Response to Changing Oceanography in the Dove Time Series: a Northumberland Plankton Community Study

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Abstract

The Dove Time Series is a plankton monitoring station in the Northumberland coastal sea which has been sampled since 1969. Over the 20th century, major changes have occurred in the North Sea plankton which have in part correlated with oscillation in atmospheric mass over the Northern Hemisphere, the North Atlantic Oscillation (NAO). Westerly winds when the NAO is positive phase block northern low pressure systems and transport warm Atlantic water into the North Sea extending stratification, leading to greater phytoplankton biomass. Phytoplankton biomass in the central North Sea reached a sustained higher level after 1985. Phytoplankton, zooplankton and ichthyoplankton datasets were created or extended from the Dove Time Series to study the effect of oceanographic change at this location. There was a change to a high abundance community 10 years later, in 1995. The most important predictor of phytoplankton abundance was not the NAO index, but the Atlantic Meridional Oscillation (AMO), which exhibits 60-100 year and subordinate 11 and 14 year periodicity, describing a deviation from the long term sea surface temperature (SST) mean in the North Atlantic. Phytoplankton periodicity partly matched the 14 year period in the AMO, which correlates with a feedback mechanism of westerly versus northerly wind in the North Atlantic, regulating ocean-atmosphere heat flux. Zooplankton abundance was predicted by SST and ratio of maximum to minimum abundance by phytoplankton/AMO. Oceanographic conditions that were contemporary with the state of the AMO anomaly after 1995 promoted higher spring phytoplankton abundance and neritic copepod abundance peaks. Ichthyoplankton variability was not synchronous with these lower order changes, probably as a result of different effects on adult fish. The cyclical nature of the AMO means both low and high biomass communities observed in the Dove Time Series are part of one regime.

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Chapter 1. A Description of Oceanographic Change in the North Sea and the Responses of the Plankton

1.1 The North Atlantic, North Sea, North Atlantic Oscillation, and the Atlantic Multidecadal Oscillation

The North Atlantic Gyre is a circulation system that transports surface water clockwise, transferring heat from the western North Atlantic to the eastern North Atlantic along the northern boundary of the gyre (Thornalley *et al*, 2011). The Gulf Stream is the current that runs from the American coastline on the western North Atlantic Atlantic to approximately 55°N, at which point its northern extension, the North Atlantic Current (NAC; Taylor, 1995), transports warm water across the North Atlantic to Europe (NAC). The latitude of the north wall of the Gulf Stream has correlated with statistically significantly less frequent cyclone formation close to the United Kingdom (Taylor, 1996). The NAC reaches the European shelf, where it splits into currents that travel northwards around Iceland and combines with southward moving water originating in the Barents sea, and a current that proceeds to the Faroe-Shetland Channel (Figure 1.1). Most water that enters the northern North Sea does so through the Faroe-Shetland Channel, exiting through the Norwegian Channel (Figure 1.3). Additionally, water to the south of the Faroe-Shetland channel reaches the shallow coastal margin and joins a coastal current that travels from the west of Scotland through the Pentland Firth and and flows southwards along the NE coast of England (Turrell, 1992; Figure 1.3).

The North Sea is a large sea adjacent to the northwest coast of Europe. It is bordered on the west by the British Isles, to the South by France and the low countries, to the east by Denmark and Norway, and to its North is the Norwegian Sea, and Atlantic Ocean. Its surface area is 750,000km^2 and its total volume is 94000 km^3. The average winter temperature over the whole sea is 6ºC and the average summer temperature is 17ºC. It is relatively shallow versus the Atlantic Ocean with an average depth of 95 metres though along the Norwegian coast the trench depth reaches 700m (Hinrichsen, 2001). There are three regions in the North Sea from north to south; these regions coincide with the three amphidromic points at which tidal amplitude is zero (Dyke, 2007; Figure 1.3). The succession of high tides around these points acts to reinforce an anticlockwise circulation in the North Sea.

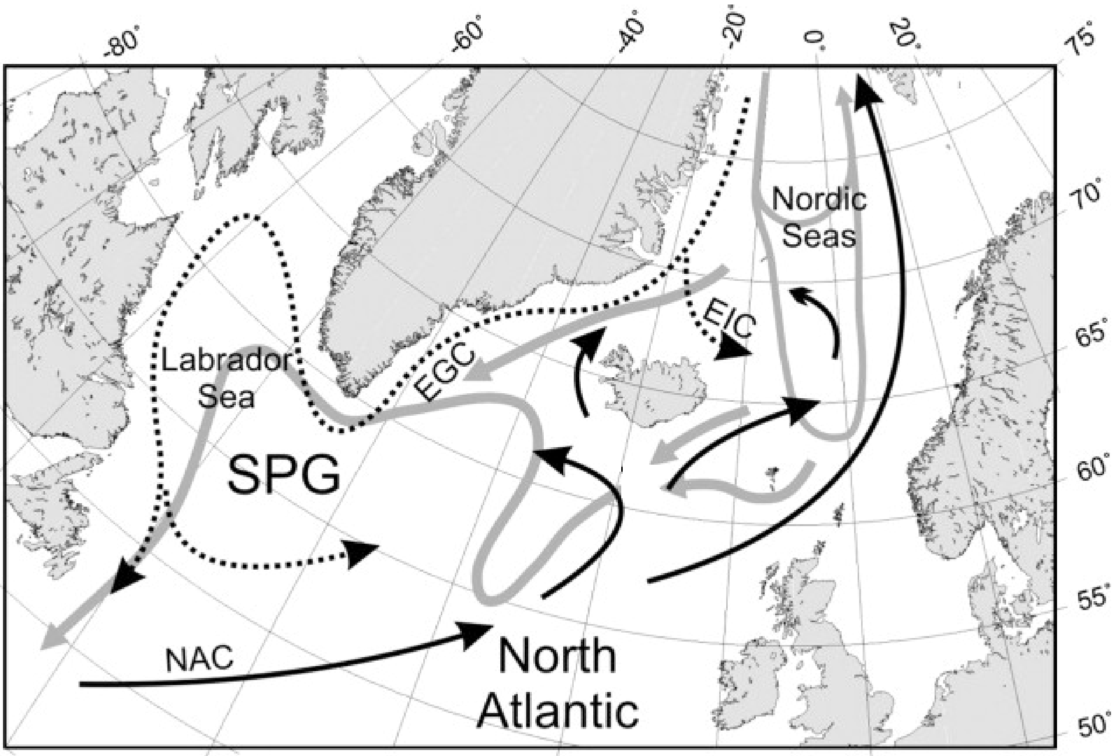


Figure 1.1 – Circulation of the North Atlantic, from Thornalley *et al* (2011). Grey arrows are deep water currents, black arrows are surface currents. SPG: subpolar gyre, NAC: North Atlantic Current, EGC: East Greenland Current, EIC: East Iceland Current.

The northern North Sea is the area between the Shetland Islands on the west, and the Norwegian coast on the east, at 61ºN (IHO, 1953), extending to the easternmost tip of Morayshire in Scotland and the western edge of the Skaggerak (ICES, 2012). This area of the northern North Sea is strongly influenced by inflow of Atlantic water. The Norwegian Trench is the one region of the North Sea with depths in excess of 500m. The northern North Sea is approximately 200 metres deep north of 56°N (Ducrutoy *et al,* 2000) and thermocline formation occurs at a depth of approximately 50 metres (Warrach, 1998).

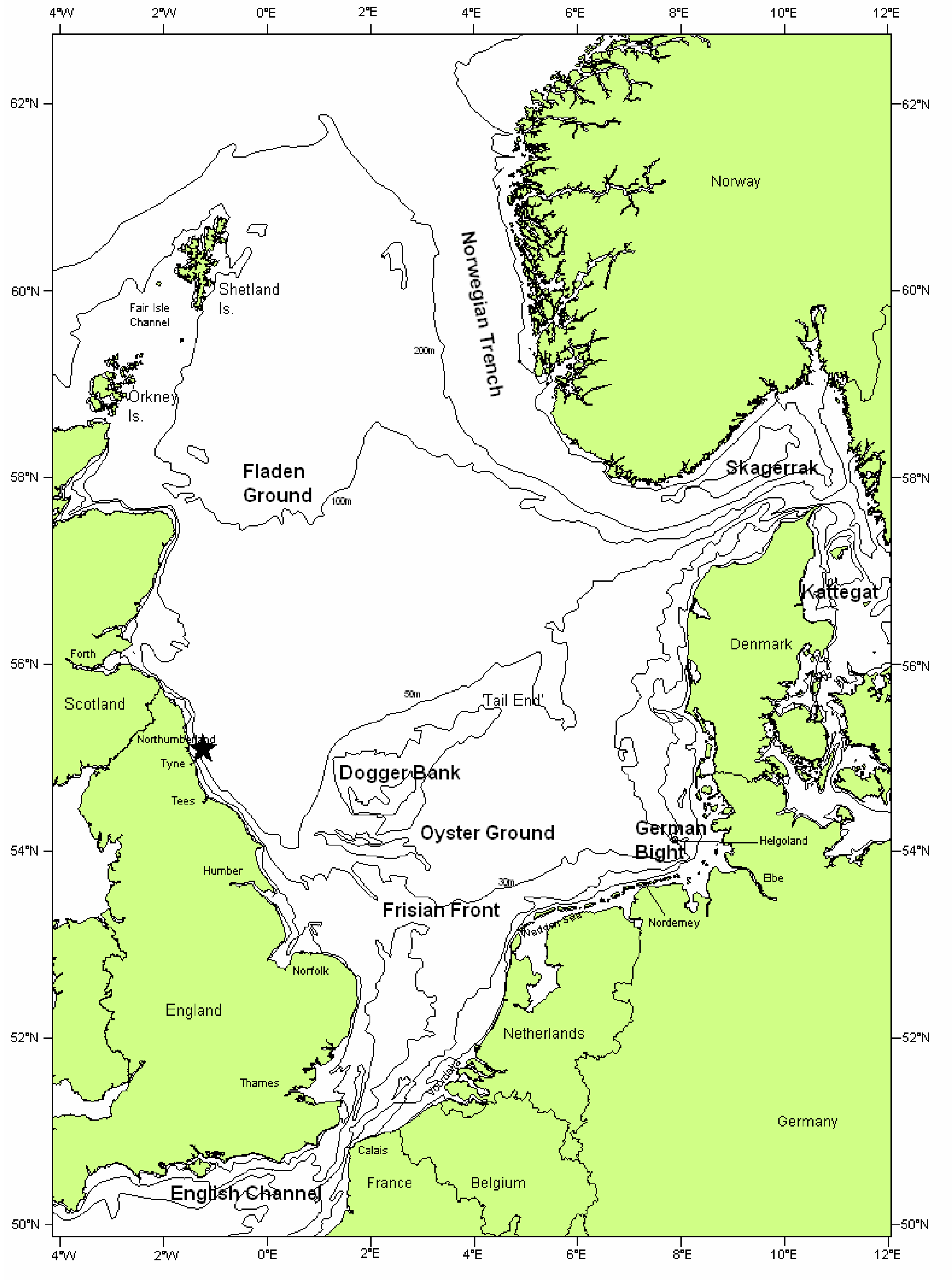


Figure 1.2: Bathymetric map of the North Sea. Dove Time Series location (★) on the Northumberland coast. Map reproduced from Rees *et al* (2007). The outer isobath along the Northumberland coastline is 50m, site is in 54m of water.

In the central part of the North Sea the depth is between 50 and 100 metres

(Figure 1.2), with weak stratification along the coast in the vicinity of the Dove Time Series (DTS) in summer (AWI, 2012). This region is more weakly influenced by the Atlantic Ocean than is the open northern North Sea. Scandinavian snow melt, and the Baltic Sea and its Skaggerak interface with the North Sea, are sources of low salinity water in this area (116km^3 year^{-1} – Ducrutoy *et al,* 2000). This obviously has a strong east to west gradient in increasing salinity until the coastal zones of the UK are reached (Beare *et al,* 2002). Freshwater inputs to the North Sea from the Scottish and eastern English coasts constitute 48 km^3 year^{-1} (Ducrotoy *et al,* 2000). The Dove Time Series (DTS) is situated off the Northumberland coast, United Kingdom, at 55° 07'N 1° 20'W (Figure 1.2), within the coastal waters of the central North Sea. The sampling location is in 54 metres of water, which places it on the edge of an isobath between inshore and offshore water, meaning it is likely to sample at a point with mixed tidal and stratification influence on hydrodynamics (OSPAR, 2000). The southern edge of the central North Sea lies along the Flamborough Front, on the Yorkshire coast of the United Kingdom (Hill *et al,* 1993) – this extends to Helgoland in the German coastal sea (Ducrotoy *et al,* 2000). In summer the regions of the North Sea on either side of this front are thermodynamically separated from each other (OSPAR, 2000).

The southern North Sea is the region along the coasts of France, Belgium, the Netherlands and Germany that is the most shallow part (a few tens of metres: Rees *et al,* 2007) and as a result does not experience widespread thermal stratification of the water column in summer (Leterme *et al,* 2006). Salinity induced stratification in the vicinity of river mouths is common (De Kok, 1996). The English Channel is the main source of marine water ingress, while substantial freshwater flows from the large river systems in the area contribute a large proportion of nutrients to the region. The freshwater inputs to the southern North Sea are approximately 123 km^3 year^{-1} , 2-3 times that of the western central North Sea (Ducrutoy *et al,* 2000). Large river systems export yellow substance (Warnock *et al,* 1999), which may reduce light attenuation and thus limit growth of phytoplankton.

The nutrients in the northern zone are powerfully influenced by the residual transport westward and southward of water from the North Atlantic Ocean. Approximately twice as much nitrogen, and ~7 times as much phosphorous are transported into the North Sea via the Atlantic than by rivers (OSPAR, 2000). As the coastal current moves southward it takes on additional nutrients from river systems along the Scottish and northern English coasts. Additionally as this water mass is kept entrained along the coast, there is less possibility of these nutrients being wholly dispersed into the open North Sea, due to the coastal front dynamics (Pingree and Griffiths, 1978). In the southern zone, the large river systems along the German, French and Low Countries coastlines contribute the majority of the nutrients to the sea (OSPAR, 2000). This leads to problematic eutrophication responses in the southern zone along the continental coastline (e.g. De Leeuw *et al,* 2003), though offshore seas in the southern zone are not considered eutrophic. Through its shallowness, the southern zone remains mostly euphotic regardless of stratification, but is sensitive to mixing induced turbidity (Gayer *et al,* 2006). The northern zone has sufficient depth for discrete euphotic and aphotic zones, remaining clearer than the southern zone as a result, although suspended particulate matter remains a factor in inshore waters with tidal influence (Gayer *et al,* 2006).

The inshore waters bordering the British coastline of the western central North Sea is influenced by the tides (AWI, 2012). Stratification below Sverdrup's critical depth occurs approximately 10km from the shoreline, in the vicinity of the Dove Time Series site (Hill *et al,* 1993). This varies with the lunar cycle, and wind driven surface mixing can induce a seaward retreat of this tidal front by a further 10km (Hill, 2005). Wind driven eddies can develop into 25-40km scale phenomena that may straddle the frontal zone and transport water and plankton from within the coastal sea to the outside area otherwise blocked by the frontal barocline (Simpson, 2005). In the Northumberland coast, these eddies exchange water across the tidal front in summer (Brown *et al,* 1999). The Dove Time Series has unfortunately not had temperature and salinity profile data recorded alongside the plankton data, with which to construct density anomaly profiles from temperature and salinity data, which is particularly important given the transitional nature of front formation in the region (Pingree and Griffiths, 1978; AWI, 2012).

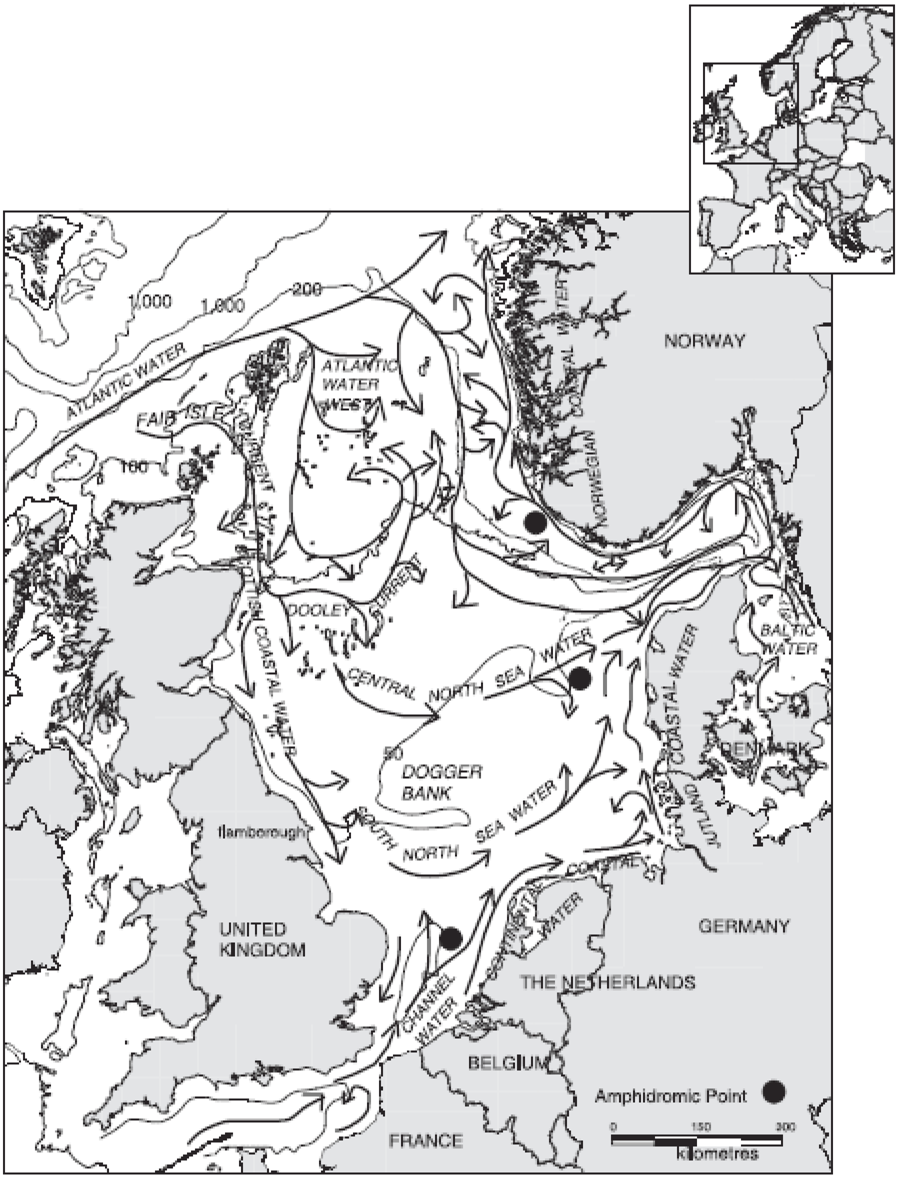


Figure 1.3: Map of the North Sea showing Oceanic inputs and circulation patterns. Amphidromic points where tidal range is zero are marked by black circles. Source: Ducrutoy *et al* (2000).

As described earlier, the circulation in the North Atlantic transports heat from west to east through the North Atlantic Current. The northern extent, or Gulf Stream North Wall (GSNW; Taylor, 1995) affects the European climate, by regulating the penetration of cold weather systems to the north. In two freshwater lakes in England, more northern GSNW promoted earlier stratification (George and Taylor, 1995), indicating covariance with air temperature must occur. The GSNW is correlated with the

North Atlantic Oscillation Index (NAO – Hurrell *et al*, 2003), at a two year lag (Planque and Taylor, 1998). The NAO is the difference in sea level pressure between either Lisbon, Portugal, Ponta Delgada, Azores or Gibraltar and either Stykkisholmur or Reykjavik, Iceland (Hurrell *et al*, 2003; Osborn, 2006; though see NAO derived from hemispheric PCA analysis of sea level pressure – Hurrell, 2012). The Winter NAO is the mean normalised difference between December and March for a given year. Because air flows in opposite directions in cyclonic and anticyclonic systems, positive phase NAO (high pressure) stimulates westerly winds and negative NAO (low pressure) depresses westerlies. The NAO in winter is the time of strongest NAO stimulated winds, due to the tilt of the earth maximising the difference in insolation of the suptropical and subarctic seas. At 12000m altitude these winds reach up to 40m s^{-1} at middle latitudes (Hurrell *et al*, 2003). In periods sustained positive phase NAO, GSNW becomes more northern, and low pressure storm tracks travel to the north of the British Isles (Chelton *et al,* 2004), explaining the finer weather that lead to earlier stratification as observed by George and Taylor (1995). Looking at the effects on plankton, Taylor *et al* (1992) noted that lagging the signal of GSNW with marine plankton abundance did not lead to stronger correlations. This indicates that the key effect of the organisation of the North Atlantic system is the much faster atmospheric signal communicated by the NAO through wind effects on mixing, stratification and air temperature, rather than the transportation of warmer water itself, explaining the lag between GSNW and NAO.

