness of the model. Then an optimisation experiment will be conducted with fishing data from north Atlantic fisheries (catch and size frequencies). The model will be validated by evaluating its skill in predicting spatio-temporal changes in the various albacore fisheries over the last fifty years. Further, since the feeding habitat is defined based on accessibility to diverse prey functional groups (Lehodey et al., 2010a), the model predicts also the diet by age and its spatio-temporal variability. These predictions will be compared to the information collected at sea (e.g., Lezama-Ochoa et al., 2010). Finally, climate change impacts on albacore population will be explored using environmental forcing produced by IPCC climate models (Lehodey et al., 2010b).

The foraging and spawning migrations of albacore and bluefin tuna have several implications for the fisheries management of both stocks. First, many of the migrations involve movements across stock management boundaries, and rates of migration across the stock boundary can be high. For example, as many as 60% of sampled juvenile bluefin tuna in west Atlantic foraging areas were diagnosed as having been born in the Mediterranean Sea (Rooker et al., 2008). These movements and contributions to neighbouring stock dynamics and fisheries need to be incorporated into stock assessment models and fisheries management policies. Secondly, the possibility that some bluefin tuna do not spawn in some years implies that reproductive potential might vary among years, even if the spawner biomass or its age/size composition does not. IBM approaches should help to identify the link between spawning potential and environmental conditions and provide a way to introduce additional uncertainty to stock-recruitment relationships and models of stock dynamics. New modelling for the migratory behaviour of bluefin tuna will be developed to simulate migrations of adult tuna between spawning and feeding areas. A detailed description of the size-specific food and temperature requirements of individual tunas and the coupling with available physical and mid trophic layer models will allow disentangling proximate and ultimate causes of bluefin tuna migrations in the North Atlantic. Predation impacts of bluefin tuna in the simulated habitats will be predicted using a size-structured mass-balanced model (Andersen and Pedersen, 2010) to assess potential top-down effects on the local fish community.

For blue whiting a spatially-explicit closed life-history model driven by physical and biological output from coupled physical/biological ecosystem models will be developed. The population model will be based on the discrete-time length-structured approach by Andrews et al. (2006) in which increase in body size occurs through progression along a set of length-classes obtained from a linear transformation of von Bertalanffy growth. In space, the population will be distributed over a discrete matrix of cells. The spatial transport of pelagic eggs and larvae using a method developed for zooplankton in which transport occurs at discrete transport events (Speirs et al. 2005; 2006). At a transport event the time-dependent proportion of the population moving between cells is derived in advance from Lagrangian tracking from flow fields output from the physical models developed in Euro-Basin. Adult movement will be based on a combination of diffusive movement and seasonal active movements to the known spawning areas along the continental shelf edge. The computational efficiency of the SU discrete-time-discrete-space approach permits the practical exploration of variety of different movement rules (Andrews et al., 2006).

7 Conclusions

This review showed that there are generally few differences in distribution patterns and life history parameters between stocks of the same species of small pelagics on either side of the North Atlantic, though migration distances and the overal spatial extents are much larger on the eastern side. In contrast there are bigger differences among species. For example, two small pelagic species might use broadly the same area for spawning, though at different times of the year, as is the case for mackerel and blue whiting in the NE Atlantic. Not all reviewed species have been studied with the same intensity so that there are a number of knowledge gaps, in particular with respect to structuring and critical environmental conditions for certain small pelagics and most of the large pelagic species. A striking difference between the small and large pelagic species reviewed here is that the former can be strong food competitors at times and excert both top-down and bottom-up control, while the later seem to occupy more separate trophic niches and if they are controlling food webs, this control is limited in space and time. Finally, the review demonstrated that the information required to apply the new more holistic spatially explicit modelling approaches outlined above is sufficient except for the identified knowledge gaps, which are currently being addressed in the Euro-Basin project.