There are actually four climate regimes in the North Atlantic atmosphere: NAO negative, NAO positive, described above; an anticyclonic "blocking" system over Scandinavia and an anticyclonic system off western Europe possibly associated with the mid-Atlantic Ridge, all four occurring on 20-30% of days (Figure 1.4; Hurrel and Deser, 2010). The blocking and ridge systems, recently described, may be more indicative of warm weather in western Europe than the traditional positive winter NAO indicator. Approximately 25% of the variation in sea surface temperature (SST) in the North Sea can be attributed to fluctuations in the NAO index which is correlated with winter-spring westerly winds. Winter flows into the northern North Sea are dependent on westerly wind strength so are strongly correlated with the NAO index. It was in negative phase for much of the 1960s, and was in positive phase from the late 1980s to the 2000s (Hurrell *et al*, 2003).

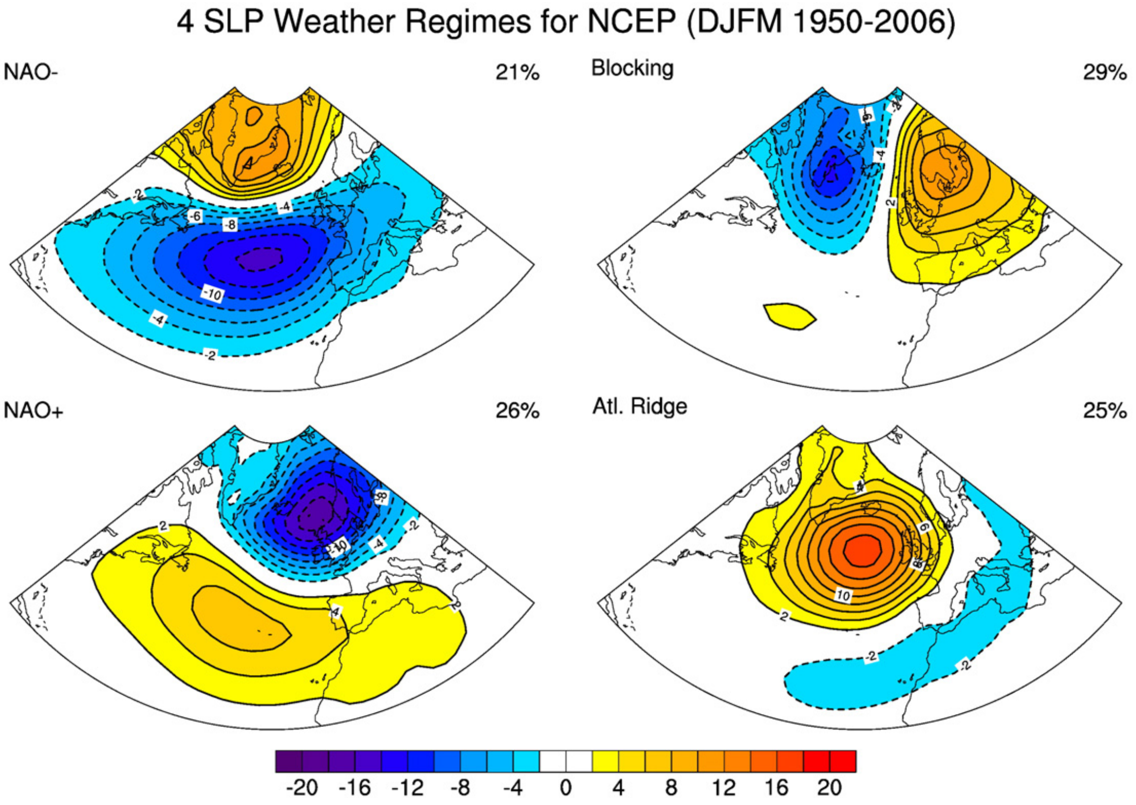


Figure 1.4: Boreal winter (December to March) sea level pressure conditions using daily data. The percentages indicate the frequency of occurrence of a regime of all winter days between 1958 and 2006. From Hurrell and Deser (2009).

There have been two periods in the late 20th and early 21st centuries when unusual deviations from long term average oceanographic conditions have persisted in the Northeast Atlantic, contemporary with persistent negative (1970s) and positive (late 1980s) phases of the NAO. The first of these was an advective process where uncharacteristically fresh water circulated from Iceland, west to the Labrador Coast, into the North Atlantic Current and consequently the North Sea and then towards Greenland. Dickson *et al* (1988) provide a summary of the phenomenon, which was observed from subpolar latitudes to as far south as 41°N. High air pressure over Greenland in the 1960s caused persistent strong northerly wind to cool and freshen the East Greenland (EGC) and East Iceland Currents (EIC). The EIC began to transport icebergs in the 1960s when it had been ice free for the preceding 15 years. The EGC expanded in volume. The water became too fresh to become dense enough to sink and mix with underlying warm saline water, thus preserving the upper 200-300m of water across the Northeast Atlantic from the usual winter mixing processes.

The overlying cold, fresher water spread westwards to the Labrador sea in the early 1970s, where it flowed southwards and then began to transport eastwards across the mid-Atlantic (complicated by the removal of ocean weather stations precisely when they were needed to confirm this to be the case! – Dickson *et al*, 1988). By the mid 1970s the water mass had reached the Faroe-Shetland Channel. An offshoot penetrated the North Sea and began the southward circulation described earlier along the eastern British Isles. The remaining water proceeded northwards along the Norwegian coast and entered the Arctic in 1979. Salinity minima in 1981-2 in the sea to the east of Greenland represent the probable last observation of the signal, though this may have been confounded by coastal mixing processes. This phenomenon was termed the "Great Salinity Anomaly" (GSA) by Dickson *et al,* (1988) and represented over the period of its transit the removal across the North Atlantic of approximately 72 billion tonnes of salt, compared to the preceding long term average.

The second major deviation from long term conditions was initially an advective event in the late 1980s that led to a long period of warm weather in the Northeast Atlantic, sustained by strong westerly winds in winter. The dependence of winter flows to the North Sea on westerly winds and thus the NAO index (Stephens *et al,* 1998) indicated advective input to be the source of the late 1980s temperature anomaly (anomaly used here and throughout as a deviation from a mean). Beginning in 1987, warm January sea surface temperature anomalies on the western and eastern sides of the North Atlantic developed, merging in 1990 (Hansen and Bezdek, 1996). Modelled winter inflow to the North Sea from north of Orkney, Shetland and Norway increased by approximately 0.5 Sverdrup after 1988 (Reid *et al,* 2001). This process succeeded cold anomalies covering 1968 to 1986. In the period from the 1960s to the 1980s, the winter NAO was in negative phase (Hurrel and Deser, 2010), which undoubtedly contributed to the persistence of the cold, fresh upper layer across the North Atlantic manifest as the GSA. The winter NAO phase changed sign in the late 1980s, which strengthened west to east heat transport and circulation (Hurrell, 1995). This lasted until the mid 1990s, when the NAO began to fluctuate between signs (Robson *et al,* 2012a).

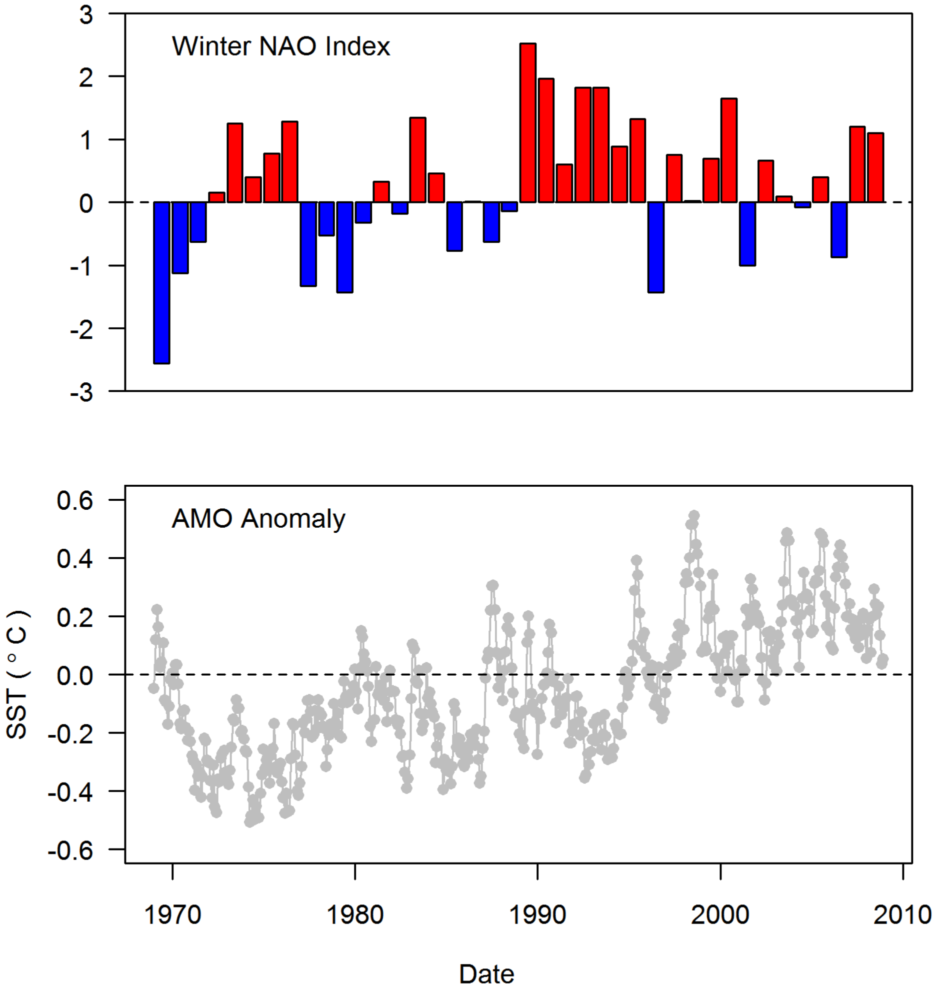


Figure 1.5: The winter NAO index and the AMO anomaly from 1969 to 2008.

The winter of 1995/6 was very cold and with low rainfall (Wilby *et al,* 1997). The Atlantic subpolar gyre (SPG), to the north of the GSNW, warmed by approximately 1°C in 2 years in 1995/6, which was the point at which the prolonged positive phase winter NAO changed to strongly negative and continued to alternate between positive and negative phase after this point (Figure 1.5), the continued warm state of the North Atlantic after this point apparently a result of anomalously strong Atlantic Meridional Overturning Circulation (Robson *et al,* 2012a), which had been brought about by enhanced westerly winds through the positive phase of the NAO in the 1980s (Hurrell, 1995). Wyatt *et al* (2012) demonstrated the NAO be a 9 year lagged atmospheric response to negative SST anomaly across the North Atlantic (Figure 1.5). So the cold

GSA event of the late 1970s represented negative heat flux in the Atlantic Ocean, this heat transferring to the atmosphere, leading to stronger westerlies (Dong and Kelly, 2004), and therefore the positive phase of the NAO in the mid-late 1980s. In this regard, both the GSA and the 1980s warm water event can be considered the oceanic and atmospheric manifestations of the same underlying cyclicity of the Atlantic Multidecadal Oscillation (Dima and Lohmann, 2007; Wyatt *et al,* 2012).

1.2 Phytoplankton in the North Sea and North Atlantic

Phytoplankton is the term for microalgae that inhabit lakes, rivers and the seas. Phytoplankton biomass tends to be dominated by three groups: diatoms, dinoflagellates and microflagellates. The diatoms are obligate autotrophic algae of the class Bacillariophyceae. They are characterised by their utilisation of free silicate (SiO_4^{4-}) to create a permeable barrier between the cell and its environment, called a frustule, the two valves of which are held together by one or more girdle bands (Horner, 2002). They can be radially symmetrical as in the order Centrales or bilaterally symmetrical as in the order Pennales, though there are genera within these orders that superficially appear to be of the opposite symmetry (Round *et al*, 1990). They adopt a wide variety of shapes, from quite simple glass boxes to intricate setose or heavily silicified forms that variously act as flotation aids, arrays for the situation of chloroplasts and grazing defences. Silica frustules diffuse incident light and thus ensure that as far as possible those chloroplasts shaded by the cell and other organelles are able to photosynthesise alongside those in direct path of sunlight. Diatoms can occur as single units common among *Coscinodiscus* spp., or in long colonial chains either held together by interlocking setae as is the case in the genus *Chaetoceros,* or by interlocking tubules as is common among the genus *Thalassiosira*, or by mucilaginous pads as can be seen in *Thalassionema nitszchioides* (Jeffrey *et al*, 1997).

Dinoflagellates are motile unicellular phytoplankters of the order Dinophyceae. They possess two flagellae, one resting in a groove around the cell called a cingulum, and another resting in a perpendicular groove called a sulcus. Their nutrition is divided into autotrophic (such as *Ceratium fusus*, Olseng *et al*, 2002), mixotrophic (such as *Ceratium furca,* Baek *et al*, 2009; and *Dinophysis norvegica,* Carvalho *et al*, 2008) and heterotrophic types (such as the genera *Protoperidinium,* e.g. Naustvoll, 2000, Buskey, 1997, Menden-Deuer *et al,* 2005; and *Fragilidinium,* Jeong *et al*, 1996). Some forms have cellulose plates covering the cell (here termed thecate), while others do not (here termed athecate or naked). Their abundance is generally subordinate to that of diatoms through the year, though they can reach very dense blooms in certain conditions (Smayda and Reynolds, 2001). Often the larger size of dinoflagellates can mean relatively small numbers can constitute high chloropyll concentrations (M. Baptie, pers. obs.). As the dinoflagellates are motile, they are better able to maintain their position in the euphotic zone than are diatoms, and are able to retreat to deeper water to take advantage of newly entrained nutrients. This strategy has in the temperate zone favoured population growth of dinoflagellates in the summer when these traits provide them with an advantage over diatoms (e.g. Margalef, 1958, Holligan and Harbour, 1977, Pingree et al, 1978).

Microflagellates is a loose term to describe small flagellated unicellular algae which variously perform autotrophic or heterotrophic functions in the plankton trophic web. They are generally present in high abundance year round compared to diatoms or dinoflagellates (e.g. Rodriguez *et al,* 2003; Peperzak *et al,* 2000; Skogen *et al,* 2004). Heterotrophic forms capitalise upon the bacterial growth that succeeds the termination of diatom or dinoflagellate blooms and tend to peak in summer, in the microbial loop foodweb (Azam *et al,* 1983), supporting microzooplankton populations (Dolan and Gallegos, 1991). They were not sampled adequately for consideration of their response to changing hydro-meteorological status of the DTS in this study, for reasons that are explained in chapter 2.

Autotrophic phytoplankters use the energy in sunlight and CO_2 to fix carbon by the process called photosynthesis. Nitrogen is a major component of amino acids which are the building blocks of proteins. Phytoplankton absorbs dissolved inorganic nitrogen in the form of nitrate, nitrite and ammonia ions (de Baar, 1994). Convective turnover of water that has spent many years in the deep ocean brings nitrogenous nutrients to surface water in the oceans. In the ocean, this means all nitrate has originated from nitrification of detrital organic matter by bacteria (new production – Dugdale and Goering, 1967). Further post-bloom growth of successive phytoplankton species occurs as a result of ammonia and phosphorous that has been made available by the excretion of zooplankton grazing upon phytoplankton, and associated higher trophic level grazing (regenerated production – Dugdale and Goering, 1967; Pomeroy *et al,* 1963). The post-bloom period in summer in temperate seas is characterised by this quasi-stable system of nutrient uptake by phytoplankton and nutrient replenishment by zooplankton grazing upon phytoplankton and subsequently excreting. As the sea warms and the thermocline deepens, additional new production can occur based upon previously unavailable nutrients, which is what leads to the second bloom in autumn in temperate seas.

In coastal waters the situation is made more complicated by agricultural use of nitrate by humans results in leaching of fertilisers from the soil into rivers, which are then transported to the sea, enriching the nutrients in the coastal margins further. Sewage from urban areas and livestock represents a large source of ammonia that is transported by rivers (OSPAR, 2010a). As a result, these additional sources (and the shorter distance remineralised nutrients must travel to reach the euphotic zone) mean new production accounts for 30% of primary production, rather than approximately 13% in temperate oceans (Eppley and Peterson, 1979).

Adenosine triphosphate is the principal molecule broken down for energy to support metabolic pathways involved in protein and lipid synthesis. Phosphate ions are absorbed in order therefore to generate energy for metabolism. Phosphates used in new production do not have an organic origin, coming from the weathering of apatite rocks (Guidry and Mackenzie, 2000). Acid erosion of rocks by rainfall, or physical erosion of submerged rocks by the movement of water over them releases soluble phosphorous, which can then enter biogeochemical cycles through uptake by plants, consumption of those plants by animals, excretion and death of those animals and so on. This is washed into the sea by rivers, introduced by rainfall, or slowly introduced by the disturbance of sediments and erosion of exposed rocks in the sea (Froelich *et al,* 1982). In some coastal waters with high N loads, phytoplankton growth is P-limited (Harrison et al, 1990).

In addition to N and P nutrients, diatoms also require silicate. This is provided by input from rivers, as well as volcanic conversion of carbonate sediments to silicates (DeMaster, 1981). During the year, some silicate in frustules is released through dissolution after cells die and some through release of non-frustule silicate during degradation of cells by bacteria (Bhattacharyya and Volcani, 1980). Experiments in the open ocean or on deck with iron enrichment have suggested that particularly in areas with high nitrate and low chlorophyll concentration that this trace metal is an important and limiting element in phytoplankton metabolism (e.g. Abraham *et al,* 2000). Iron is required to catalyse chlorophyll-*a* synthesis, and several nitrogen reduction enzymes (de Baar, 1994 and references therein). The eruption of the Icelandic volcano Eyjafjallajökull in 2010 lead to enhanced nutrient uptake suggestive of a plankton response to the ash deposition at sea (Achterberg *et al*, 2013).

Sunlight of course is the ultimate energy source for photosynthesis, and in coastal zones where rivers and tidal stirring maintain levels of turbidity higher than in seasonally stratified offshore waters, cells can be light limited before the nutrient supplies in the vicinity of the population can be exhausted (e.g. Irigoien and Castel, 1997). In extreme circumstances cells can be concentrated to such an extent that light limitation is caused by the shading of cells by other cells (e.g. Morin *et al,* 1999).

Temperature is a relatively minor factor in its effects upon phytoplankton physiology, by virtue of its narrow range of values compared to nutrients or light availability. Temperature can vary by perhaps one order of magnitude and blooms can occur at temperatures approaching freezing, due to inhibited grazing (Townsend *et al,* 1994). However, temperature has increased across the world's seas over the last century (IPCC, 2007) and therefore has potential to have an effect upon plankton that is major, if not direct. Warming seas are indicative of the combination of warmer air temperature and residual solar warming of seawater carrying over from one year to the next due to its latent heat capacity. Each year, insolation energy required to thermodynamically separate the upper layer of the sea from underneath diminishes. The effect is to promote earlier stratification of the sea, lengthening the part of the year in which phytoplankton can be net producers of carbon (OSPAR, 2010b). This alters the nutrient dynamics in a number of ways. Earlier stratification may decouple seasonal cycles of herbivorous zooplankton from the seasonal cycles of phytoplankton (Mackas *et al*, 2007), or inhibit phytoplankton population growth by promoting greater zooplankton abundance (Oviatt *et al,* 2002). This then potentially continues to propagate upwards in the food web, altering biomass at all trophic levels (e.g. Aebischer *et al,* 1990; Frank *et al,* 2005; Möllmann *et al* 2008). This may upset the balance of overwintering versus non-overwintering zooplankton (Dupuis and Hahn, 2008; Ji *et al,* 2010).

In shelf seas of the temperate North Atlantic, plankton groups cycle according to the supply and exhaustion of nutrients, during times of suspension in the euphotic zone. Winter is the period of the year in which nutrients are made soluble in the water column, ready to be used up by phytoplankton in the coming year. For silicates and phosphates, this is ultimately an inorganic process (though one with potential to include biological steps, such as zooplankton excretion – Pomeroy *et al,* 1963). In coastal waters, rivers are the main source of these nutrients. The atmosphere additionally supplies coastal waters with nutrients via rainfall, snowfall and wind transported particulate matter. Nitrates as described earlier originate in the nitrification of detrital organic matter by bacteria in the aphotic zone, and in sediments (Trimmer *et al*, 1999). Replenishment occurs as a combination of local nitrification of DOM, atmospheric inputs and horizontal transport into the area in question by residual current flows, originating in this case in the Northeast Atlantic Ocean (OSPAR, 2000).

All of these nutrients are variously important in structural or metabolic roles, however the key component missing from the system in the early winter, is sufficient light to allow rates of growth to utilise the available nutrients. Diatoms are negatively buoyant, hence the many evolutionary developments to retard the process of sinking. They require to remain in suspension in the euphotic zone. This zone is variable in depth and is dependent upon the clarity of the water. In the North Sea, this depth is approximately 10-20 metres depth (Olesen and Lundsgaard, 1995; Aarup, 2002; Gazeau *et al,* 2004). In order for this to happen, the phytoplankton must become separated from the aphotic zone by a density gradient, and this separation must occur above the critical depth at which photosynthesis production gains exceed respiration losses (Sverdrup, 1953). Usually this occurs as a result of warming, but in coastal waters there is also the possibility of haloclines, and of tidal stirring disrupting the formation of a stable thermocline, and in these conditions the spring bloom may be brought forward, delayed, or it may not occur at all. In the central North Sea a spring bloom does occur, and production near the DTS site peaks in May-June (Joint and Pomroy, 1993).

Sea density is a function of temperature, pressure and salinity (Pond and Pickard, 1983). Fresher water is less dense than saline water, and colder water is more dense than warmer water, so the combination of salinity, temperature and depth determines density. In winter, high mixing combined with low light attenuation limits algal growth rate so abundance remains low. In spring, the warming effect of sunlight begins to induce differential warming of the upper zone compared to deeper water, causing a density gradient to form. Rainfall and snow melt can mean a halocline can develop before a thermocline, leading to an earlier spring bloom (Tett *et al,* 1986). By mid spring stratification is sufficient to divide the water column into two isolated mixed zones – an initially shallow upper mixed layer (Joint and Pomroy, 1993). In the stratified parts of the North Sea this reaches approximately 30m (Becker, 1981, in Richardson and Pederson, 1998) to 50m (Warrach, 1998). In shallower coastal waters, it can be closer to 5m depth, though this is usually the case with strong salinity or tidal influences on stratification (M. Baptie, pers. obs.). This depth is variously defined as that at which temperature is 0.2ºC (de Boyer Montegut *et al,* 2004), 0.5ºC (Levitus, 1982) or 0.8ºC (Kara *et al,* 2000) colder than at the surface, or where density anomaly (σ_T) is 0.125 lower than at surface (Levitus, 1982).

As small-sized, r-strategist diatom cells are capable of growing at the fastest rate in the initially dim and turbulent conditions in late winter to early spring, because of their high photosynthesis to respiration efficiency (Tett, 1990), it tends to be these groups that constitute the first peak in chlorophyll. Initial spring bloom phytoplankton populations are relatively shielded from copepod grazing as early moulting adults use more winter body reserves to reproduce rather than grazing on phytoplankton (Fransz and Giezkes, 1984), and low temperature inhibits zooplankton activity. Re-suspended dormant cysts from the previous year of predatory phytoplankton (such as *Polykrikos* and *Protoperidinium*) return to vegetative action, and zooplankton begin to feed upon the abundant supply of phytoplankton (Nehring, 1996). As the combined negative factors of diminishing available nutrient concentration above the thermocline, and increasing grazing pressure with zooplankton population growth, reach a critical point, the diatom blooms rapidly collapse. The balance of nutrients available slows the rate of one or more cellular processes to an extent that the community cannot replenish losses to grazing. Following the first spring bloom, the upper mixed layer enters a state where the production lost by zooplankton grazing upon phytoplankton is balanced by regenerated production from the nutrients liberated from zooplankton excretion. Mineralisation of phytoplankton and zooplankton excreta that sink below the thermocline continues through summer, but further exponential growth does not occur until the density gradient deepens, usually because of the latent warming of surface seas. By autumn, light is decreasing and so the bloom does not tend to match that of the spring bloom in its magnitude.

At this point two forms of phytoplankton are observed to dominate. One is high aspect ratio, large diatoms (e.g. *Guinardia* types) and the other is larger, motile dinoflagellates (such as *Ceratium* spp.). These larger phytoplankton grow because their large size and low surface area to volume ratio means they are able to photosynthesise effectively, resist sinking, and resist grazing (Reynolds, 1996). Additionally, the lower surface area to volume ratio, combined with colonial chain growth, increases drag and decreases sinking. Motile dinoflagellates are also able to migrate to both access untapped nutrient supplies below the 1% light attenuation depth, and to avoid photosynthetic quenching which can occur in summer when water is at its clearest (Long *et al*, 1994).

Time and sunlight begin to dictate the rates of growth of phytoplankton – as the sea begins to cool once more, the pycnocline that has held the upper mixed layer separate from the lower mixed layer begins to weaken. This accelerates sinking, and thus dilutes the upper mixed layer of its particles. In inshore seas, the weaker insolation leads to increased wind and tidal dominance in determining water column structure. Herbivorous zooplankton populations decline, and their predators begin to curtail their own reproduction, in order to focus energy on maintenance through the lean winter months (Verity and Smetacek, 1996). Those forms able to encyst or form resting cells do so and enter the sediments (Reid, 1978). Nutrient concentrations begin to rise, as phytoplankton become light limited, leaving bacteria to recycle detrital organic matter. So ends the year, and as poorer weather becomes the norm, the process of weathering, mixing and precipitation begins once more to replenish nutrients which will be used in the subsequent year (Nixon, 1982).

As a consequence of changing climate in the North Sea, the phytoplankton community has changed considerably in the last half century, and this is viewed against a context of potentially major change in phytoplankton globally (Boyce *et al*, 2010; although see criticisms by McQuatters-Gollop *et al*, 2011; Mackas, 2011; Rykaczewski and Dunne, 2011). Contrary to Boyce *et al,* (2010), phytoplankton biomass in the North Sea has been increasing since 1958, but the constituents of biomass have changed, with greater effects in the northern North Sea than further south. In the northern North Sea, diatom biomass decreased by 20% in the period 1958 to 2002, while dinoflagellate biomass increased by 15%; no change was observed in central (covering the Dove site) and southern parts of the North Sea. These changes were correlated with warming sea surface temperature (Leterme *et al*, 2006).

While phytoplankton growth is dependent on the requisite nutrients, for the most part the long term plankton surveillance programmes in the North Sea and North Atlantic (e.g. Continuous Plankton Recorder, CPR; Colebrook, 1979) do not have simultaneously sampled nutrient data at their disposal. In any case, no trends in nutrients were observed in the central North Sea between 1955 and 1993 by ERSEM hindcasts (European Regional Seas Ecosystem Model; Pätsch and Radach, 1997), and no increases have been observed subsequent to this period in the southern or northern regions of the North Sea (Skogen *et al,* 2009; Grizzetti *et al,* 2011). Attention has therefore focused on the physical trends, revealing strong response of plankton to the warming of the sea that has occurred over the last century. Phytoplankton colour index (PCI; Batten *et al,* 2003) values were at local minima during the proposed transit dates of the GSA (Edwards *et al*, 2001). Change in biomass moved abruptly higher in the North Sea following a reorganisation of the community in the late 1980s. During the late 80s warm water event, the response of phytoplankton was reflected in phytoplankton colour index that was nearly 3 standard deviations above the long term mean which remains the highest value recorded in the North Sea (Edwards *et al,* 2001). Since this large increase, phytoplankton colour index in the central North Sea has maintained a level nearly double the annual average prior to 1987 (Reid *et al*, 2001). Outside the North Sea, the same phenomenon was observed in PCI in the Northeast Atlantic by Reid *et al,* (1998) and Edwards *et al,* (2002). This was coincident with the change in sign of the winter NAO (Hurrel and Deser, 2009; Beaugrand *et al,* 2008). Similarly timed shifts in phytoplankton abundance or biomass in the late 1980s were observed in the southern zone of the North Sea by Schlüter *et al* (2008) and Weijerman *et al* (2005). Weijerman *et al* (2005) observed that coincident warming of the sea was the most important indicator of this 1980s community reorganisation in the southern North Sea. Dinoflagellate abundance increased in this period to a greater degree than did diatom abundance (Edwards *et al,* 2002). Beaugrand *et al* (2008) found warming SST to be most strongly correlated with the first principal component of their analysis of this phenomenon across the North Sea and North Atlantic. SST does not directly operate on phytoplankon population growth in the same way that a pulse of nutrients would, as it is generally limited in its range relative to other factors (de Baar, 1994). The effect is indirect promotion, signified by the NAO and AMO, of conditions that support phytoplankton growth, such as earlier stratification with longer duration and altered wind and cloud conditions in spring (Stenseth *et al,* 2002).

Nehring (1998) described spread of several new thermophilic phytoplankton species in the North Sea: *Corethron criophilum* is a recent invader in the North Sea, recorded beginning in 1990. *Dinophysis odiosa* is a genuine thermophile, one that is an example of a species that cannot colonise the North Sea due to low temperatures (Nehring, 1998). *Coscinodiscus wailesii* invaded the Northeast Atlantic in 1977 (Edwards *et al*, 2001). *Mediopyxis helysia* was recently described from the North Sea (Kuehn *et al*, 2006). It is an invasive species, achieving local dominance in the Wadden Sea in 2009 (Meier, 2010). It first appeared in Scottish North Sea waters in 2005 (McCollin, 2008). *Thalassiosira punctigera* is an invasive species from the south Atlantic Ocean, resident in the North Sea since 1979 (Hasle, 1983). These species, possibly introduced by ballast water exchange, persist in an area that is not in their natural range – that they are notionally warm water species suggests a role of warming seas in their continued presence.

While Irigoien *et al* (2004) published a study of global patterns in phytoplankton and zooplankton diversity, the majority of their source data were not time series, so no global study of long term change in phytoplankton diversity exists. Leterme *et al* (2005) described changing diversity of selected species for the North Atlantic, the main study into shifting composition of phytoplankton, by Leterme *et al* (2006) is restricted to division into diatoms and dinoflagellates. Bresnan *et al* (2009) identified shifts in composition of the phytoplankton at the Stonehaven monitoring site, particularly a shift from *Chaetoceros* spp. dominated blooms to *Skeletonema* spp. dominated blooms. Edwards *et al* (2002) remarked that phytoplankton diversity in the continuous plankton recorder was at a low in the late 1970s. Reid *et al* (1990) showed relative abundance of diatoms, dinoflagellates and *Ceratium* spp. but did not present trends in diversity through an index or species richness, or otherwise. Widdicombe *et al* (2010) in the English Channel provided time series data at marginally greater group resolution, revealing declines in diatoms, increases in coccolithophores and both total and heterotrophic dinoflagellates.

Changes in abundance, biomass and diversity have been accompanised by phenological changes, variously moving peak abundance later (Wiltshire *et al*, 2008), merging or disappearance of peaks (Bresnan *et al*, 2009; Edwards *et al*, 2002) or earlier (Sharples *et al*, 2006; Edwards and Richardson, 2004). In the Northern Hemisphere, peak chlorophyll estimated from satellite data around the European continental shelf has moved earlier between 1997-2009 (Kahru *et al*, 2011). With a longer time series and more consistent spatial coverage, Edwards and Richardson (2004) found peaks in dinoflagellates when considered collectively had advanced by 23 days, and bimodally abundant diatoms unchanged in spring and earlier by 5 days in autumn. Over the whole North Sea, phytoplankton colour index has moved from two peaks, to one unbroken season, beginning in the late 1980s (e.g. Beaugrand, 2004; Burkill and Reid, 2010). To the north of the Dove Site, modelling validated with field data indicates earlier growth of phytoplankton caused by earlier stratification (Sharples *et al*, 2006). Still further north, Bresnan *et al* (2009) have noted mixed seasonal patterns when examining functional groups and individual species. Edwards *et al* (2001) presented a move two months later in phytoplankton peak biomass in the southern North Sea. At Helgoland Roads, warmer autumn temperatures correlated with delayed spring phytoplankton blooms, in this area due to a greater proportion of zooplankton surviving the winter and being able to graze more intensely on the following year's phytoplankton community, before it could grow at a greater rate than it was cropped (Wiltshire and Manly 2004).

1.3 Zooplankton in the North Sea and North Atlantic

The North Sea mesozooplankton is a key trophic group, grazing upon phytoplankton and providing food to larval and some adult fish, euphausiids, amphipods, chaetognaths, polychaetes, gelatinous zooplankton and even seabirds (Christensen, 1992). They therefore have the capacity to rapidly transmit climate impacts upon their phytoplankton prey in both directions in the food web through changed grazing impact (Fauchald *et al*, 2011). Mesozooplankton in UK waters tends to be dominated by a few highly abundant species, which means the dynamics of unusual forms can be informative of underlying change in circulation (Bonnet *and* Frid, 2004; Edwards *et al*, 2001). Here follows an introduction to the ecological importance and diversity of zooplankton in the North Sea, their geographic differences within the basin, historic trends from other time series, and the climate effects already known about.

Copepods dominate the North Sea zooplankton community. While at certain times of years polychaete worms, barnacle larvae or echinoderm larvae become numerically dominant, and euphausiids can become the dominant biomass fraction (Williams and Lindley, 1980), annual numerical and biomass dominance is overwhelmingly retained by the copepods (Fransz *et al*, 1991; Lindley and Batten, 2002). A small number of species make up the large part of copepod biomass: *Acartia* spp., *Pseudocalanus elongatus, Paracalanus parvus, Microcalanus pygmaeus, Temora longicornis, Oithona* spp. and *Calanus* spp. (Lindley and Batten, 2002). Non-copepod taxa as pointed out can achieve seasonal dominance. The appendicularia *Fritillaria borealis* and *Oikopleura dioica* can achieve numerical dominance when copepod abundance is low but apparently are negatively impacted by high copepod abundance (Stibor *et al*, 2004). The hyperiid amphipod *Parathemisto* spp. can reach neritic abundances high enough to leave visible tide marks as they are starved of oxygen and are washed ashore (M. Baptie, pers. Obs.).

Within the zooplankton are several co-occuring groups of species that have been considered representative of different environments within the sea. Beare *et al* (2002) divided species of copepods into three groups, as have some other authors: Boreal Atlantic, represented by *Calanus finmarchicus*, Temperate Atlantic, represented by *Calanus helgolandicus, Candacia armata* (Beaugrand *et al*, 2002; Kirby *et al*, 2009) and *Centropages typicus* – with an association with the FIC, and finally a neritic index of resident species, *Centropages hamatus* (Krause *et al*, 1995; Beaugrand *et al*, 2002) and *T. longicornis*. Other authors highlight other zooplankton groupings: Corten (1990) included *Metridia lucens* and the polychaete worm *Tomopteris helgolandica* in a warm temperate/temperate Atlantic affinity group. Willis *et al* (2006) however suggested a boreal Atlantic centre of distribution for *Tomopteris helgolandica*. Species level identification of preserved *Tomopteris* is difficult due to the diagnostic tail often being lost, which may explain some of this confusion between authors. Edwards *et al* (2001) noted the presence of Lusitanian fauna, the large predatory copepod *Euchaeta hebes* and the large calanoid *Rhincalanus nasutus* in the zooplankton as a signifier of highly unusual sea circulation in the North Sea. Lindley *et al* (1990) considered the copepod *Candacia armata* to be a significant resident of the North Sea as it was representative of northern Atlantic ingress and had persisted in the North Sea with a wider distribution since 1987. The chaetognaths *Sagitta maxima* and *Eukrohnia hamata* are indicators of cold Atlantic water and tend to die upon entering the North Sea, being replaced mainly by the warm Atlantic immigrant *Sagitta elegans* from the north in strong Atlantic inflow years and to a lesser extent by the North Sea resident *Sagitta setosa* in weak Atlantic inflow years (Fraser, 1937; Fraser 1939; Russell, 1939). In an early publication from the Dove Marine Laboratory, Meek (1928) observed a shift in the dominance of *S. elegans* and *S. setosa* in the sea off Northumberland that was associated with the seasons. A finding by Evans (1968) was that the principal amphipod in DTS samples, *Parathemisto gracilipes,* may at that time have been the dominant hyperiid amphipod in waters off Northumberland through its affinity with warmer water than *Parathemisto gaudichaudi.* These groups aside, the copepod *Oithona similis* (Martens and Brockmann, 1993; Martens and van Beusekom, 2008), the siphonophore *Muggiaea atlantica* (Lindley *et al*, 1990; Greve, 1994), the cladocerans *Evadne* spp. and *Podon intermedius* (Austen *et al*, 1991; Gieskes, 1971), the larvaceans *Fritillaria borealis* and *Oikopleura dioica* (Wyatt, 1973) have all been identified as indicators of hydrographic change.

Stephens *et al* (1998) described a decline in zooplankton from 1950 to 1980 in the North Sea, which following work by Edwards *et al* (2002) seemed to have recovered to be close to the long term North Sea mean in the succeeding 20 years after 1980. Beaugrand and Ibanez (2004) showed that after the end of the 1980s, zooplankton had undergone a step change in abundance. The warm-temperate and temperate species associations identified by Beaugrand *et al* (2002) both increased in abundance after the mid 1980s. The variability in the plankton community in the North Sea has decreased, indicating the change in zooplankton abundance was part of a regime shift (Beaugrand *et al*, 2008). At the Dove Time Series site, the decline in zooplankton was also observed (Roff *et al*, 1988), however unlike the North Sea as a whole, Clark *et al* (2001) showed a decline in zooplankton abundance continuing into the 1990s. Near to this, the Stonehaven time series of zooplankton has shown no trend in abundance from 1997 to the mid 2000s (Valdes *et al*, 2005). Though not in the North Sea, the Atlantic influenced L4 station in the neighbouring English Channel had observed generally stable zooplankton abundance (Eloire *et al*, 2010). Zooplankton population dynamics can be highly variable, and only through long term monitoring can the signal be distinguished from the noise attributable to seasonal and irregular factors.

Across the whole North Sea, small calanoids in the 1960s to 1980s declined to a minimum in 1981 (Broekhuizen and McKenzie, 1995). The majority of small calanoid copepods fall into the genera *Pseudocalanus, Microcalanus, Paracalanus* or *Acartia.* The cyclopoid copepods of the genus *Oithona* are the other type most commonly observed. The decline in the *Pseudo/paracalanus* group reversed to an extent in the 1980s but has subsequently continued (Fauchald *et al*, 2011). In the North sea, it is small (less than 500μm) copepods who were observed to have the greatest grazing impact upon phytoplankton (Morales *et al*, 1991). This could have a major effect on copepod-phytoplankton dynamics. For example, secondary production by the small copepod *Paracalanus parvus* in the Georges Bank has been modelled as greater than that of *Calanus finmarchicus* (Davis, 1984). *Oithona* also decreased in abundance (Beaugrand *et al*, 2003). However, total copepod abundance increased after the 1980s (Taylor, 2002). It is warm temperate groups, in particular species such as *Acartia clausi*, *Temora longicornis* and *Calanus helgolandicus,* that have increased in distribution and numerically (Beaugrand *et al*, 2003; Fauchald *et al*, 2011). In the late 1980s to mid 1990s, warm water species such as *Eucalanus crassus, Euchaeta hebes* and *Rhincalanus nasutus* increased in abundance (Lindley and Batten, 2002). *Acartia clausi* and echinoderm larvae have been the most abundant taxa in the North Sea near to Northumberland since the 1960s. Jellyfish in the North Atlantic shelf have in recent years increased in abundance, likely due to changing circulation and warming seas (Gibbons and Richardson, 2009). After the mid 1980s, jellyfish were present in 30-40% of North Sea CPR samples throughout the year, previously being restricted to the second half of the year (Attrill *et al*, 2007). Abundance of decapod larvae have increased after the 1980s warming event (Lindley *et al*, 2010). These observations reflect a change in the gelatinous and meroplankton contribution to zooplankton abundance, with undoubted consequences on the functioning of the community. Additionally, change in meroplankton from benthic adults is indicative of change outside the plankton.

The changes and appearances of unusual forms are as a result of major northward movement in assemblages of copepods since the 1980s. Beaugrand (2004) demonstrated nearly opposite trends of temperate versus boreal copepod species richness, with decreases in copepod diversity as a whole until the 1980s (Beaugrand, 2003). Total zooplankton and calanoid copepod diversity increased between 1958 and 1995 across several diversity indices (Lindley and Batten, 2002). In the southern North Sea, copepod diversity has increased linearly over 40 years between 1975 and 2005 (Wiltshire *et al*, 2008). Latitudinally in the northwest Atlantic, diversity increases the further south one examines (Beaugrand *et al*, 2002). There has been a northward extension of all copepod assemblages in the northeast Atlantic by more than 10º in latitude (Beaugrand, 2003). The gradient in diversity outside the North Sea but in the vicinity of the region, and the increasing diversity observed in the North Sea in all parts itself suggests there are several simultaneous influences on zooplankton diversity.

Warming seas are a major factor in these changes. Temperature explained 90% of variance in growth rate across 33 copepod species (Huntley and Lopez, 1992). Temperature change is a key succession mechanism; for example as well as limiting growth, breeding is stopped in *Centropages hamatus* in the southern North Sea due to cold conditions in winter – this may change in future (Halsband and Hirche, 2001). Warming seas have contributed directly to declining populations of *Evadne* spp. (Greve *et al*, 2004). *Oithona similis* abundance has increased in the Wadden Sea as SST and wind speed has increased (Martens and van Beusekom, 2008). The onset of population growth of *Oikopleura dioica* and *Temora longicornis* in the southern North Sea are negatively predicted by increasing SST prior to their peak season developing (Greve *et al*, 2001). Changing cloud patterns may also be an influence on plankton. For example in the Gulf of St. Lawrence, Kouwenberg *et al* (1999) estimated UV-B based mortality of *Calanus finmarchicus* eggs to be 50% at the sea surface.

Predation on zooplankton comes from a variety of sources. Euphausiids are present in the North Sea. Båmstedt and Karlson (1998) found prey clearance rates of krill (*Meganyctiphanes norvegica*, and three *Thysanoessa* spp.) on copepods of up to 4 individuals h^{-1}, and a preference for *C. finmarchicus* when grazing on mixed copepod food. Approximately 6% of omnivorous zooplankton were inferred to have been consumed by the chaetognath *Sagitta elegans* in the Dove zooplankton time series by Clark *et al* (2003), who suggested a wind/SST mediated effect on *Sagitta elegans* abundance and therefore copepod population growth rate. *Sagitta* spp. abundance follows abundance of offshore and neritic copepods (Krause *et al*, 1995), indicating a climate mediated effect would apply to a wide area of the North Sea, assuming equivalent predation between areas. Changing fish predation upon zooplankton can mediate species balances – changing dominance of pelagic fish by either herring or sprats in the North Sea affects the relative abundance of *Calanus helgolandicus* and krill (Fauchald *et al*, 2011). Munk and Nielsen (1994) estimated grazing impact of a mixed larval fish assemblage in the Dogger Bank at 3-4% of copepod stock day^{-1}, compared to a combined chaetogath/scyphomedusa predation rate of 1-3% day^{-1}. This suggests an increasing gelatinous plankton fraction will place further pressure on zooplankton. *Hyperia galba* is a hyperiid amphipod that is parasitic on jellyfish (Dittrich, 1988) that may benefit indirectly from increased jellyfish abundance. Free-swimming hyperiids have generally been considered a subordinate predation factor to other predatory groups, however in a Southern Ocean system with a similar level of mesozooplankton predation to the North Sea (generally less than 5%, up to 44% of standing stock) they can take a daily ration of 11.5% of dry body weight, suggesting that short term increases in the abundance of their North Sea confamilials could have major effects on mesozooplankton (Froneman *et al*, 2002). Clark (2003) acknowledged fish and amphipod predation may be more active than chaetognath predation, through greater activity was offset against lower abundance.