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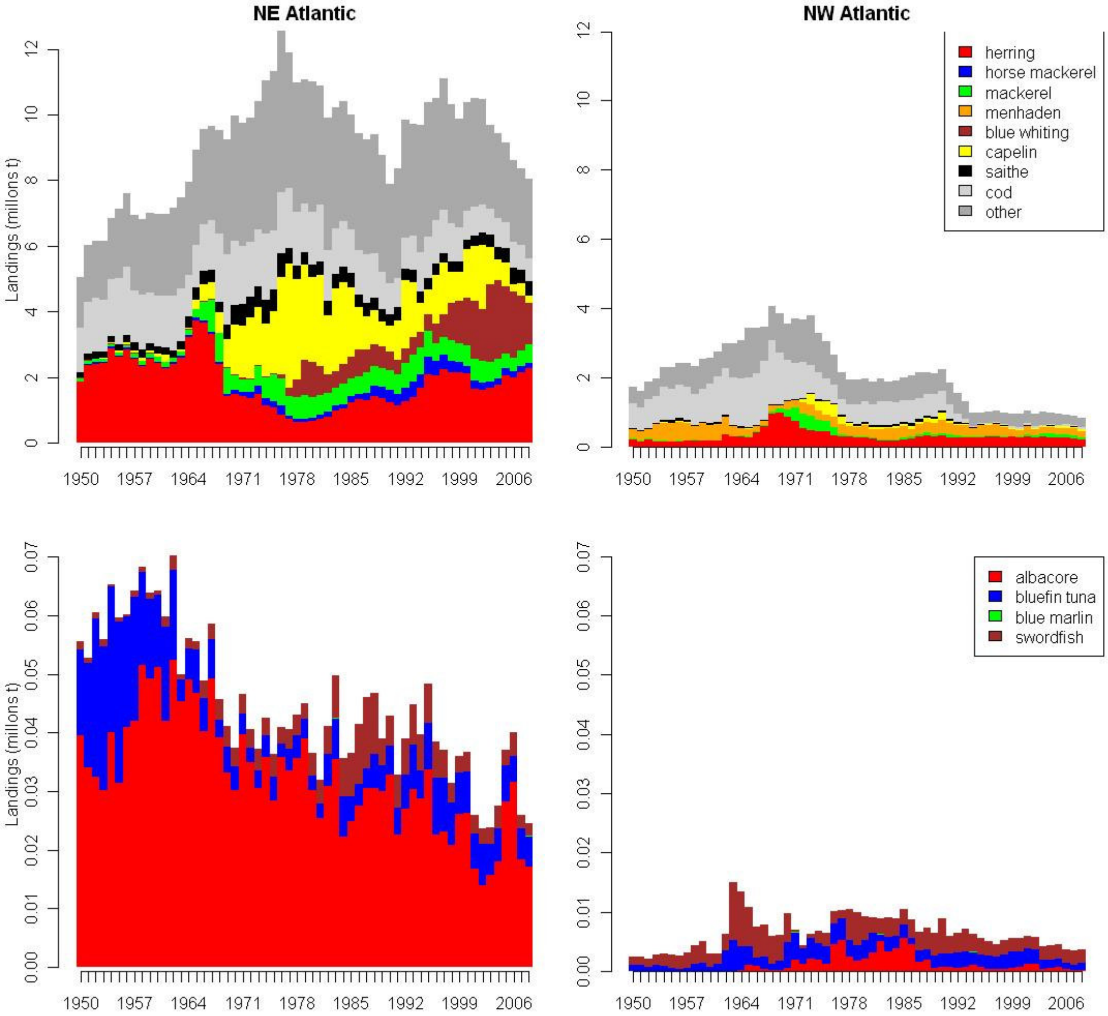
Figure legends

Figure 1. International fisheries landings in NE Atlantic (FAO area 21) and NW Atlantic (FAO area 27) from FAO (2010). FAO area 27 covers from 90°W to 42°W and from the North pole down to 35° S; FAO area 21 is from 42° E to 68.5° E and from the pole down 42° S.

Figure 2. Map of important physical oceanographic features in North Atlantic, with coloured arrows illustrating major currents: Gulf Stream, North Atlantic Current (NAC); Continetal Shelf Current (CSC); Eastern Greenland Current (EGC); Labrador Current (LC); Western Greenland Current (WGC); Subarctic Front (SAF).

Figure 3. Schematic map of feeding areas of adult parts of key pelagic fish species in the North Atlantic.


NE Atlantic
NW Atlantic
Landings (millons t)
0
2
4
6
8
10
12
herring
horse mackerel
mackerel
menhaden
blue whiting
capelin
saithe
cod
other
1950
1957
1964
1971
1978
1985
1992
1999
2006
Landings (millons t)
0.00
0.01
0.02
0.03
0.04
0.05
0.06
0.07
albacore
bluefin tuna
blue marlin
swordfish