Calanus spp. has been studied extensively in the North Sea and the North Atlantic, due to its important trophic position and the temperature mediated change in dominant species over the last half century. Fransz *et al* (1991) described in detail the sea circulation processes governing supply of the North Sea with *Calanus finmarchicus*. The CPR however has allowed confirmation on the scale of the entire Northeast Atlantic of the effects of change in this process. CPR abundances of *Calanus finmarchicus* populations in the North Sea have collapsed. The seasonally average abundance in the northern North Sea in 1998 was 5% of the seasonally averaged abundance in 1958 (Beare *et al*, 2002), as a result of weakened deep water advection of CV copepodites in spring (Heath et al, 1999). Outside the North Sea *Calanus finmarchicus* has shown a decline in the waters around Iceland particularly to the north (Beare *et al*, 2000) indicating that conditions have ceased to be conducive to widespread *Calanus finmarchicus* breeding off the European continental shelf. Breeding *Calanus finmarchicus* found in the North Sea have spent winter in diapause in the deeper water of the North Atlantic. As such the abundance of this species in the North Sea is strongly influenced by the strength and scale of transport onto the shelf that occurs at the end of winter (Stephens *et al*, 1998; Heath *et al*, 1999). *Calanus helgolandicus* can overwinter and sustain a resident population in the North Sea due to its tolerance of milder temperatures and its 'natural' range in more southern latitudes, exhibiting residency without true diapause at depth (Bonnet *et al*, 2005; Beaugrand *et al*, 2002). Across the North Sea, *Calanus helgolandicus* has become the more abundant of the two congeners (Reid *et al*, 2003).

Atmospheric regulation of thermal range distribution has affected the biogeography of zooplankton (e.g. Reid *et al*, 2001; Beaugrand, 2004). The NAO has been implicated as a signal of these changes through its rapid transmission of the climate signal resultant from the latitude of the GSNW in a given year. Fromentin and Planque (1996) attributed 58% of interannual variability in *Calanus finmarchicus* abundance to the NAO index, while *Calanus helgolandicus was* much less strongly driven, by only 18%. This meant that as the NAO ceased to be in persistent negative phase and conditions became on the whole more favourable to warm-temperate species, positive regulation of *Calanus finmarchicus* distribution and survival gave way to increased *Calanus helgolandicus* growth to the North Sea. Boreal assemblage copepod abundance was positively correlated with salinity in the northwestern North Sea and negatively correlated in the northeastern North Sea, indicating an Arctic influence in transport of this group (Beare *et al*, 2002). Beaugrand (2003) found positive correlations between *Calanus helgolandicus* presence and warming SST and positive NAO index, the reverse for *Calanus finmarchicus*. He suggested the increased calanoid copepod diversity observed in all regions was a result of northward movement of zooplankton ecotones, brought about by changes in Northeast Atlantic circulation to allow domination of saline Atlantic water. Planque and Taylor (1998) suggested the NAO effect upon SST alters stratification and either increases or decreases interspecific competition between species with discrete thermal optima depending on NAO phase.

Late advection of water from the North Atlantic into the North Sea in high NAO years disproportionately harms *Calanus finmarchicus* populations, while having little effect on copepods without a diapause overwintering strategy. Southward *et al* (1995) identified the same switch from *Sagitta elegans* to *Sagitta setosa* with cold/warm waters as observed by Russell in the 1930s, a decline in *Calanus helgolandicus* (in this more southerly latitude a 'cold' water representative) and a pattern of community shifts associated with cold or warm water that oscillate for several years between each community. Piontkovski *et al* (2006) regressed NAO index against copepod abundance in Helgoland Roads and L4, finding significant positive effects on copepod abundance, but only at lags of 3-4 years. The authors suggested this represented a signal transmitted by the NAO but manifest as advection via the English Channel, rather than changed nutrient input or stratification.

Phenological change in peak abundance has occurred in the zooplankton. This is observable across the Northern Hemisphere, and peaks move earlier in each case (e.g. Mackas and Tsuda, 1999; Batten and Mackas, 2009; Costello *et al*, 2006; Sullivan *et al*, 2007). Data from several sampling programmes across the North Sea reflects similar trends. In the same study noted above, Edwards and Richardson (2004) also found copepod peaks had moved earlier by 10 days. Meroplankton is affected too: there were significantly earlier peaks in zoea larva abundance of 4 crab species and 1 crab family in CPR area C2 (North England and Scotland) during 1989 compared to 1981 (Lindley *et al*, 1993; Lindley 1987), associated with exceptionally warm sea temperature at this time, presumably changing adult spawning time. Peak abundance of decapod larvae in general has moved earlier (Edwards *et al*, 2006). The southern North Sea also exhibits such a pattern, with several zooplankton species peak abundance moving earlier as sea warms (Greve *et al*, 2001, Greve *et al*, 2004).

The North Sea zooplankton is a copepod dominated community, with occasional biomass or numerical dominance achieved by seasonal spikes in non-copepod taxa, such as euphausiids, echinoderm larvae, polychaete worm larvae and barnacle larvae. Diversity has been increasing and the main reason suggested for this is the northward progression of Northeast Atlantic zooplankton communities which has affected the composition of the species that are advected into the North Sea via the Faroe-Shetland Channel, as represented by the change in prevalence of the boreal affinity *Calanus* *finmarchicus* to its more temperate affinity congener *Calanus helgolandicus*. The CPR is the principal source of information on spatial trends in the zooplankton, revealing the NAO to have driven conditions critical to *Calanus finmarchicus* advection, weakening after the 1980s. It may have several different avenues of effect as suggested by long time lags in its effect upon Helgoland Roads and L4 copepod abundance, as well as the community shift revealed by the CPR occurring shortly after switch in phase of the winter NAO index. The community now is more stable than during a period of change in the 1980s, though continued climate change, particularly increasing wind, salinity and SST suggest further changes are likely. The Dove Time zooplankton time series had only been studied to the end of 1996 and it remained to be seen if the large scale changes in zooplankton observed in the North Sea as a whole have been similarly observed in the more recent years of the DTS.

1.4 Ichthyoplankton in the North Sea and North Atlantic

Ichthyoplankton is the eggs and larvae of fish. They are small, temperature sensitive, and vulnerable to predation at these stages (Rijnsdorp *et al*, 2009). Their presence in the plankton is dependent on adult spawning and this can mean this group is particularly prone to trophic mismatch difficulties in a time of community reorganisation. Their mode of hunting for prey, often visually, means changing weather and sea state are other factors that may exert themselves particularly strongly, which will be explained in this section. Of course they ultimately mature into adult fish which are often of commercial importance to humans as food or aquaculture fish meal. The group have not been studied in detail in the Dove Time Series.

Species level descriptions of long term trends in fish larvae are quite rare in the North Sea. A nearby published example exists at station L4 in the English Channel (Genner *et al*, 2010). The Stonehaven time series samples ichthyoplankton but no study of the full community has been published, focusing instead on species of interest (Heath *et al*, 2009). ICES have sampled the larvae of herring for stock assessment models since 1967 (1972 with consistent methodology; Gröger and Schnack, 1999). Fish larvae had not been identified beyond “fish larvae” in the continuous plankton recorder time series (Warner and Hays, 1994), but Edwards *et al* (2011) released information on 5 species and 5 families. These data revealed southward shifts in the larval distribution of clupeids, northward movement in the larval distribution of cod. Peak abundance had moved later in mackerel, earlier in whiting and dab. Pipefish were a newly abundant group in the Atlantic, being observed at greater abundance after the 2000s in summer. Older larvae can spot and avoid sampling gear (Brander and Thompson, 1989). As the CPR aperture is narrow this resource is likely to be restricted to younger individuals.

Looking at these single species assessments can still be useful, particularly in the case of the ICES herring larvae surveys which are extensive in time and space. Across the North Sea, the Larval Abundance Index (LAI, abundance per 30x30 nautical mile square) has increased. In the central North Sea ICES region, there were peaks in LAI in the 1980s and 2000s, with lower LAI in the 1990s (Rohlf and Gröger, 2009). The 2000s saw a decline in sandeel larvae at Stonehaven (Heath *et al*, 2009). Genner *et al* (2010) published a time series of ichthyoplankton community structure which illustrated increasing abundance of larvae of summer spawning adults.

Diversity of ichthyoplankton in the North Sea before this study was not understood, and few recent time series studies are published. Diversity of ichthyoplankton in a time series from outside the North Sea, in the Bay of Biscay, has increased through the 2000s (d'Elbée *et al*, 2009), but contemporary trends in diversity in the North Sea itself are rare. Malzahn and Boersma (2007) presented a short study of the fish assemblage in the southern North Sea which showed relatively stable communities, with the exception of higher abundance of lesser sandeels *Ammodytes marinus* in 2004 compared to 2003 and 2005.

There are many studies published on the seasonal or even more acute effects of environment, food and predation on survival of fish larvae. These are valuable in understanding the tolerances of fish larvae, and the extent to which survival depends upon the conditions encountered. Temperature is a key limiter of individual fish larva growth. As a baseline, 5-10% of an ichthyoplankton cohort die per day from all causes (Cushing, 1983). Temperature is a key factor of larval dynamics. The larva is the stage most prone to heat stress (Rijsndorp *et al*, 2009), with suboptimal growth or feeding inhibition observed if larvae encounter unsuitable temperatures observed in a range of North Sea species, such as witch flounder *Glyptocephalus cynoglossus* (Bidwell and Howell, 2001), haddock *Melanogrammus aeglefinus* (Laurence, 1978), cod *Gadus* *morhua* (Buckley *et al*, 2004; Peck *et al*, 2006), anchovy *Engraulis encrasicolus* (Hunter, 1980) and herring *Clupea harengus* (Moksness, 1991, Munk *et al*, 1991). The ranges of adult fish in the North Sea are changing due to temperature, for example relatively greater abundances of deep living fish have been observed as bottom temperatures rise (Dulvy *et al*, 2008). This will inevitably have an effect on the makeup of the larval community in the plankton, which may or may not thrive relative to the trends in their food.

Their principal prey is mesozooplankton and with a few exceptions, principally copepods (Turner, 1984; Mousseau *et al*, 1998; Cushing, 1983). *Calanus* spp., *Temora* spp., *Pseudo-calanus* spp., *Paracalanus* spp. and *Acartia* spp. are as noted earlier the most abundant copepods in the North Sea zooplankton and unsurprisingly also the most heavily grazed by fish larvae, though the grazing effect of fish larvae is generally low (<10% of copepod secondary production; Gissel and Munk, 1998). There are little data on the grazing rates of fish larvae in the vicinity of the DTS though in a Newfoundland study area, Pepin and Penney (2000) found that most species (many present also in the North Sea) consumed 30-70% of body weight daily, but biomass was so low (0.005-0.5mg m^{-3}) that the grazing impacted upon less than 0.1% of available prey. Plaice, *Pleuronectes platessa,* is a common species with conspicuous larval dependence on predation upon larvaceans *Oikopleura* and *Fritillaria borealis* instead of copepods (Last, 1978, Shelbourne, 1957). Lesser sandeels *Ammodytes marinus* also feed upon *Oikopleura* (Cushing, 1983).

The low impact of larvae upon prey demonstrates the normal situation is for prey plankton to exert bottom up control on fish larvae. In this case, fish larvae have a relatively minor impact upon the zooplankton community and are generally not food limited. An energy web model indicated plankton secondary production (66.4g DW m^{-2} $year^{-1}$) is sufficient in the North Sea to provide the energy needs of planktivorous (in energy surplus 3 quarters out of 4) and benthivorous (in surplus 4 quarters of 4) adult fish (Greenstreet *et al*, 1997). The low biomass of fish larvae relative to copepod biomass would suggest that at a North Sea scale, fish larvae are not food limited (Cushing, 1983), though local starvation and other factors regulate populations. Heath (2005) described similar energy surpluses with a taxonomically varying planktivorous fish community that is energetically stable. Once larvae become juveniles, top down control can occur, and may be a symptom of climate change. Frank *et al* (2007) suggested top down control to be a function of species richness and temperature, with warmer, richer systems being controlled by a bottom up pathway, and cooler, less rich systems being top down controlled. Top down control of zooplankton abundance by fish is likely to be deleterious to fish abundance eventually as copepods are the most strongly positive impacting group on the widest range of North Sea fish species (Christensen, 1995). In the Baltic sea between 1988 and 1996, top down control at times of temperature induced stress in copepod populations was observed between Sprats and *Temora longicornis* and *Pseudocalanus elongatus* while the temperature insensitive species *Acartia clausi* was unaffected and increased in abundance (Alheit *et al*, 2005; Möllmann and Koster, 2002). *Calanus finmarchicus* peak abundance coincides with *Ammodytes marinus* spawning and is therefore crucial to early larval survival, while *Calanus helgolandicus* abundance does not coincide with spawning and therefore its rise in abundance and partial ecological replacement of the niche of *Calanus finmarchicus* has contributed to the decline in *Ammodytes marinus* recruitment in the North Sea (van Deurs *et al*, 2009). Reid *et al* (2000) noted strong correlations between fishing intensity and zooplankton abundance, particularly for the period 1978-1982 when sandeel fisheries were at their peak, and zooplankton abundance in the CPR record was at a minimum. This suggested rapid development of a top down control system, alternating with the bottom up status quo. There can also be sublethal effects of changing zooplankton patterns; the energy content of sprats and sandeels have declined, indicating their diet has altered through contact mismatch between zooplankton and ichthyoplankton (Wanless *et al*, 2005).

Specific copepod abundance can also negatively affect recruitment, even contributing to wider marine community change. Sherman *et al* (2002) found high growth of planktivorous larvae of pelagic fish during a period of zooplankton growth while demersal stock fishing was restricted in the western Atlantic. Bottom up (food limiting) control of cod larva population growth coupled with altered plankton community composition has inhibited cod recovery in the North Sea despite fishing restrictions (Beaugrand *et al*, 2003). Further to this, warming sea temperature has allowed expansion of the highly territorial grey gurnard, *Eutrigla gurnardus*, (Amorim and Hawkins, 2005) into the role once dominated by adult cod, and predation by it upon juvenile cod when they attempt to settle into the demersal stage of their lifecycles, has also been suggested as a reason for the lack of recovery of this important commercial stock (Floeter *et al*, 2005).

Predation based mortality either through cannibalism or direct predation can be a significant source of mortality (van der Veer, 1986). Other fish are an important predator of ichthyoplankton. Greater sandeel *Hyperoplus lanceolatus,* sprat *Sprattus sprattus* and small sandeel *Ammodytes tobianus* predation maybe a significant top down effect on juvenile herring recruitment (Fuiman and Gamble, 1988). A cause for some concern in future is the risk posed to ichthyoplankton by predation from jellyfish. Lynam *et al* (2005) distinguished jellyfish in the northern Scottish seas from other areas based on the strength of their response to the NAO index and GSNW, and suggested top down and competitive control of fish recruitment could be enhanced through the positive feedback between warm water and jellyfish abundance. Moon jellyfish *Aurelia aurita* in Limfjorden in Denmark reduce half life of fish larvae to 1 day or less in periods of high abundance (Hansson *et al*, 2005). Attrill *et al* (2007) forecast several scenarios of warming and NAO index fluctuations, all resulting in an increase of jellyfish over the coming century.

Many fish species have specific spawning grounds, from which their larvae can disperse rapidly. As an example, *Clupea harengus* larvae dispersed from a central isopleth of 1000 larvae m^{-2} to 100 larvae m^{-2} in 7 days in the Hebrides in 1984, travelling 30' N in the process (Heath and MacLachlan, 1987). This of course depends on the location of spawning and dispersal is highly sensitive to the fine scale hydrographic processes in the area, such as tides and eddies (Simpson, 1971), a feature of dispersal probably underestimated by simple oceanography (Cowen *et al*, 2000). Tidal front zones appear to be a good environment for fish larvae, presumably due to mixing and concentration of particles as water masses drag against each other. This is true of whiting *Merlangius merlangus* (Munk *et al*, 1999), *S. sprattus* (Berntsen *et al*, 1994), *Gadus morhua* and *Melanogrammus aeglefinus* (Lough and Manning, 2001) and dab *Limanda limanda* (Lee *et al*, 2006). More mixed inshore areas appear to promote survival of young larvae which then migrate offshore with age (Dickey-Collas *et al*, 1996), this process can occur in reverse too, with offshore larvae recruiting to inshore populations (Knutsen *et al*, 2003).

The CPR demonstrates the broad scale representation of oceanographic change among some fish larvae (Edwards *et al,* 2011). Vilchis *et al* (2009) found shifts in stratification in the Pacific which brought about changes in ichthyoplankton composition associated with cold and warm El Niňo/Southern Oscillation events. Swedish herring catches going back to the middle ages have been affected by changing wind stress driven by the NAO (Alheit and Hagen, 1997). Attrill and Power (2002) demonstrated the NAO to be the most important factor influencing juvenile fish assemblages in the Thames estuary, generally increasing species richness when in positive phase. This has been commented on in the UK historically: Storrow (1932) noted unusual water masses in the Atlantic coinciding with increased pteropod abundance in the North sea and reduced salmon catches in coastal sea near the Tyne. Russell (1939) linked poor herring spawning in the English channel with high abundance of certain phytoplankton species, and noted a relationship between *Sagitta setosa* and poor Herring landings on the Northumberland coast. He suggested chaetognaths could be indicators of *Calanus* abundance in Northumberland waters, a key food item of herring (Last, 1989). He suggested chaetognaths could be indicators of *Calanus* abundance in Northumberland, a key food item of herring (Last, 1989). Perry *et al* (2005) found predominantly northwards shifts in range of species that were at the margins of their range in the North Sea. The most conspicuous example of modern times is the appearance of the snake pipefish, *Entelurus aequoreus* in the plankton (Ewards *et al,* 2011). It has increased in abundance in the Northeast Atlantic since 2003 and has been a factor in reduced seabird breeding success due to the inability of chicks to swallow the rigid bodies, causing starvation and choking mortality (Harris *et al*, 2007; Kloppmann and Ulleweit, 2007). It has also been found as far north as Svalbard in 2006 (Fleischer *et al*, 2007). Horse mackerel *Trachurus trachurus* are another example of a species found out of range recently in the North Sea, associated with altered North Sea flows. It has increased in abundance since the 1980s (Beare *et al*, 2004a) and Rijsndorp *et al* (2009) consider it to represent Lusitanian faunal progression to the North Sea. It has been transported into the North Sea and the catch of adults by Norwegian vessels is strongly correlated at a 6 month lag with the strength of Atlantic inflow to the North Sea (Iversen *et al*, 2002). Warming events have caused temporary incursions of a variety of Lusitanian fish into the Southern North Sea (Corten and van de Kamp, 1996; Bergstad, 1990; Rijsndorp *et al*, 2009).

Changing patterns of fish abundance impact upon the human economy; it has created fisheries that had no historic precent, and decimated those that already existed. In the 1970s, landings of adult sprat at eastern English ports were in the range of 20000-50000 tonnes (MMO, 2010). Reduced residual currents from the Atlantic Ocean moved sprat larvae slowly enough to encounter ideal overwintering grounds off Northumberland (Corten, 1990). Currents in the 1970s did not transport the usual stock of herring larvae far enough south and recruitment collapse resulted from very high mortality in the unsuitable open North Sea (Corten, 1986). Herring fishing was opened in 1983 after closure due to catastrophic collapse of the fishery beginning in the 1960s (Yang, 1982). The same phenomenon appears to be important in the proliferation of sardines in the North Sea, beginning in 1995 (Beare *et al*, 2004b) in the Northern North Sea, and 2002 in the Southern North Sea (Voss *et al*, 2009). Mackerel are a normal North Sea resident species, but one at potential risk of trophic mismatch occurring. Both Castonguay *et al* (2008) and Runge *et al* (1999) have demonstrated strong relationships between mackerel recruitment and zooplankton abundance. MacKenzie and Koster (2004) and Ottersen *et al* (2010) highlighted the importance of temperature in a wide range of aspects of fish population dynamics, including recruitment. Increased summer temperatures cause earlier arrival of mackerel in spawning areas and earlier timing of peak spawning in the North Sea (Jansen and Gislason, 2011). Climate induced mismatch may well occur in this species with obvious implications for the veracity of the models of recruitment coupled with copepod prey biomass and production and their use in mackerel stock assessment. As Hunt and McKinnell (2006) point out, lower copepod prey availability may increase ontogenetic cannibalism, already well known for mackerel and further depensating the juvenile population (Peterson and Ausubel, 1984). Other species present in the modern DTS, considered representative of community change in the North Sea are Norway bullhead *Micrenophryis lilljeborgii* (Neudecker *et al*, 2006), Norwegian topknot *Phrynorhombus norvegicus,* lesser weaver *Echiichthys vipera* (Heessen, 1996), and poor cod *Trisopterus minutus* (Heessen and Daan, 1996).

The key position occupied by planktivorous fish as one of the primary consumers affected by alterations in prey phenology (Platt *et al*, 2003), or the phenology of their own spawning parents, is recognised by Ji *et al* (2010). Greve *et al* (2005) noted shorter middle seasons with greater winter SST and later seasons developing from 1990 to 1999 in larval *Solea solea*. Genner *et al* (2010) similarly found SST driven change in larvae, but this was to a later peak in spring spawner offspring and earlier for late spawner offspring, in the English Channel.

Fish larvae suffer very high mortality due to the stressful environment they hatch into, with high daily rations required for growth and specific thermal niches to exploit, while spending early life as passive drifting organisms within the plankton (Rijnsdorp *et al*, 2009). Temperature has the major effect upon fish larva behaviour and growth and therefore is crucial to larvae making contact with prey. Fish larvae have a low impact upon their prey, through their relatively low density. They are therefore normally bottom up controlled, though top down control can occur if other negative effects are exerted upon prey organisms, leading to community stress. Wind and currents appear to concentrate larvae near tidal fronts, which appears to increase chances of feeding and therefore survival. Currents represented by different fish species, both larval and adult have been manifest in the North Sea and surrounding area for at least the last century. Several warm water species appear to have occupied niches of more northern temperate species in the North Sea recently. There is a clear effect of climate on all life stages of fish, though larval fish are less studied than mesozooplankton.

1.5 Plankton science: field sampling, laboratory analysis and data interpretation of long term trends

In the following sections covering trends and effects in the plankton, information has been gathered from a number of studies which all describe long term change, but do so based on data gathered and analysed in different ways. The Dove Time Series is a time series of data derived from averaged vertically and horizontally hauls using nets of 63µm, 200µm and 1mm mesh sizes (Evans and Edwards, 1993). This offers the benefit of sampling the entire water column, leading to high confidence in estimates of zooplankton abundance, which has led to important studies of the zooplankton in the region (e.g. Roff *et al*, 1988; Evans and Edwards, 1993; Clark and Frid, 2001). Size classes from phytoplankton to adult jellyfish are captured by the programme.

Phytoplankton incidentally sampled by the 63µm mesh method is poorly sampled by this technique, being highly underestimated if one was to attempt enumeration and quantitative analysis. Delicate forms are likely to have been damaged by the mesh. North of the Dove is a sampling site at Stonehaven, Northeast Scottish coast. Zooplankton is sampled in a similar location (open coastal sea), in a similar way to the DTS, towed vertically with a 200µm mesh since 1997 (see Heath *et al*, 1999; 350µm after 1999 – Heath *et al*, 2011). Phytoplankton at Stonehaven are estimated quantitatively from integrated 0-10m depth water samples (see Bresnan *et al*, 2009). The time series offers a valuable insight into more northern plankton with greater proximity to the Atlantic Ocean than the Dove plankton. In the southern North Sea, Helgoland Roads zooplankton is sampled with oblique net tows, while quantitative phytoplankton samples are taken at the surface (Greve *et al*, 2004; Wiltshire and Manly, 2004). This time series is among the finest resolution time series worldwide, with weekday scale analysis, since 1962. Plymouth Station L4 in the English Channel is sampled in the same way for zooplankton as the DTS (Eloire *et al*, 2010). Phytoplankton at the site is sampled at a depth of 10m (Widdicombe *et al*, 2010). L4 has been sampled consistently since 1988. Covering the North Atlantic, including the North Sea, is of course the continuous plankton recorder (CPR), sampled with the same methodology since 1948. This is towed behind merchant vessels of opportunity (see Warner and Hays, 1994) and has contributed the most to knowledge of the plankton in the Northern Hemisphere (e.g. Reid, 1977; Colebrook, 1979; Reid *et al*, 1990; Beaugrand, 2000; Edwards *et al*, 2002; Beaugrand, 2004; Batten and Welch, 2004).

The majority of these time series are methodologically straightforward to compare (though no empirical meta-analysis has been made in this thesis). Phytoplankton is the exception, as they are very poorly sampled by nets. This means one should treat quantitative results from net based surveys with caution. SAHFOS do report log transformed abundance of phytoplankton (see http://www.sahfos.ac.uk/taxonomy/phytoplankton.aspx), and CPR studies have been published with data in this format (e.g. Head and Sameoto, 2007). The numbers are actually abundance proxies based on a scoring system (Warner and Hays, 1994), and should therefore be viewed as a guide of trends, rather than as genuine abundances. As a reinforcement of this, cell counts are orders of magnitude lower than depth integrated based phytoplankton time series (e.g. Bresnan *et al*, 2009). CPR studies also have phytoplankton colour, a quasilogarithmic proxy for biomass, though the spread in correspondence between this and *in situ* chlorophyll is wide (Batten *et al*, 2003). UNESCO (1968) zooplankton sampling, as is undertaken at the Dove, and Plymouth L4 also produces individual counts much higher than those of the CPR (Clark *et al*, 2001). Net studies, particularly when deployed through the water column, can offer a counterpoint to phenomena observed in CPR samples across the wider scale. For example Jónasdóttir and Koski (2011) found *Calanus finmarchius* and *Calanus helgolandicus* continue to alternate in having the higher relative secondary production in the North Sea when not sampled by means other than the CPR, indicating undersampling due to specific vertical migration behaviour of *Calanus finmarchicus* during summer.

Previous DTS authors (Evans and Edwards, 1993, Clark and Frid 2001, Bonnet and Frid, 2004) have used a combination of vertical whole water column (WP2; UNESCO, 1968) samples and larger mesh samples towed horizontally for a period of time (WP3) and combined per m^3 calculated from one or the other dependent on the organism. Evans and Edwards (1993) considered relative density of an organism between WP2 and WP3 nets to be an acceptable measure of which abundance value was representative of per 'true' m^3 abundance. The advantage of this approach is the much better sampling of larger organisms by the wider mouthed WP3 net compared to WP2, allowing a wider size range of groups to be represented in the final data. The WP3 horizontal tow has no analogue in the other North Sea time series. The serious disadvantage of this approach is in treating abundance in individuals m^{-3} determined by vertical near bottom to surface hauls and restricted horizontal tows with equivalence. Plankton is patchily distributed in space and time. To take midwater horiztonal and vertical samples from a nominally monthly time series risks greatly reducing accuracy of per m^3 counts for those taxa sampled with the midwater WP3 net. Only by sampling the whole water column can one draw conclusions on per m^3 counts without *caveats*.

Laboratory analysis generally involves subsampling or counting in full. Phytoplankton analysis was undertaken using variants of the Utermöhl technique (Utermöhl, 1958) in Stonehaven, and L4. The Lund method (Lund *et al*, 1958 essentially the same as the Utermöhl technique) was employed at Helgoland Roads. The

CPR involves estimation of abundance and allocation to categories in both phytoplankton and zooplankton. Zooplankton estimation in the other time series involved full enumeration of suitably diluted samples. Taxonomic resolution in all cases has been to the highest level that can be reliably identified. New technologies become available to accelerate analysis, such as FlowCAM (e.g. Poulton and Martin, 2010). Steinberg *et al* (2011) studied several counting techniques including FlowCAM and found it to compare favourably with others. This technology was employed in Chapter 3.

Plankton is patchily distributed and therefore often in weekly or monthly time series this translates into high variability in estimates of abundance and diversity. This makes determining the response to changing climate a challenging task. Several studies have focused on a restricted number of species, sensitive to their environment to a greater degree than other plankton, to resolve a climate signal from biological time series. This approach has at its heart recognition that plankton do grow differentially in different water masses and there are some relatively stable associations against which change can be measured, as was described earlier. Beare *et al* (2002) and Beaugrand *et al* (2002) independently described change in distribution of mesozooplankton with certain geographic affinities, using different approaches. Beare *et al* (2002) grouped species by similar seasonal cycles and trends. Beaugrand *et al* (2002; but see also Beaugrand, 2000) used multivariate analysis to group species co-occuring in space (see Beaugrand *et al*, 2003 for detailed descriptions). Briefly, principal component analysis (PCA) ordinations of the species against PC axes determines linear gradients of conditions under which those species are more often observed at abundance than not. The advantage of PCA is one can discuss biological or environmental variability independent of each other. For example McQuatters-Gollop and Vermaat (2011) measured species sensitivity by correlating biological time series with the principal components of a PCA of environmental variables. PCA is problematic in that when β-diversity is high (which it can be along a gradient of time in a region that appears to have undergone considerable change in weather and oceanography), linear gradients may not be valid and presence on an axis may be distorted (Palmer, 2008).

Constrained (or canonical) correspondence analysis (CCA) is a technique more often used in terrestrial vegetation ecology than in marine ecology (see Alves-de-Souza *et al*, 2008 for an application linking marine phytoplankton with their environment). It has some features that make it intuitively interpretable and, being one of a family of analyses collectively called direct gradient analysis, directly linked to knowledge of the environment. Where PCA maximises variance explained in a biological dataset and correlates this with predictors, or vice versa, sample scores in CCA are constrained to be linear combinations of explanatory variables. While a contributing variable can be correlated with a CCA linear constraint, this serves to guide the analyst in interpreting the likely importance of this variable in determining the linear constraint, and should not be misconstrued as indicating the analysis to be correlative. CCA is a parametric analysis that divides variability into that which can be combined into a linear constraint descriptive of species abundance and compositition, and further (unconstrained) variability that cannot be ascribed to the input variables. The disadvantage of this approach is that by constraining axes to represent variability of known predictors, the maximum variability may be explained by combinations of unmeasured variables. Therefore a CCA will always describe lower variability than an unconstrained CA or PCA. The temptation then is to add more and more explanatory variables, but this makes the method vulnerable to overfitting (a 'shotgun' approach of including all possible predictors risks confounding explainable variability, Oksanen, 2010). As each axis is a different combination of the same variables, 'partialling out' the relative importance of individual predictors can be complicated by finding their contribution to be indistinguishable from variability shared by all axes, if collinear with other variables. If one is selective with predictive variables by choosing those that optimise a goodness of fit statistic to avoid these pitfalls, the axes along which variability is arranged are analogous to uncorrelated gradients of condition sets. The approach is therefore a multivariate multiple regression and the combined linear constraints themselves therefore imply causation over correlation. In Chapters 2, 3 and 4 this approach was taken to advance analysis of the DTS beyond correlations.

Time series analysis of ecological data needs to identify trends and variability operating at interannual and intra-annual time series. There are many approaches to this, a major form has been that of an autoregressive integrated moving average (ARIMA) model. These models combine a locally varying regression component and a moving average component with estimates of the terms of the autoregressive component being made by Kalman filtering, that is continually updated estimates as new observations are made (e.g. Harvey and Phillips, 1979). 'Goodness of fit' is determined by maximum likelihood estimation of model terms (Gardner *et al*, 1980). An alternative time series approach, as used by Boyce *et al* (2010), is to apply a generalised additive model (GAM; Wood, 2006) with time as smoothing predictor. The disadvantage of a GAM is the need to carefully check for all the normal parametric conditions (e.g. structure-less residuals, independent observations, bias from outliers). Furthermore both of these modelling approaches are problematic when it comes to making predictions. As the smooth term of a GAM is determined by completing iterations of the model for any number of degrees of freedom using the known predictor and response data, the end result nonlinear contribution of the smoothing predictor to variability in the response necessarily means that it is impossible to make a prediction, as the knowledge of the slope of the smooth term is not known outside the observed data. An ARIMA model can make forecasts but these are linear in nature and unbounded by the trends present in the observed time series. Kalman filtering is genuinely a state space approach, however a time varying ARIMA is not actually a model of the data, but the data subtracted from a stationary equivalent model. As a time series model, ARIMA therefore is parameterising the residual differences between these two. Structural models were the advance from ARIMA that explicitly partitioned variance in models according to its underlying structure (Ripley, 2002). Nonetheless this model was a Gaussian state space model, i.e. overdispersed data, as they almost always are, are not well descibed by these models. Dethlefsen and Lundbye-Christensen (2006) wrote an R package that could describe Gaussian or non-Gaussian state space models (SSM) in a generalised linear model (GLM) like framework to separately consider seasonal, interannual trend and level components of variance. Petris *et al* (2009) advanced this to fully Bayesian estimation of variance of all of these structural time series components and allowed specification of types of structures to model each term, terming these dynamic linear models (DLM). This has allowed short term forecasting, with forecasts bounded by the specified structure as determined through examination of models of observed data. These models were applied to the Dove Time Series data to describe the likely consequences of change in abundance of species with affinities determined through relationships with combined linear constraints.

1.6 Thesis Aims

The aim of the thesis was to look at the long term variation in three trophic levels of the plankton represented by the phytoplankton, zooplankton and ichthyoplankton sampled at the site. The Dove Time Series is a coastal time series, and given the variable nature of stratification and thus front formation along the Northumberland coast, it was expected to exhibit its own time series patterns compared for example to the Continuous Plankton Recorder time series. Chapters 2, 3 and 4 describe the time series of each group in turn. The response of plankton to changing oceanographic state over time was explored through variability in gross abundance, community composition and seasonality. Chapter 5 describes a modelling technique to project the probability of presence of an organism according to its statistically defined niche, which was carried out in order to determine if the approach could be used to estimate the extent of coastal versus open sea habitat near to the Dove Time Series, and if the plankton aspect of the North Sea regime shift as described in numerous Continuous Plankton Recorder papers had lead to conditions more or elss favourable to plankton at the Dove Time Series site. Each chapter has its own aims and hypotheses, to which the reader is referred.

Since regime shift has been described (and disputed) in the North Sea, it was a thesis aim to resolve whether change in the plankton at Dove Time Series was consistent with an ecosystem-wide regime shift, through its similarity with observations made elsewhere. As a whole, the thesis tested the null hypothesis that there had been no plankton response in abundance, composition or phenological events to changing oceanographic state of the sea, inferred from oceanographic and meteorological data as well as ocean climate indices.

Chapter 2: Long Term Hydrometeriological and Biological Variability and its Effect upon Phytoplankton at the Dove Time Series

2.1 Introduction

The North Sea and the wider North Atlantic have been the site of major alterations in the pelagic ecosystem (Edwards *et al*, 2001, Edwards *et al*, 2002, Edwards and Richardson, 2004) that have led some authors to consider them supportive of the concept of a regime shift having occurred (Weijerman *et al*, 2005, McQuatters-Gollop *et al*, 2011, Alheit and Niquen, 2004; Ji *et al*, 2010). Phytoplankton is recognised to be of critical importance in the food webs that lead to successful population growth of commercially important fish species in the North Sea (Kirby *et al*, 2007), and therefore study of the fluctuating dynamics of the phytoplankton component of the ecosystem is key to understanding the implications of continuing climate change and its direct economic impact upon humans. The Dove Time Series has incidentally recorded phytoplankton in fine mesh net tows since 1971. Over this period there have been in the North Sea incursions of exceptionally fresh water of Arctic origin (Dickson *et al*, 1988), and incursions of exceptionally warm water associated with stronger westerlies leading circulation from the North Atlantic to the North Sea (Greene and Pershing, 2003). The location of the time series is in a part of the North Sea where currents are quite weakly affected by oceanic ingress (Stephens *et al*, 1998; Turrell, 1995; Pingree and le Cann, 1989), having an along shore coastal current (Gmitrowicz and Brown, 1993) not associated with ingress events as observed in the northern North Sea. The proximity of the DTS to the coast makes it of interest to study as a counterpoint to the well known work on the continuous plankton recorder (Edwards *et al*, 2001, Burkill and Reid, 2010, Beaugrand *et al*, 2008).

Phytoplankton has long been considered indicative of sea conditions (Russell, 1935). In the North Sea they have been demonstrated to be responsive to change in oceanographic conditions driven by large scale pressure differential systems such as the North Atlantic Oscillation index (Irigoien *et al*, 2000, Edwards *et al*, 2002, Sharples *et al*, 2006), the Arctic Oscillation (Hop *et al*, 2006, Skogen *et al*, 2007) and further afield, the El Niňo/southern Oscillation (Lenarz *et al*, 1995, Sanchez-Velasco *et al*, 2002). The sea level pressure (SLP) anomaly resultant from heat transfer from sea to atmosphere that is the NAO has made the climate around the North Sea warmer when in positive phase, and cooler when in negative phase. When the NAO is in positive phase, westerlies over Europe are over 8 m s^{-1} greater than in negative phase (Hurrell, 1995). Thus, colder Arctic air is kept away from western Europe by a warm high pressure weather system, and the water of the North Atlantic Current continues to surrender its heat to the atmosphere at latitudes off Ireland. The winter NAO index has been in positive phase for much of the period between 1980 and 2002, coincident with increases in SST and wind speed. 75% of covariance in SST and SLP are explained by the phase of the NAO index (Hurrell, 1995). Wyatt *et al* (2012) found a teleconnection between the 70-130 year period hemispheric SST anomaly described by the Atlantic Multidecadal Oscillation Index (AMO) and the NAO index, such that the water based AMO correlates with a 30 year period moving average of the atmospheric NAO index. The two indices thus both describe ocean climate variability in the Atlantic at different frequencies, in different media.

The NAO has spent periods being in sustained negative phase, notably in the 1960s (Hurrell, 1995) and as described above, in the 20th and 21st centuries it has been generally more positive than the normalised mean 0. When SST anomalies such as the AMO are at their lowest, oceanic heat transport is at its minimum, while atmospheric heat transport is at its maximum, resulting in peak NAO index (e.g. the Atlantic Sub-polar Gyre region having cooler SST when the NAO is in positive phase – Robson *et al*, 2012a). Because positive phase NAO is associated with deeper winter mixing in the Atlantic Ocean (Robson *et al*, 2012b), positive phase NAO correlates with greater oceanic supply of nitrate, and longer phytoplankton growing periods along the western margin of the European continental shelf, as the greater air temperature promotes earlier thermal stabilisation of the water column (Racault *et al*, 2012). Sea surface temperature minima occur in March when NAO is positive, and April/May when NAO is negative (Pingree, 2005), indicating the different strength of North Sea ingress under either condition though as noted before, SST itself is unlikely to limit phytoplankton growth, rather the degree of winter mixing and timing of stratification is the relevant consequence of these hemispheric processes.

Remote sensing of chlorophyll globally has confirmed that warmer seas in temperate and high latitudes correlate with longer growing periods (Racault *et al*, 2012), and that in the North Sea, the peak in chlorophyll has moved earlier (Kahru *et al*, 2011). Phytoplankton colour index (PCI, a proxy for chlorophyll concentration) data from the continuous plankton recorder programme has revealed a correlation with oceanographic events (Burkill and Reid, 2010). The Great Salinity Anomaly described in chapter one, minima in salinity and temperature recorded around the North Atlantic from 1968-82 (Dickson *et al*, 1988) was contemporary with minimal values in PCI in accordance with the transit of the GSA. Low biomass was recorded in the offshore northern north sea in 1976 when the GSA transited through this region in 1976-1977. The CPR recorded low PCI in the Central and British Coastal North Sea in 1977, the GSA transited this region in 1977-78 and low PCI in 1979 coincided with transit of the GSA in the southern continental North Sea, also in 1979 (Edwards *et al*, 2001). The second period in the North Sea represented a warm water event in the late 1980s characterised by high salinities and anomalously warm winters (Becker and Dooley, 1995). SST across the North Sea in 1988-89 was 1-3°C above the 1960-1990 average. Anomalies in PCI increased exceptionally high after 1985, reaching their 3 standard deviation peak in 1989, and peak PCI in the central North Sea was 1 month later in 1990-95 than 1960-1990 (Edwards *et al*, 2001). Enhanced PCI score was observable in the central and southern oceanic regions, the implication being stronger nutrient overturn and stratification had occurred in these regions (Edwards *et al*, 2001). Averaged across the whole North Sea, PCI seasonal patterns moved in the late 1980s from a moderate biomass, bimodal annual cycle to a high biomass, uni-modal cycle, where both bloom periods merged (Beaugrand, 2004). Following the 1980s, the reduced advection of *Calanus finmarchicus* in spring, and the late summer peak abundance of *Calanus helgolandicus* would appear to mean significant grazing pressure on phytoplankon has meant production continues to outpace grazing through the summer.

The CPR is a valuable resource but it is by convention studied with reference to spatially averaged boxes, representative of the central North Sea, northern north Atlantic etc. This is problematic when it comes to inshore seas, which have oceanography influenced by the presence of thermohaline frontal zones which occur as a result of dissipated tidal energy in deeper water causing a density gradient to develop. Offshore seas achieve thermal stratification for longer through the year, while the tides inshore will be of key importance in determining where stratification can occur (Sharples *et al*, 2006). Salinity from rivers and estuaries can make a significant contribution to the formation of frontal zones (Salinity below 35.45 is indicative of some freshwater input – O'Boyle and Raine, 2007). In their study of phytoplankton community composition in the continental shelf sea off northwestern Ireland, O'Boyle and Raine (2007) found a diatom dominated phytoplankton assemblage on the coastal side of the thermohaline front that forms between the ocean and coastal waters. Dinoflagellates dominated the oceanic water. Likewise the waters off Northumberland have a frontal zone, with a clearer distinction between inshore mixed water, and stratified water approximately 10-15km offshore (Gmitrowicz and Brown, 1993). This boundary and alongshore wind are important in forcing inshore currents, and there is a less uniform response of currents to wind inshore than offshore, presumably because of tidal and local bottom entrainment effects. Gmitrowicz and Brown (1993) did not consider large scale North Sea circulation to be important in determining mean flow in the northeast English coastal sea because of the strong density gradients and wind forcing they described. There is therefore a strong reason to investigate the extent to which the phytoplankton in the Dove Time Series are responsive to local phenomena versus the ocean climate indices, the NAO and the AMO.