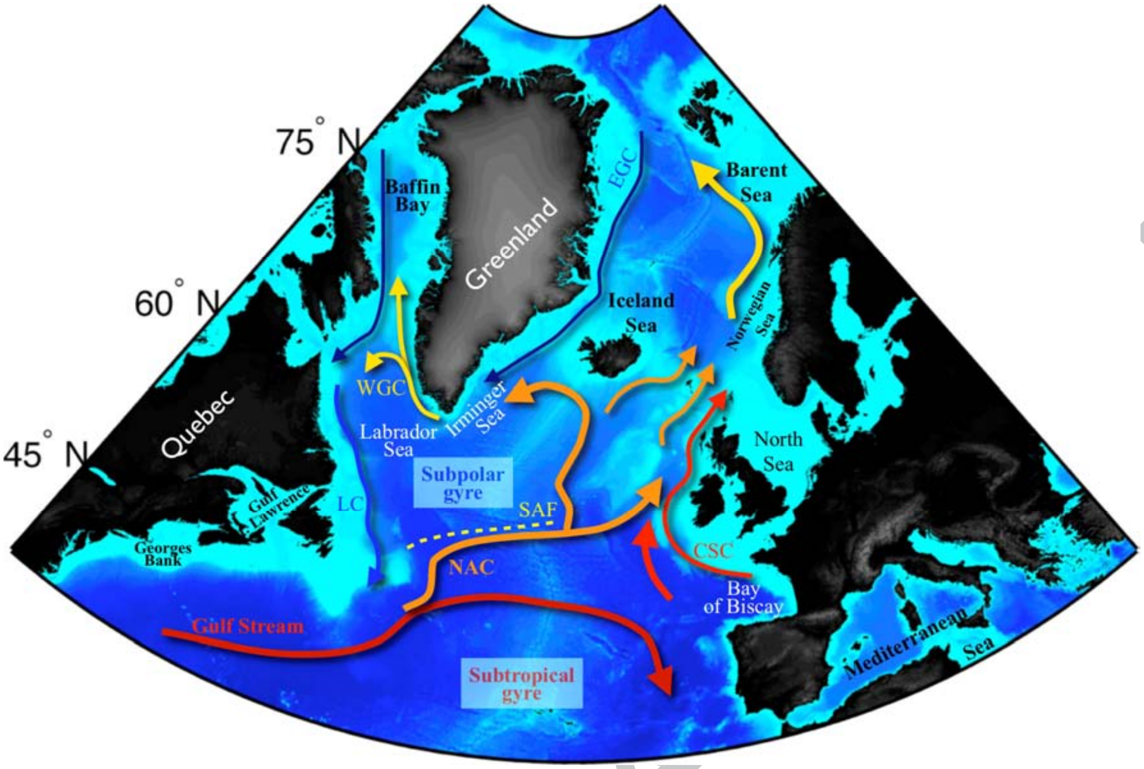
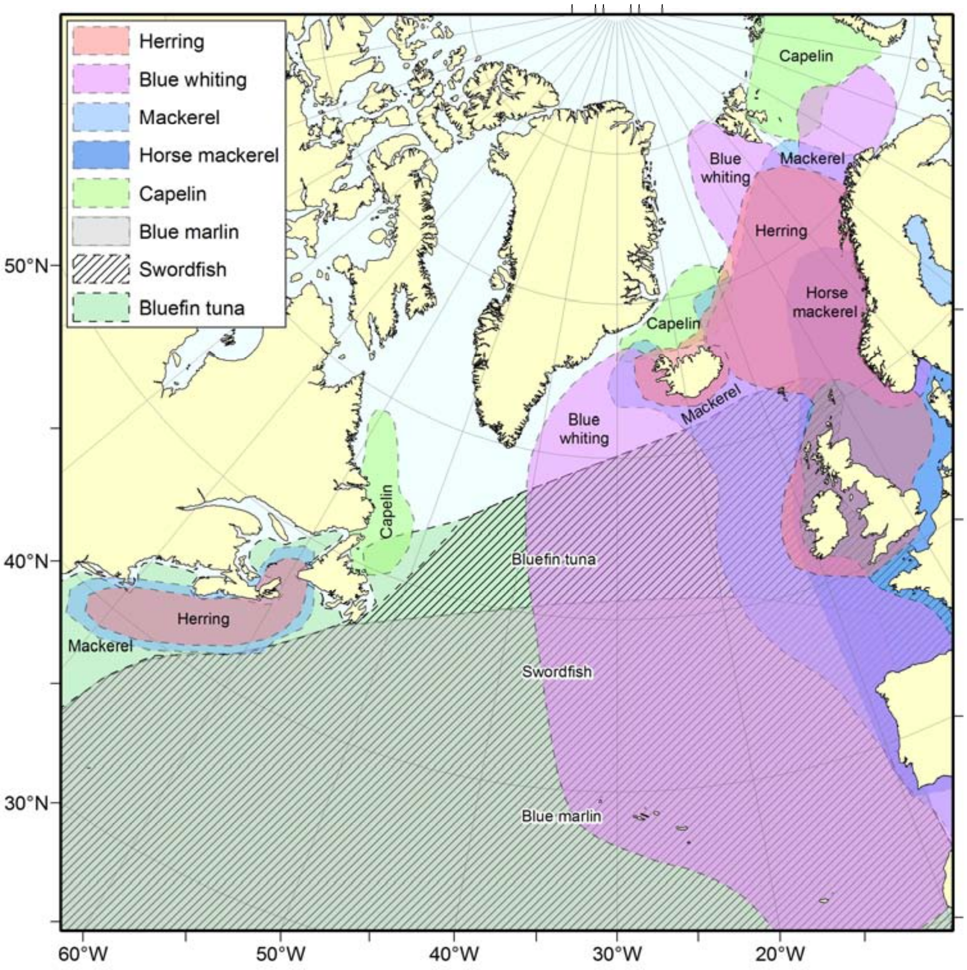

75° N
60° N
45° N
Baffin Bay
Greenland
EGC
Barent Sea
Iceland Sea
Norwegian Sea
Quebec
WGC
Labrador Sea
Irminger Sea
North Sea
Subpolar gyre
Gulf Lawrence
LC
SAF
Georges Bank
NAC
CSC
Bay of Biscay
Gulf Stream
Subtropical gyre
Mediterranean Sea

Figure 2



Herring
Blue whiting
Mackerel
Horse mackerel
Capelin
Blue marlin
Swordfish
Bluefin tuna
Capelin
Blue whiting
Mackerel
Herring
Horse mackerel
Capelin
Blue whiting
Mackerel
Capelin
Bluefin tuna
Herring
Mackerel
Swordfish
Blue marlin
50°N
40°N
30°N
60°W
50°W
40°W
30°W
20°W

Figure 3

Table 1. Summary of current knowledge of environmental and biological drivers for life history and spatial distribution as well as food web roles and interactions for selected small and large pelagic species in the North West and North East Atlantic (NEA). Major knowledge gaps are identified.

Environmental drivers: temperature (T), salinity (S), large scale oceanographic pattern (O) (incl. NAO, wind, turbulence), oxygen (O2).

Biological drivers: density dependent (D), body condition/prey availability (B), predation pressure (P), unknown (?).

Food web role/control of species: top-down effect of species on its prey; bottom-up effect of species on its predators; resource or predator impact on species population dynamics; competition; ? suspected.

Species	Stock structure	Migration/distribution changes	Spawning timing	Maturity & fecundity	Recruitment/larval survival	Growth	Food web role/control	Differences between NE & NW Atlantic	Important knowledge gaps
herring	several stocks in NE & NW Atlantic	D, T, P	T, D	B	T, O, P	D, T	top-down & bottom-up; resource controlled; competition with mackerel	oceanic feeding and overwintering only in NEA	Env. and stock size impact on migration, recruitment processes; top-down pressure.
mackerel	uncertain - probably weak structure in NE & NW Atlantic	T	T	?	B, O	D, T	bottom-up?; competition with herring	oceanic feeding only in NEA	Env. and stock size impact on migration. Stock structure
capelin	several populations in NE & NW Atlantic	T, O	?	D	T, O, P	D, T, B, O	top-down & bottom-up; predator controlled	higher fecundity at age/length in NW; NE deep-water and NW beach spawning	Recruitment processes, response to climate changes, food web role
blue whiting	uncertain in NE Atlantic	O, D	T, S	?	P	D, T	predator control; competition with capelin, herring?	mainly in NEA	stock structure, food web role, dynamics of southern part/population
horse mackerel	several stocks in NE Atlantic	O, T	T	?	T, O	D, B	competition with mackerel, blue whiting, sardine?	only in NEA	food web role
albacore	single population in N Atlantic	T, O, O2	T	?	O	T	none	single population	food web impact
bluefin tuna	stocks in E & W Atlantic	D, O, B	T?	B?	?	?	top-down?, resource controlled?	maturation, abundance	spawning areas, food web impact
sword-fish	possibly NE and NW population	O	T	?	?	?	none	stronger effects of ocean currents on distribution in NWA	NE-NW Atlantic mixing uncertain
blue marlin	single population in Atlantic	O2, T	?	?	?	B?	none	single population	Migration patterns, spawning areas, juvenile distribution and ecology