Besides those described above for CPR and remotely sensed datasets, varying phenological patterns have been observed in the North Sea. Sharples *et al* (2006) modelled chlorophyll peaks in the coastal North Sea off the Firth of Forth, Scotland, and found the signal of the winter NAO important in determining wind stress and thus bloom onset, bringing the bloom forward by approximately 10 days between 1974 and 2003. The effect of wind was strong before 1990, and weaker after this point. At Stonehaven, northeastern Scottish coast, peak diatoms moved earlier in the 1990s and early 2000s, but this trend vanished in the later 2000s. Dinoflagellate peak moved later (1997-2006; Bresnan *et al*, 2009). The pattern in the southern North Sea was for later peaks. At Helgoland Roads peaks have moved later (1962-2002; Wiltshire and Manly, 2004), again by 10-15 days. In the English Channel, no phenological changes were described for phytoplankton phenology at the Plymouth L4 station between 1992 and 2007, though diatoms and *Phaeocystis* had declined in abundance (Widdecombe *et al*, 2010).

As the DTS is in a coastal sea, close to the point at which seasonally stratified and tidally mixed seas form a frontal zone (Hill *et al*, 1993; Gmitrowicz and Brown, 1993), it was not known if inshore or offshore conditions were more important in the seasonal cycle of phytoplankton. The coastal and open North Sea appear to have different contributing factors to biomass (McQuatters-Gollop and Vermaat, 2011). Two sets of environmental data representing conditions close to the coast, and conditions more distant from the coast were used. These are explained more fully in methods below.

2.1.1 ***Aims***

The changing oceanographic and meteorological conditions in the region of the North Sea sampled by the Dove Time Series are likely to have altered the time of year at which water column stability develops, determining the position of phytoplankton in the water column and thus the availability of light and nutrients that are necessary for growth. The aim of this chapter was to determine what change, if any, had there been in phytoplankton abundance, the timing of phytoplankton peak abundance, and the composition of the phytoplankton assemblage. As frontal zone dynamics are likely to impact upon the oceanography in the vicinity of the DTS site, a further aim was to determine which of two sets of data representative of inshore or offshore sea best described variation in the phytoplankton assemblage.

2.1.1.1 ***Null Hypotheses***

- Changing oceanographic and meteorological conditions have had no effect on phytoplankton assemblage composition.

- Changing oceanographic and meteorological conditions have had no effect on phytoplankton abundance.

- Changing oceanographic and meteorological conditions have had no effect on phytoplankton phenology.

- There will be no difference in goodness of fit of multivariate models of phytoplankton assemblage composition using either inshore or offshore predictor variables.

2.2 Methods

2.2.1 *Field sampling*

Phytoplankton were sampled at monthly resolution since 1971 with a methodology that was consistent between years at a site in the North Sea off Northumberland approximately 10km offshore between the Blyth and Tyne Estuaries, at 55° 07'N 1° 20'W. The net size used was a Plymouth 200 (P200) net (UNESCO, 1968) with 63µm mesh and 63µm filtering cod end. The samples retained by such a net were extremely poor at sampling many phytoplankton species due to their small size relative to the coarseness of the net; the phytoplankton sampled were only done so incidentally as the principal target group of the net was small sized zooplankton. The site is approximately 54m deep and each month sampling was undertaken aboard the *R.V. Bernicia*. The P200 net was hauled vertically from 50m depth to the surface four times. The sample in seawater was fixed with buffered formaldehyde to an approximate final concentration of 12% by the addition of 40% formaldehyde in an approximate 30/70 v/v mix shortly after sampling. Mesozooplankton and ichthyoplankton were sampled alongside the phytoplankton using different mesh sizes (200µm net with 200µm cod end, and 1mm net with 200µm cod end respectively). Their communities are described in Chapters 3 and 4, and their total abundances were used as candidate predictors in this chapter.

2.2.2 *Sample analysis and data manipulation*

Samples were analysed using an Olympus CKX31 microscope in brightfield and phase contrast illumination at magnifications of 200-400x. Samples, in 100ml jars, were gently inverted for approximately 1 minute to thoroughly mix the contents and 1ml of suspension was added to a Sedgewick-Rafter counting chamber. This was left to settle for 10 minutes before scrutiny. If it was excessively dense with cells lying on top of each other, another 1ml was diluted with tap water to a suitable working suspension. No obvious damage was observed to cells on taking this step, though future dilutions should probably be conducted with filtered seawater (Ozbay and Jackson, 2010). Chambers were scanned horizontally at a continuous slow pace. Organisms crossing the top of a grid square were considered part of that transect, while organisms crossing the bottom of a grid square were not. Individual cells of colonial organisms, rather than simply the colonies themselves, were considered in abundance class scoring. As samples had been taken with a net it was determined to be inappropriate to attempt quantitative analysis of the samples due to the poor filtration efficiency of the 63µm mesh when considering some small but ecologically important species.

A semi-quantitative approach to analysis was undertaken. Taxa were given a score from 0 to 4 (similar to Škaloud *et al*, 2006; Table 2.1) to describe their level of abundance in the sample and it is this abundance class that was used for all subsequent statistical analyses where abundance was the variable of interest.

Abundance Class	Description
0	Not present in the sample
1	Few (typically <10) in the entire counting chamber
2	Few (typically <10) in a horizontal traverse of the counting chamber
3	Many (typically >10) in a horizontal traverse of the counting chamber
4	Many (typically >10) in a single field of view of the counting chamber

Table 2.1. Semi-quantitative rank classification used for the purposes of estimating phytoplankton abundance in the Dove Time Series fine mesh samples. Due to the coarse mesh size (63μm) fully quantitative analysis would have led to misleading conclusions.

This approach represented the greatest information pay off for analytical effort (Legendre and Legendre, 1998) but was not without *caveats*. Firstly, the abundance class bands were not equal. A single grid square of a Sedgewick-Rafter cell is 1/1000 of the area of the entire chamber, while a horizontal traverse is 1/20th of the entire area of the chamber, thus implying for example that an organism at the classification threshold of Class 4 is 50x more abundant than an organism at the classification threshold of Class 3.

Aside from the quasi-logarithmic ranking progression, the second and more important issue was the filtration efficiency of the P200 net meant certain small taxa were disproportionately predisposed to being classified at a lower abundance class than would be the case had sampling historically been conducted with a Lund tube (Lund and Talling, 1957) or other integrated depth sampling device. To control for this to a limited extent, morphometric data from a range of sources used as identification guides (Tomas, 1997; Horner, 2002; Hoppenrath *et al*, 2009; Throndsen *et al*, 2007; Kuylenstierna and Karlson, 2006; Round *et al*, 1990; Dodge, 1982; Konovalova *et al*, 1989, Plankton*Net - *planktonnet.awi.de* and Algaebase- *www.algaebase.org*) was used to determine the filtration efficiency of the net according to the following equation (Equation 2.1; Hays, 1994):

$$\mathrm{FE} = \frac{1}{1 + \exp\left(-8.9 \times M\hat{L}D - 1\right)} \tag{2.1}$$

Where FE is filtration efficiency and MLD is average maximum linear dimension. From this, the conversion factor FE_{conv} was calculated as (Equation 2.2):

$$\mathrm{FE}_{\mathrm{conv}} = 1 + \left(1 - \mathrm{FE}\right) \tag{2.2}$$

The effect of this manipulation was to weight the abundance class of organisms that were inefficiently sampled by the P200 net, whilst leaving the abundance class of organisms sampled with reasonable efficiency unchanged. The abundance classes recorded in initial analysis were multiplied by $\mathrm{FE}_{\mathrm{conv}}$. These data were not in the scale of 0 to 4 and were rescaled by multiplication of the corrected data by 4 and division by the maximum corrected abundance class value of that taxon. This value was then rounded up to the nearest whole number, resulting in a rebalanced dataset. The effect of these manipulations are shown in Figure 2.1. The mean abundance class for April was 12.5% higher in the converted dataset than in the raw dataset. By comparison, in August when there were proportionately fewer small taxa present, mean abundance class was 8.1% higher in the converted dataset than in the raw dataset. Removal of small taxa whose abundance class would be modified at all abundance classes resulted in the loss of substantial information about the spring growth period that would result from exclusion of these taxa. Nonetheless spring abundance was clearly still underestimated and all conclusions about change in abundance class of spring organisms was not considered relative to the summer/autumn growth period, and *vice versa*.

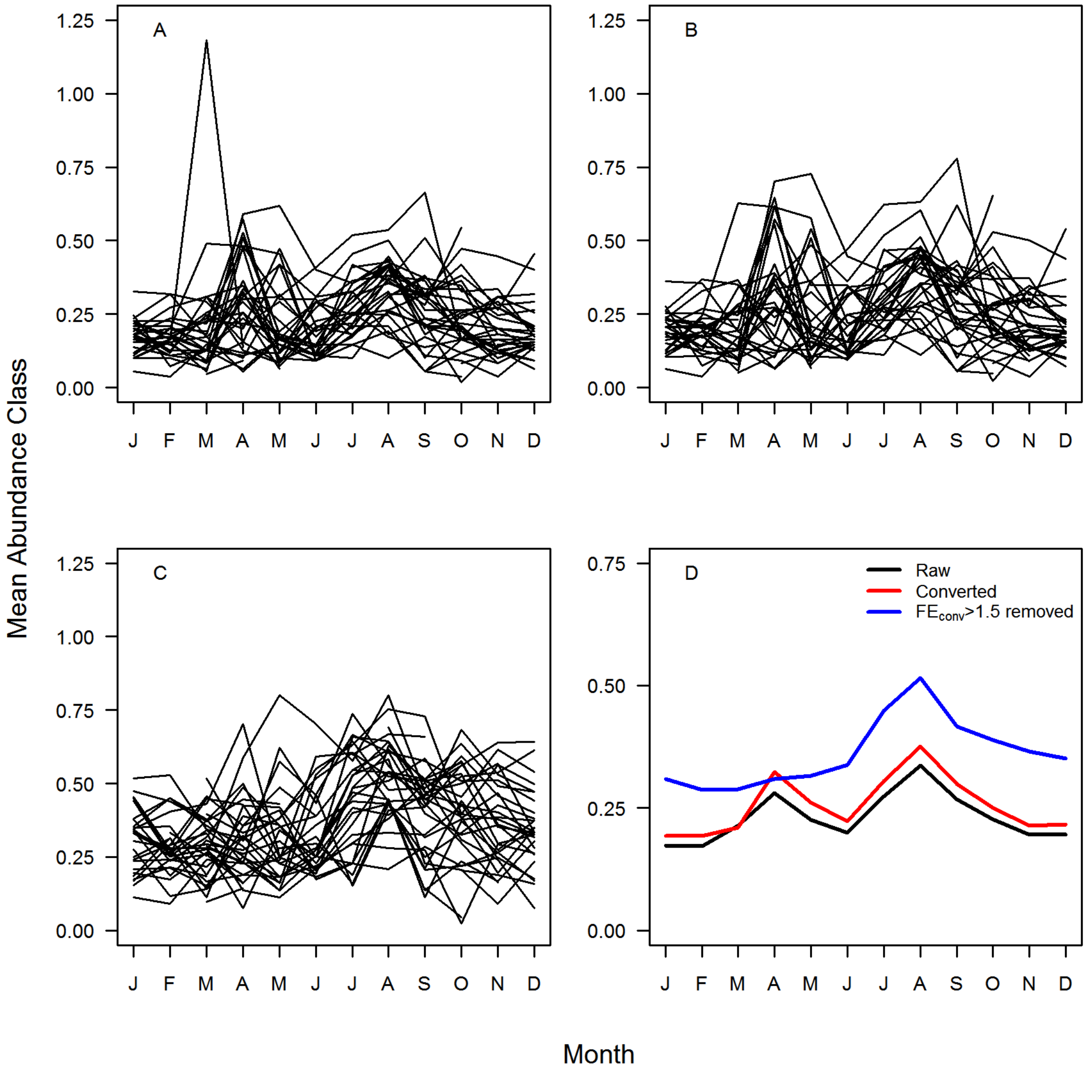


Figure 2.1: The Dove phytoplankton time series. A: Raw abundance class, B: Rebalanced, rescaled abundance class, C: Rescaled abundance class but calculated with taxa with FEconv >1.5 removed, D: Mean abundance class in each case.

2.2.3 *Interpolation of missing values; consideration of approach*

At a monthly resolution, the DTS from January 1971 to December 2008 is a time series 456 rows of data points in length. Due to breakages, missed surveys, sample desiccation and other losses, 121 of these 456 rows of data points were missing. This posed a problem for further analysis as they represented 26.54% of the total dataset. As data from 1989 were missing entirely there were considerations regarding modelling and making predictions from such patchy input data that clearly required attention. It was decided to interpolate missing data points using a method that took into account both inter- and intra-annual variability and was appropriate for ordinal data.

Nearest neighbour, linear model, cubic spline, and autoregressive integrated moving average model approaches to filling missing values were all evaluated and rejected. Nearest neighbour interpolation simply calculates the mean of y_{n-1} and y_{n+1} to interpolate y_n. This results in aesthetically pleasing interpolation where neighbouring values of y are similar, but where there are large differences between y_{n-1} and y_{n+1} or the interpolation is between y_{n-1} and y_{n+a} where a is a number of missing values greater than 1, abrupt and clearly unrepresentative straight lines of points are plotted on a graph of (x_n,y_n). Linear interpolation goes a step further by relating changes in y to changes in x by determining linear regression coefficients across a range of points either side of a missing value with similarly unacceptable straight line interpolation across larger gaps.

Cubic spline interpolation calculates *n* piecewise cubic polynomials of x and as such was considered a candidate operation for bridging gaps in the DTS due to the approximation of seasonal variation afforded by a higher order polynomial function. The function provided an excellent approximation of original data where missing values were small, however the DTS is characterised by high variability between points due to its seasonal nature that induce overshoot and undershoot problems. This is caused by the cumulative sum of the 2nd derivative terms of the surface taken over each point in the surface being minimised, resulting in a minimum curvature of the spline, represented where there are sharp gradients between data points by overshoots or undershoots. As these overshoots in a number of cases broke the maxima and minima of y across the whole time series, cubic spline interpolation was not chosen as a method of interpolation.

2.2.3.1 *Interpolation stage 1: Stineman interpolation*

Stineman (1980; R implementation by Johannesson *et al*, 2009) developed this simple method initially for less computationally intensive interpolation of sparse points compared to linear interpolation of many points. Taking points 1, 2, 3 as one triangle, the midpoint of line (1,3) here called point 4 is used to be a vertex of another triangle made of points 1, 4 and 5, the point beyond line (1,2) that forms the triangle. Lines (1,5) and (3,2) represent tangents of the circle that passes through points 1 and 3 with the midpoint of the curve passing through lines (4,5). The interpolated point 6, lies at the intersection of line (4,5) and the arc of the circle between points 1 and 3. See Figure 2.2 for a diagram describing an iteration of the process.

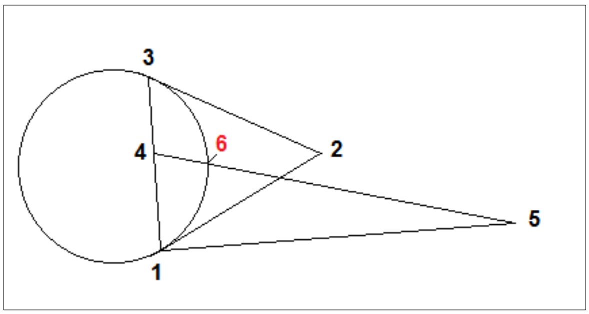


Figure 2.2: Demonstration of one iteration of Stineman interpolation. Points 1, 2 and 3 are known data points, with a missing value between them. Stineman interpolation functions by considering lines (3,2) and (1,2) to be tangents of a circle which passes through points 1 and 3. The midpoint of line (1,3), point 4, is used to make a triangle with the other vertices at point 1 and 5. The condition of Stimenan interpolation is that the line (4,5) must pass through the midpoint of the circle. Point 6, in red, is the point at which line (4,5) intersects the mid point of the arc of the circle between points 1 and 3. This, point 6, is the interpolated missing data point.

The resulting interpolated curve is monotonic between points and constrained by the need to pass through the first and last point such that oscillations manifested as overshoots in cubic spline interpolation are avoided. The disadvantage of the method was the strict monotonic condition which of course when bridging a gap of 12 data points representing 1989 replaced the expected seasonal cycle with a shallow curve.

While the Stineman method was the most conservative whilst being more informative than lower order interpolation methods, the interpolation on chronologically (year-month) ordered data was a poor approximation of expected values. Data for each taxon were subsetted by month such that a separate interpolation was applied to each taxon, by each month. Interpolations were rounded to the nearest whole number as the process took ordinal data as input but produced continuous data as output. The DTS was reassembled in its original order. Stineman interpolation cannot by its nature of calculation make forecasts or hindcasts meaning missing values were still present for January and February 1971 as well as October to December 2008, at either end of the DTS. This process reduced the missing values from 13310 to 5917. It was not possible to bridge large gaps (for example 1989 was entirely missing) whilst including seasonal variation in abundance class. For this a second stage of interpolation was required.

2.2.3.2 *Interpolation stage 2: ordinal logistic regression*

As the abundance data gathered was from an inefficient source and had been recorded as semi-quantitative ordinal data there were a number of requirements for interpolation and extrapolation that were not provided by conventional means. An ordinary least squares method of regression gives a value of y for x within certain confidence limits. Disregarding other considerations data in this format will be of little use if confidence intervals for an estimate of y are greater than ±50% of y. Similarly, time series models such as ARIMA output a mean ± error which is also impossible to reconcile with the either/or nature of the input data. Ordinal logistic regression is a special case of binomial regression which outputs probabilities that for a given x, y will be one of the range of ordinal input data (Harrell, 2009).

Data were once again subsetted by month and separate ordinal logistic models were applied to each taxon for each month. A vector of the predicted probabilities of y belonging to class 0:4, denoting every value for a given month for the period 1971-2008 were output. 34.12% of the subsets analysed were significant at alpha 0.1. Where model terms were not significant or where the model could not run (e.g. many/all 0s) missing values were left in place. Where the model was significant, the predicted class with the highest probability was used to replace the missing value. This operation resulted in 3621 cases (61.12%) being filled. Extrapolations were applied to terminae of the time series (January and February 1971 and October to December 2008) as well as being used to bridge larger gaps in the DTS.

2.2.3.3 *Replacement of remaining short gaps*

The data were reordered to the original format and Stineman interpolation was applied for a third time to replace as many remaining missing values as possible. The remaining 450 missing cases were manually inspected. It was decided it was reasonable to replace these cases with 0 where the rest of the month subset was 0, or to perform a local average of the neighbouring three points where it was not. This was expected to have negligible impact on statistics calculated from these data as those cases manually interpolated represented 0.89% of the dataset. Figure 2.3 shows the interpolated time series.

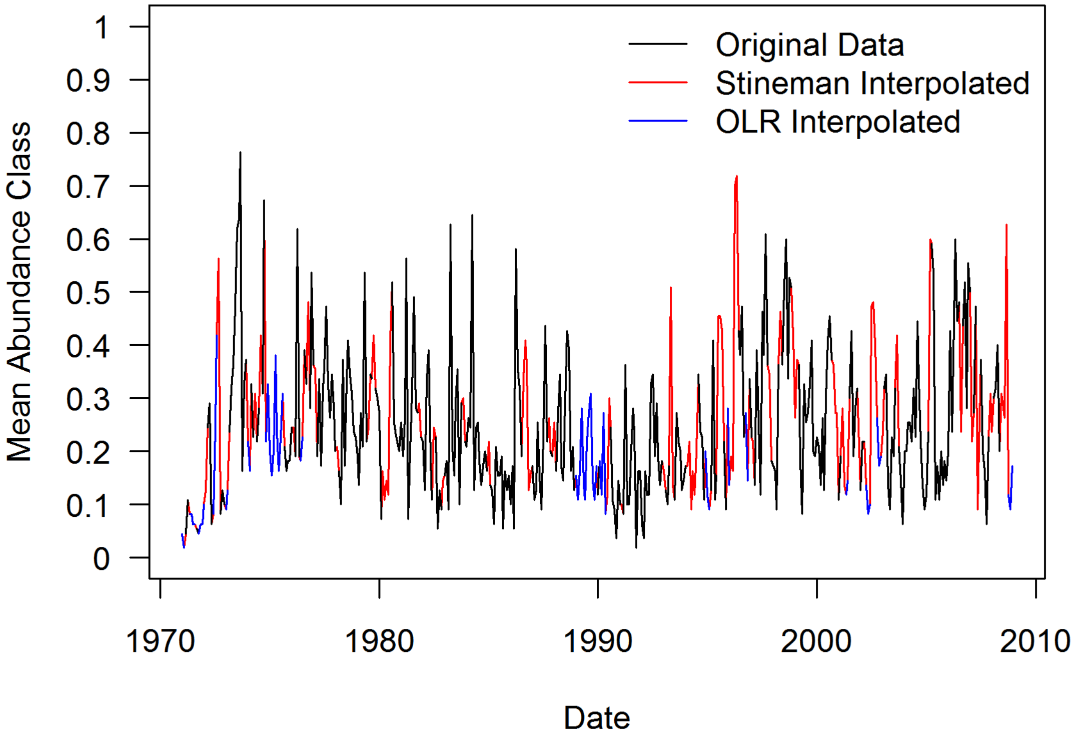


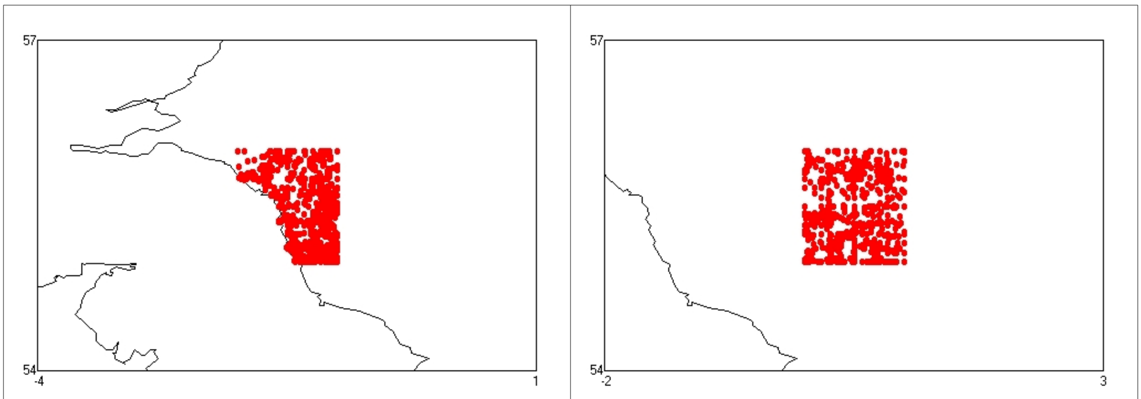
Figure 2.3: Dove Time Series after two stage replacement of missing values with Stineman interpolated (red) Ordinal Logistic Regression interpolated and extrapolated (blue) cases. Original Data are black.

2.2.4 *Identification of species affinities*

The phytoplankton record in the DTS is diverse, which complicates summarising the response of phytoplankton to external drivers of change in community and abundance class. Some way to assess the aggregate responses was required. The following analyses were conducted to identify periods in the DTS that were numerically and qualitatively distinct from neighbouring periods, in an attempt to identify candidate community shift events, and to describe variation in species with common responses to changes in these predictors. The variables used for environmental predictors are summarised in Table 2.2. Oceanographic and meteorological data were divided into inshore and offshore datasets – inshore was represented by data from within a box from 55 to 56°N and -2 to -1°E, offshore by data from within a box from 55 to 56°E and 0 to 1°E (Figure 2.4). Additionally, nutrient data were secured form the European Environment Agency from 1981-2008, but these were too patchy to be used directly in analysis. See Figure 2.23. See figures A7.2 to A7.4 in the appendix for full time series of the ICES and NOAA datasets.

Parameter	**Source**	**Units**
SST*	ICES	° C
Salinity*	ICES	none
NAO index (PC Based)	NCAR	none
AMO anomaly	NCAR	° C
Wind Speed*	NOAA (ICOADS 1°x1°)	M s^{-1}
U-wind (East-West)*	NOAA (ICOADS 1°x1°)	M s^{-1}
V-wind (North-South)*	NOAA (ICOADS 1°x1°)	M s^{-1}
Cloud Cover *	NOAA (ICOADS 1°x1°)	Okta
Zooplankton Abundance	DTS	Individuals m^{-3}

Table 2.2: Environmental and biological predictors used in this study. Values with an asterisk had inshore and offshore variants. ICES: International Council for the Exploration of the Sea. NCAR: National Centre for Atmospheric Research. NOAA ICOADS: National Oceanic and Atmospheric Administration International Comprehensive Ocean-Atmosphere Data Set. DTS: Dove Time Series.



Inshore box: 55 to 56°N and -2 to -1°E

Offshore box: 55 to 56°E and 0 to 1°E

Figure 2.4. Data boxes used for definition of inshore and offshore areas. Red points represent ICES temperature and salinity data points made during the 1969-2008 period.

An autoregressive integrated moving average (ARIMA) model was diagnosed with autocorrelation (ACF) and partial autocorrelation (PACF) functions to describe cyclical patterns in the data and interannual trends respectively. These were used to construct an initial ARIMA model of interannual variation in mean phytoplankton abundance class across all taxa. To explore the ARIMA model of mean phytoplankton abundance class (now largely excised of seasonal variation) for distinct shifts, linear breakpoint analysis was applied (Bai and Perron, 2003; Zeileis *et al*, 2002; Zeileis *et al*, 2003). The process considers a dataset with m breakpoints where coefficients of regression models applied to those data shift from one state to another, remaining stable in that segment. The model has m + 1 segments with different coefficients. The model minimises residual sum of squares (RSS) per segment thus calculating the optimal number of breaks depending on the minimum size segment specified. The lowest BIC (Bayesian Information Criterion) partition was associated with optimum breakpoints and the minima of BIC and RSS should coincide.

Constrained correspondence analysis was carried out on phytoplankton with respect to the available predictors. The responses of phytoplankton taxa to CCA eigenvectors were used to determine sensitivity to climate and other trophic level variables correlated with these eigenvectors. The R package 'vegan' (Oksanen, 2010) was used for multivariate analysis. Model selection was accomplished with the 'ordistep' function, which used minimised Akaike Information Criterion as its selection statistic. High scores represented a tendency to be more common/sparse along a gradient associated with a CCA eigenvector. Weighted average species scores on each axis were used to combine abundance class of species into one of four groups for time series analysis. Thus the collective abundance class of taxa with common affinities to the CCA axes (and thus the linear combination of the effect input predictors) could be constructed and the time series structure and behaviour described, and forecast a modest period into the future.

2.2.5 *State space time series modelling*

2.2.5.1 *Extracting seasonal peaks from coarse resolution time series*

The DTS was sampled at a roughly monthly resolution, and these data placed in idealised month boundaries, implying each sample was sampled ~30 days apart. This is of course a simplification of the reality. Compared to the level of detail present in for example the Helgoland Roads time series, which samples at daily resolution, there was a requirement to model the 96.71% of the annual cycle not so described by a monthly resolution time series, in order to identify gradual change in peak abundance class between all divisions of the DTS. To accomplish this, a State Space Model (SSM; Dethlefsen and Lundbye-Christensen, 2006; Petris, 2009) was constructed with interannual and seasonal components defined such that interannual variability in average abundance class was described by a first order polynomial function, and seasonal variability was defined by a Fourier form harmonic function with wavelength 12:

$$y_k = T_k + H_k \tag{2.3}$$

Where the trend component T_k is modelled as:

$$T_k = T_{k-1} + \beta_{k-1} + \omega_k^{(1)} \sim N(0, \sigma^2)\ ,\ \beta_k = \beta_{k-1} + \omega_k^{(2)} \sim N(0, \sigma^2) \tag{2.4}$$

Where T_{k-1} is the prior distribution of the time varying component and β_{k-1} is the prior distribution of the static component and $\omega_k^{(1)}$ and $\omega_k^{(2)}$ are error terms.
The Harmonic seasonal component is modelled as:

$$H_k = \theta_{ck} \cos\left(\frac{2\pi}{12k}\right) + \theta_{sk} \sin\left(\frac{2\pi}{12k}\right) \tag{2.5}$$

$$\theta_{\mathrm{ck}} = \theta_{c,k-1} + \omega_k^{(c)} \sim N(0, \sigma^2)\ ,\ \theta_{\mathrm{sk}} = \theta_{s,k-1} + \omega_k^{(s)} \sim N(0, \sigma^2) \tag{2.6}$$

Where θ_{ck} and θ_{sk} are the states of the Kalman smoothed sine and cosine components of the seasonal trend. Initial values for T, β, θ and ω were established by using the output of a basic structural model:

$$x_t = m_t + s_t + \varepsilon_t\ ,\ \varepsilon_t \sim N\left(0, \sigma^{2(\varepsilon)}\right) \tag{2.7}$$

$$s_{t+1} = -s_t - \ldots - s_{t-s+2} + \omega_t\ ,\ \omega_t \sim N\left(0, \sigma^{2(\omega)}\right) \tag{2.8}$$

Where m is the level component, and s is the seasonal component, ε and ω are error terms. From this the two part arctangent of coordinates made from the vectors θ_{ck} and θ_{sk} was calculated. The two term arctangent (atan2) is the angle in radians between the positive x axis and the vector (0,0) to coordinates (x,y), returned in the range –π to π. The modelled harmonic component approximated the seasonal cycle and the atan2 of this component for a given month indicated the location on the seasonal curve and therefore the location of the peak in that year. Dividing the atan2 value by 2π reduced this to range -0.5 to 0.5, multiplied by 12 the output corresponded to segments on a circle that when back transformed located the seasonal peak (Dethlefsen *et al*, 2009).

2.2.5.2 *Describing interannual cycles and forecasting into the future*

For forecasting into the future, the longer term cyclical behaviour of a model needed to be described by a similar model to that used to describe seasonal and stochastic variation (the latter model component is data dependent and therefore a poor forecasting tool). The division of the time series into taxa associated with different CCAs was used to produce state space models with components describing three different types of variation in average class. Unstructured interannual variation was described using a local linear trend model:

$$Y_t = \mu_t + \upsilon_t \, , \; \upsilon_t \sim N(0, \mathrm{V}) ,$$

$$\mu_t = \mu_{t-1} + \beta_{t-1} + \omega_{t,1} \, , \; \omega_{\mathrm{t},1} \sim N\left(0, \sigma_\mu^2\right) , \tag{2.9}$$

$$\beta_t = \beta_{t-1} + \omega_{t,2} \, , \; \omega_{\mathrm{t},2} \sim N\left(0, \sigma_\beta^2\right) \tag{2.10}$$

(2.11)

Where μ_t is the 'random walk' component composed of its prior state at t-1, its time varying slope β and the associated uncorrelated error terms υ, $\omega_{t,1}$ and $\omega_{t,2}$. The effect is to track change in Y over time without a defined structure. Maximum likelihood estimation was used to obtain values of the observation and system variance parameters.

The resulting tracked level of each time series tended to follow underlying irregular periodicity that was described in forecasts as a second interannual component IH_k, specified as a trigonometric function with period dependent on the maximum frequency of a periodogram of annually aggregated data (to avoid false identification of shorter period peaks caused by time series autocorrelation):

$$\mathrm{IH}_k = \text{¿} \sum_{j=1}^{\infty} S_j(t) \tag{2.12}$$

$$S_j(t) = a_j \cos(\mathrm{t}\omega_j) + b_j \sin(\mathrm{t}\omega_j) \tag{2.13}$$

Where $S_j(t)$ is the sum of the cosine and sine harmonics multiplied by the coefficients a_j and b_j. ω in this component was the fundamental frequency, calculated from its relationship with the period of IH_k which as stated above was estimated using autocorrelation functions at very long lags. The period, τ is related to ω by $\tau\omega = 2\pi$.

Thirdly, seasonal component was specified with a second Fourier form harmonic component, in the same manner as 2.13, however with a defined period of 12. The addition of a trigonometric function operating at timescales outside of 12 months allowed for interannual quasi-cyclic variation to be forecast. Kalman filtering was used to carry out single value decomposition of the variance matrices of the observation and error components of the model and provide fitted values (Petris *et al*, 2010). Predicted values including seasonal and non-linear interannual components were therefore possible with the models specified.

2.2.5.3 *Sensitivity analysis*

Validation of the goodness of fit of the models specified was accomplished using two approaches. Firstly Forward Filtering Backward Sampling (FFBS; Petris, 2010) was used to check the breadth of posterior distributions of the 'true' level of each time series. The process calculates a draw from the posterior distribution of the state (unstructured interannual and seasonal) vectors. 10 recursions of FFBS were run per time series validation, and each recursion used one less year of validation data than the previous recursion. A Kalman filtered state space model was used as the optimal filtered distribution upon which FFBS drew samples for intermediate distributions decrementing to the beginning of the time series from the most recent output of the Kalman filtered state space model. The closeness of each recursion was inspected visually to assess the performance of the model.

2.2.5.4 *Model validation*

To determine if predictions obtained from the models were realistic, the state space models were applied to all but the final five years of each time series and predictions were made on the 'future' state up to the end of the real time series data. The predicted final five years was correlated with the real remaining 5 years. The predicted output was complicated by the stochastic linear trend component reverting to a linear forecast from the trajectory of the most recent points. This led to a tendency for this component to drag entire forecasts upwards or downwards based on the most recent real data points, influencing forecasts where it was no longer communicating ecologically relevant information. Therefore the prediction was based on a model where interannual variation was described by the harmonic term determined from autocorrelation functions of the smoothed Kalman filtered time series and seasonal components configured to begin their prediction from the last model output of the Kalman smoothed deseasonalised model.

2.3 Results

2.3.1 *Abundance and community composition*

The Dove Time Series contained 139 distinct phytoplankton taxa matching up to date names in Algaebase as of 2008. These were at species or genus level and 2 indeterminate categories, for unidentified diatoms and dinoflagellates. The highest recorded number of taxa in a single sample was 51 (April 2006), while the lowest was 4 (March 1972). The median number of taxa for the entire time series was 21 with an interquartile range of 16 -29. Diatoms were split between 19 orders across 3 classes as well as one species *Mediopyxis helysia* that is currently *incertae sedis,* and also those diatoms that could not be identified. Dinoflagellates were spread across 8 orders as well as indeterminate specimens and cysts. Other groups recorded were Silicoflagellates, Cyanobacteria, Chlorophyceans and Coccolithophorids. Microflagellates were recorded so infrequently they were excluded from analysis. A full species list is included in appendix (Table A7.1), including indication of the months when observations were most or least frequent.

The highest number of diatom taxa found in a given month was 40 (April 2006) and there were two months (June 1987, May 1995) when there were no diatom taxa present. The whole time series median number of diatom species in a sample was 10.5 with an interquartile range of 6-17. Dinoflagellates had over the course of the time series followed a tighter seasonal cycle with a median presence of 8 with interquartile range of 5-11. A minimum presence of zero was found 4 times (March 1972, March 1985, April 1985, November 2007) and a maximum was observed in June 1996 of 20 distinct dinoflagellate taxa. Mean annual taxon richness in the DTS is shown in Figure 2.5.

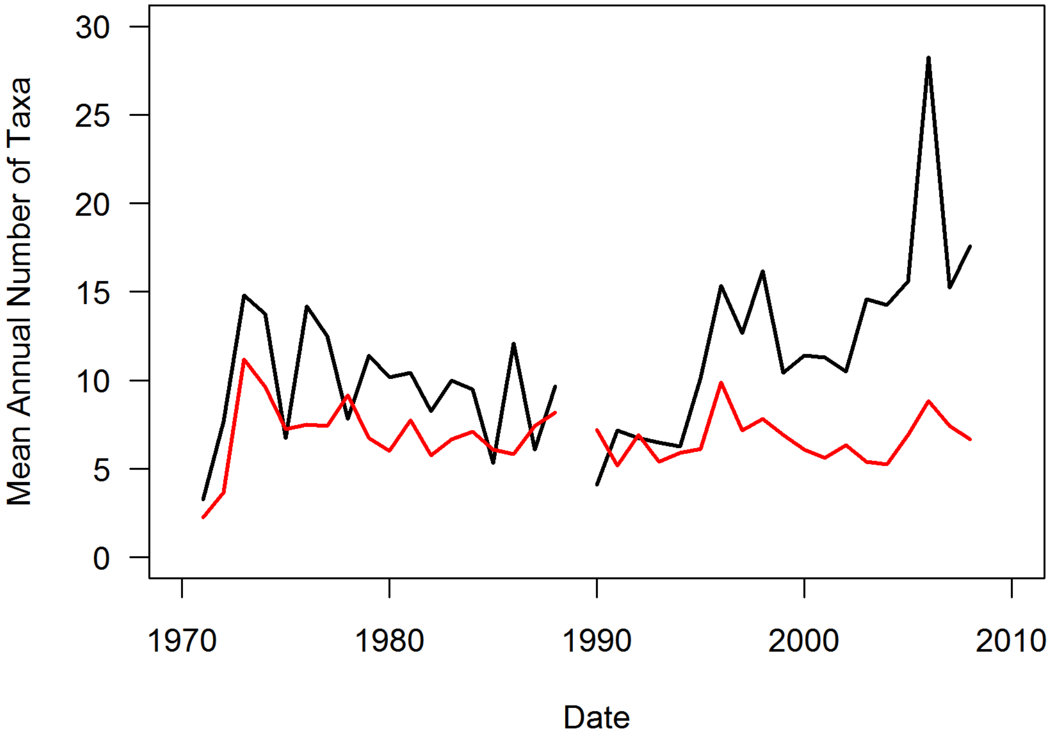


Figure 2.5: Mean annual taxon richness of the Dove Time Series Diatoms (black) and Dinoflagellates (red). 1989 is absent as full taxon richness data were used as opposed to the fully interpolated dataset that was based on a smaller number of taxa that had been corrected according to the filtration efficiency of the P200 net.

The interpolated time series contained 109 species, for which morphometric data were available to adjust abundance class. Of interest were periods of change in the mean abundance class from one stable state to another. As there was structure in both ACF and PACF graphs, and the subject of interest was the interannual change in mean class, an initial model with both autoregressive and moving average terms as well as a single degree of differencing to model trend in mean class was specified (Figure 2.6).

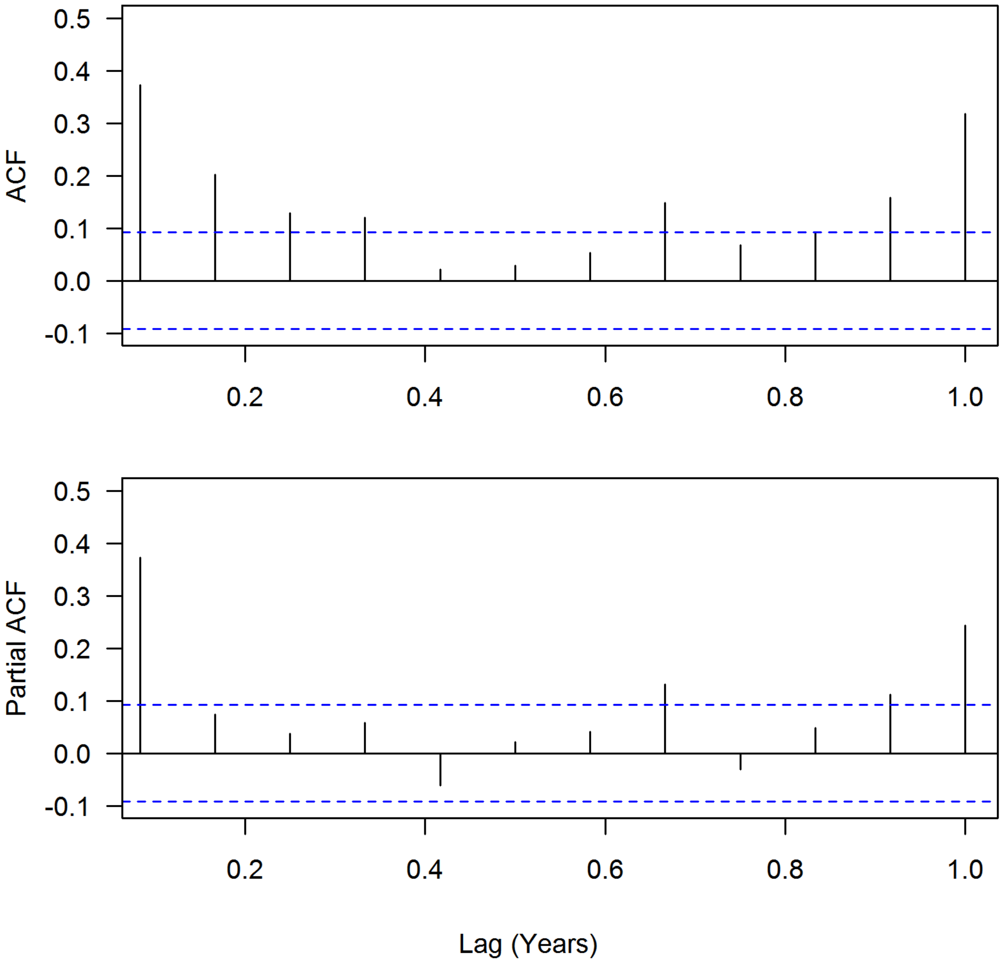


Figure 2.6: Autocorrelation (ACF) and partial autocorrelation (PACF) analysis of DTS total phytoplankton abundance class. ACF demonstrates periodicity which must be taken into account when modelling trends. PACF demonstrates a 1st order autoregressive term should be added to the model, due to the 1 year lag present.

Linear breakpoint analysis metrics diverged after an iteration with 2 breaks in the total abundance class of all phytoplankton in the DTS (Figure 2.7). The breaks identified are summarised in Table 2.3. The high range of dates on either side of the 1984 break point, from 1982 to 1988, suggested this was unlikely to be a step change in abundance, which was borne out by the lack of a step in abundance between periods. Compared to this was the second break date, 1995, which has a much narrower 95% confidence interval. Post 1995, abundance was retained at higher abundance than the preceding decade.

LL95%	Break Date	UL95%
1982-7	1984-4	1988-11
1993-4	1995-6	1996-4

Table 2.3: Dates at which breakpoint analysis achieved minimised RSS/BIC for phytoplankton time series.

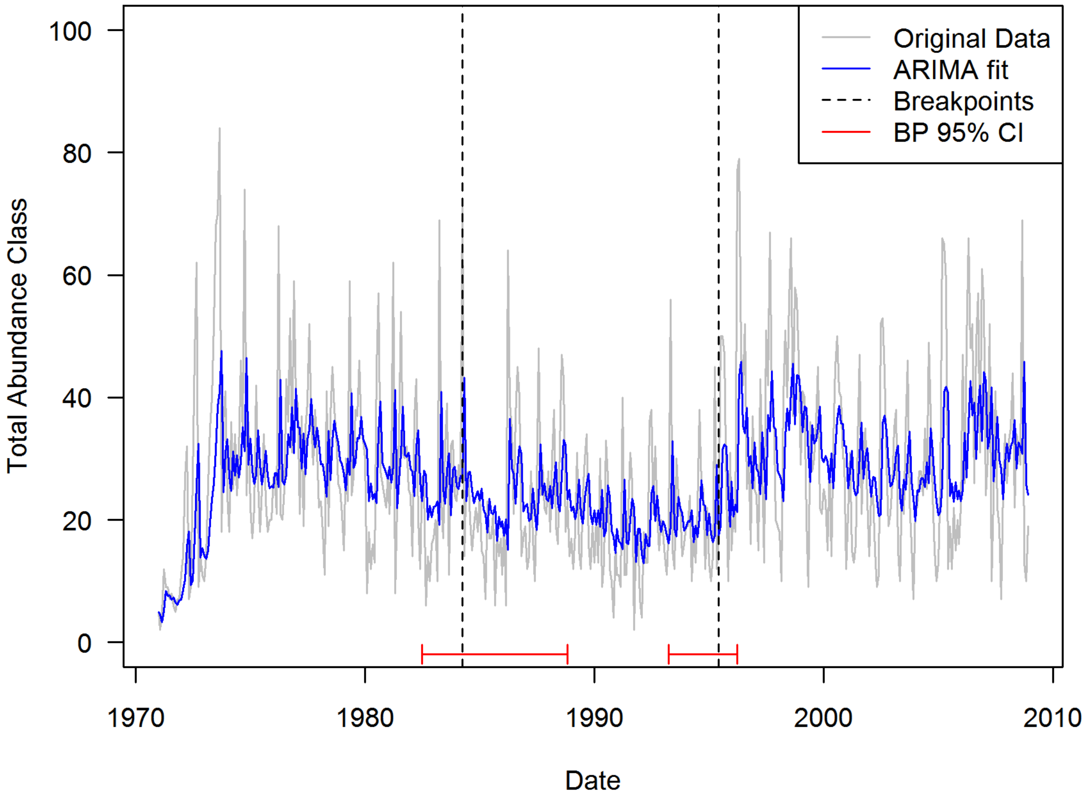


Figure 2.7: The Dove Time Series phytoplankton time series. Blue line is ARIMA model fit, dashed lines are the points at which RSS is minimised by linear breakpoint analysis, red lines are confidence intervals associated with breaks.

2.3.1.1 *Community composition*

Constrained Correspondence analysis (CCA) was performed on the community data to determine which predictors were important in organising community composition. Only species observed more than 10 times in the time series were included in analysis, reducing the number of species from 109 to 89. Model selection was achieved by minimising Akaike Information Criterion. CCA suggested strong roles in species assemblage composition for wind, SST, cloud cover, zooplankton abundance and the AMO (Figure 2.8). Higher dimension variability was explained by inshore salinity and the NAO index. AIC selection removed all wind direction data as candidate predictors. There was a selection preference for offshore variants of datasets over inshore (offshore: wind, SST and cloud cover; inshore: salinity). In the case of offshore SST and wind speed, offshore correlated strongly with inshore so it is unimportant which of those was selected at the expense of the other in model selection. Cloud cover and salinity were both weakly correlated with their counterpart time series and so their selections were indicative of an inshore water influence and an offshore meteorological influence to the phytoplankton. Correlations between the variables and axes are summarised in table 2.4.

Variable	CCA1 correlation	CCA2 correlation
SST (offshore)	0.97	0.04
Wind Speed (offshore)	-0.62	0.52
AMO	0.32	-0.44
Zooplankton abundance	0.24	-0.29
Cloud Cover (offshore)	-0.21	0.38
Salinity (inshore)	-0.08	0.03
Winter NAO	0.07	-0.05

Table 2.4: Correlation coefficients of input predictors with CCA eigenvectors. NAO and Salinity explained more variation on higher dimension axes and were uncorrelated with CCA1 or CCA2.

Splitting CCA into quadrants revealed four sets of conditions that were found at greatest abundance during the four seasons. Taking the linear constraints of these, CCA1 as expected dominated by temperature which has risen over study period in more or less linear fashion. This axis explained 41.64% of constrained variance. CCA2 showed stability to 1980s then more negative into 2000s, indicating variation partly explained by long period of the AMO. CCA2 explained 14.51% of constrained variance. These two linear constraints were used in a GLM which revealed significant effects on overall abundance class at alpha 0.1 for both sets, and significance at alpha 0.01 for CCA2. CCA1 was moderately negatively correlated with nutrients as would be expected for a summer dominant signal – lower importance of CCA1 in determining abundance class suggested weak evidence for nutrient trends at the DTS, elsewhere supported in this study. The change in conditions in 1990s and 2000s associated with CCA2 (mixed wind conditions, less cloudy, more positive AMO anomaly) supported the alternative hypothesis to no effect: meteorological and oceanographic state influenced abundance class of phytoplankton at DTS.

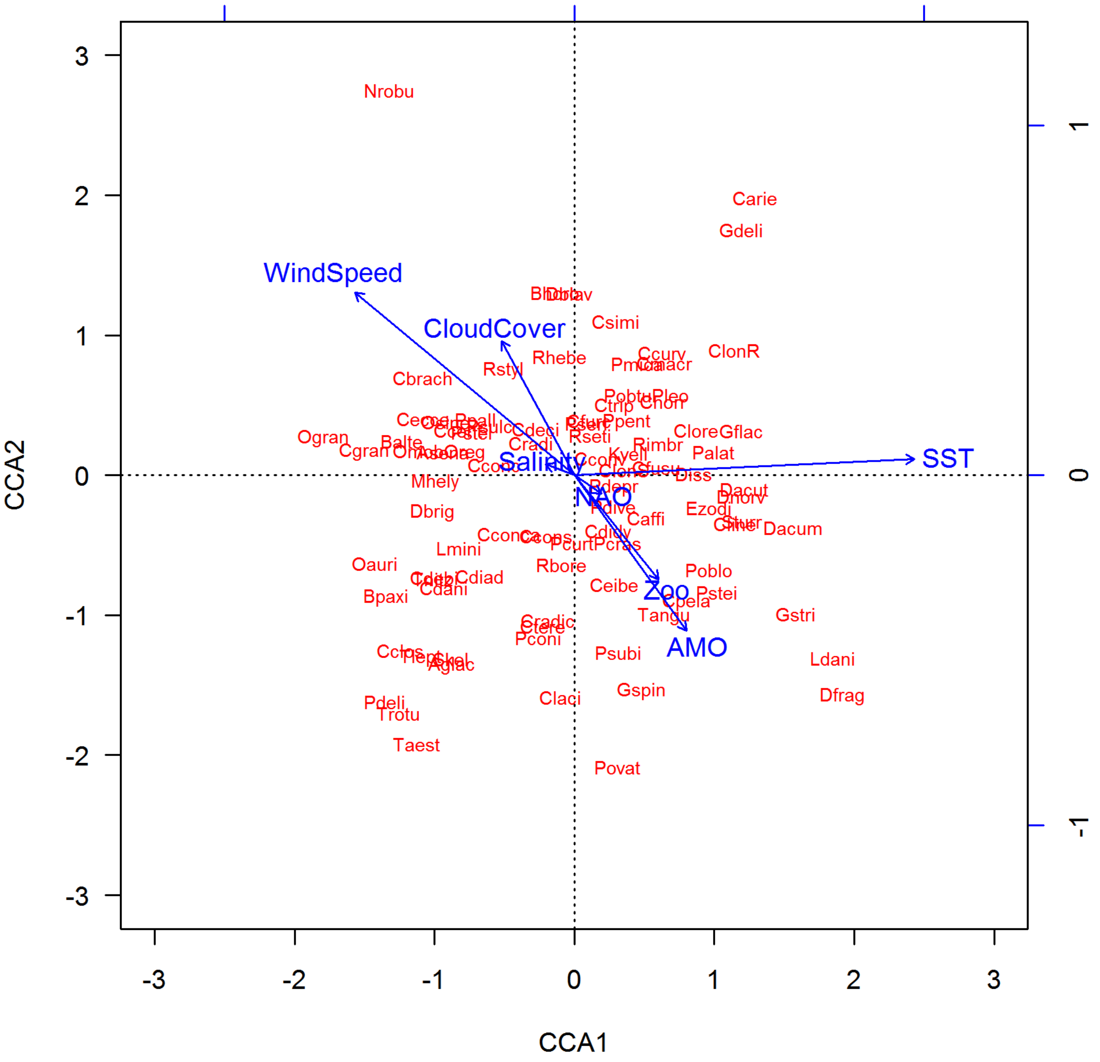


Figure 2.8: DTS phytoplankton constrained correspondence analysis, first two eigenvectors. Species codes are organised in two dimensional space according to their weighted average scores against CCA1 and CCA2. The biplot arrows are aligned according to their correlation with either axis and scaled according to the combined weighted average score of all sites against each axis. Interpretation of combinations of scores of difference sign in table 2.5.

Sign combination	**SST**	**Wind Speed**	**AMO**	**Zooplankton Abundance**	**Cloud Cover**	**Season**
CCA1+ CCA2+	Warm	Mixed	Negative	Low	High	Autumn
CCA1+ CCA2-	Warm	Mixed	Positive	High	Low	Summer
CCA1- CCA2+	Cool	Mixed	Negative	Low	High	Winter
CCA1- CCA2-	Cool	Mixed	Positive	High	Low	Spring

Table 2.5: Interpretation of conditions under each quadrant of CCA in figure 2.8. Salinity and NAO were correlated with higher dimension axes.

Species were divided according to their weighted average scores against CCA1 and CCA2. Total abundance class per month was averaged by year to describe the seasonal patterns present (Figure 2.9). This revealed two groups strongly influenced by the positivity of the CCA1 gradient, peaking in summer and autumn. Spring phytoplankton, peaking sharply in April were those with negative scores on both axes. Winter phytoplankton scored negatively on CCA1 and positively on CCA2; unsurprising as these phytoplankters are those in stationary phase over winter. The state of environment predictors in each combination above are summarised in table 2.5. As the smaller phytoplankton present in spring were poorly retained by the net, the small spring peak relative to autumn or summer is an artefact, and the level of abundance was less important than the patterns determined. Diatoms dominated the winter and spring groupings, while dinoflagellates were dominant in the summer and autumn groupings (Table 2.6). *Ceratium* dinoflagellates were mostly found in autumn, while *Dinophysis* dinoflagellates were found mostly in summer. *Protoperidinium* were found year round, with a heavy bias to summer and autumn. *Chaetoceros* and rhizosolenoid diatoms predominated in summer and autumn. *Coscinodiscus* and *Odontella* were mostly found in winter. *Chaetoceros*, *Thalassiosira* and *Skeletonema* were found mostly in spring.

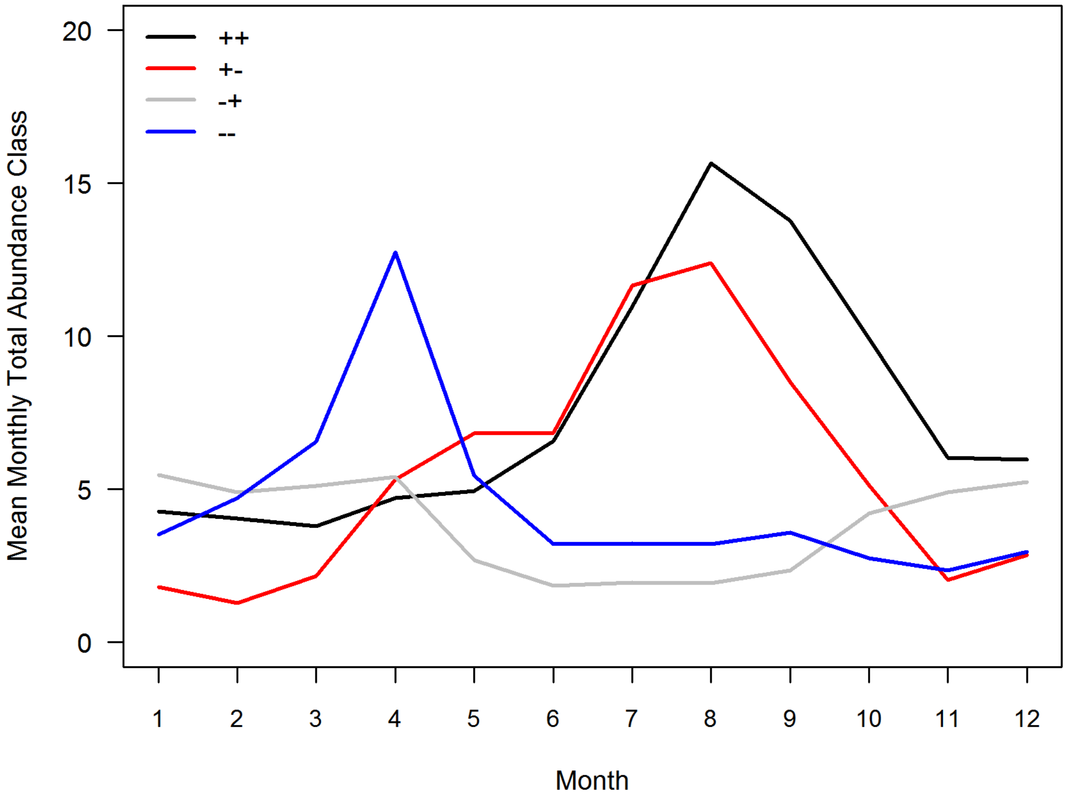


Figure 2.9: CCA partitioned phytoplankton time series. Legend indicates combination of scores against axis CCA1 and CCA2.

Group	Diatoms	Dinoflagellates
++ (Autumn)	*Chaetoceros convolutus, Chaetoceros curvisetus, Chaetoceros lorenzianus, Chaetoceros similis, Guinardia delicatula, Guinardia flaccida, Proboscia alata, Pseudo-nitschia 'seriata'* group, *Rhizosolenia imbricata, Rhizosolenia setigera*	*Ceratium arietinum, Ceratium furca, Ceratium fusus, Ceratium horridum, Ceratium longipes* (rough and smooth forms), *Ceratium macroceros, Ceratium tripos, Dissodinium* or *Pyrocystis, Kofoidinium velleloides, Prorocentrum micans, Protoperidinium obtusum* or *leonis, Protoperidinium pentagonum*
+- (Summer)	*Chaetocers affinis, Chaetoceros didymus, Chaetoceros eibenii, Cerataulina pelagica, Dactyliosolen fragilissimus, Eucampia zodiacus, Guinardia striata, Leptocylindrus danicus, Stephanopyxis turris, Thalassiosira anguste-lineata*	*Ceratium lineatum, Dinophysis acuminata, Dinophysis acuta, Dinophysis norvegica, Gonyaulax spinifera, Protoperidinium curtipes* or *crassipes, Protoperidinium depressum, Protoperidinium divergens, Protoperidinium oblongum or claudicans, Protoperidinium ovatum,*

		Protoperidinium steinii, Protoperidinium subinerme
-+ (Winter)	*Actinoptychus senarius, Biddulphia alternans, Bellerochea horologicalis, Coscinodiscus centralis, Coscinodiscus concinnus, Chaetoceros decipiens, Coscinodiscus granii, Dactyliosolen blavyanus, Neocalyptrella robusta, Odontella granulata, Odontella mobiliensis or regia, Odontella sinensis, Podosira stelligera, Paralia sulcata, Rhizosolenia hebetata, Rhizosolenia styliformis*	*Protoperidinium pallidum* or *pellucidum, Cladopyxis spp.*
-- (Spring)	*Asterionellopsis glacialis, Bacillaria paxillifera, Ceratoneis closterium or Nitzschia longissima, Chaetoceros concavicorne, Chaetoceros constrictus, Chaetoceros danicus, Chaetoceros debilis, Chaetoceros diadema, Chaetoceros laciniosus, Chaetoceros radicans, Chaetoceros teres, Ditlyum brightwellii, Leptocylindrus minimus, Mediopyxis helysia, Odontella aurita, Pseudo-nitszchia 'delicatissima'* group, *Rhizosolenia borealis, Skeletonema spp., Thalassiosira aestivalis or nordenskioeldii, Thalassiosira leptopus, Thalassionema nitzschioides, Thalassiosira rotula or gravida*	*Protoperidinium conicum* or *conicoides*

Table 2.6: Phytoplankton species assemblages as identified in CCA. Diatoms predominate in winter and spring, dinoflagellates in summer and autumn.

Plotting these groups summed as time series indicated there was clear interannual structure in abundance class for all four groups. Periodograms of detrended time series indicated the strongest signal at frequency 0.4-0.475. This meant between approximately 2 and 2.5 cycles at this wavelength were observable between 1971 and 2008 (Figure 2.10). Periods are summarised in table 2.6. Periodicity between approximately 14 and 18 years was discernible as the dominant modes of variability in the annually aggregated time series (Figure 2.11).

Group	Peak Frequency	Number of periods	Wavelength (Years)
++ (Autumn)	0.475	2.11	17.575
+- (Summer)	0.4	2.5	14.8
-+ (Winter)	0.4	2.5	14.8
-- (Spring)	0.4	2.5	14.8

Table 2.7: Spectral analysis of time series of phytoplankton species summed according to CCA axis scores. Wavelength determined as time series * peak frequency.

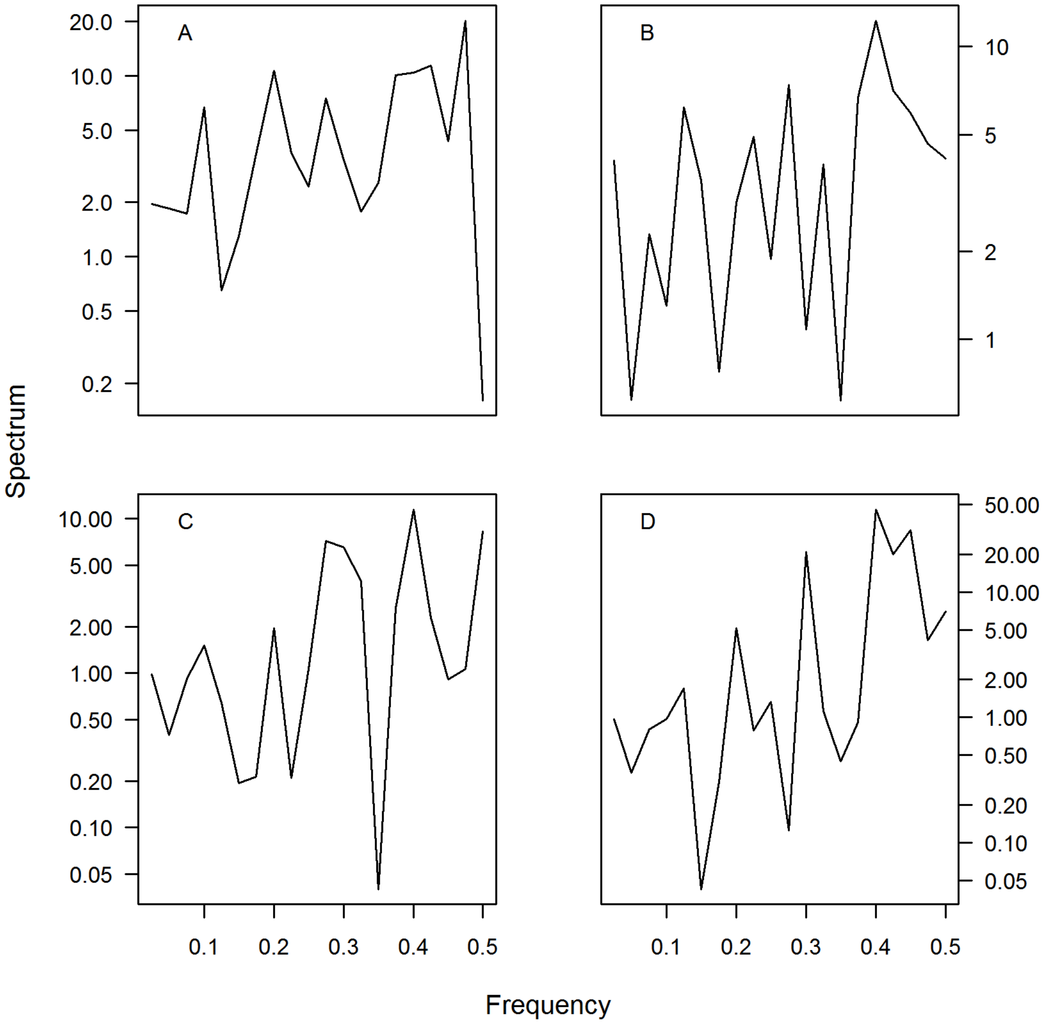


Figure 2.10: Periodograms of A: Autumn, B: Summer, C: Winter, D: Spring phytoplankton. Detrended annual mean time series were used to detect peak frequencies at which a periodic signal was strongest.

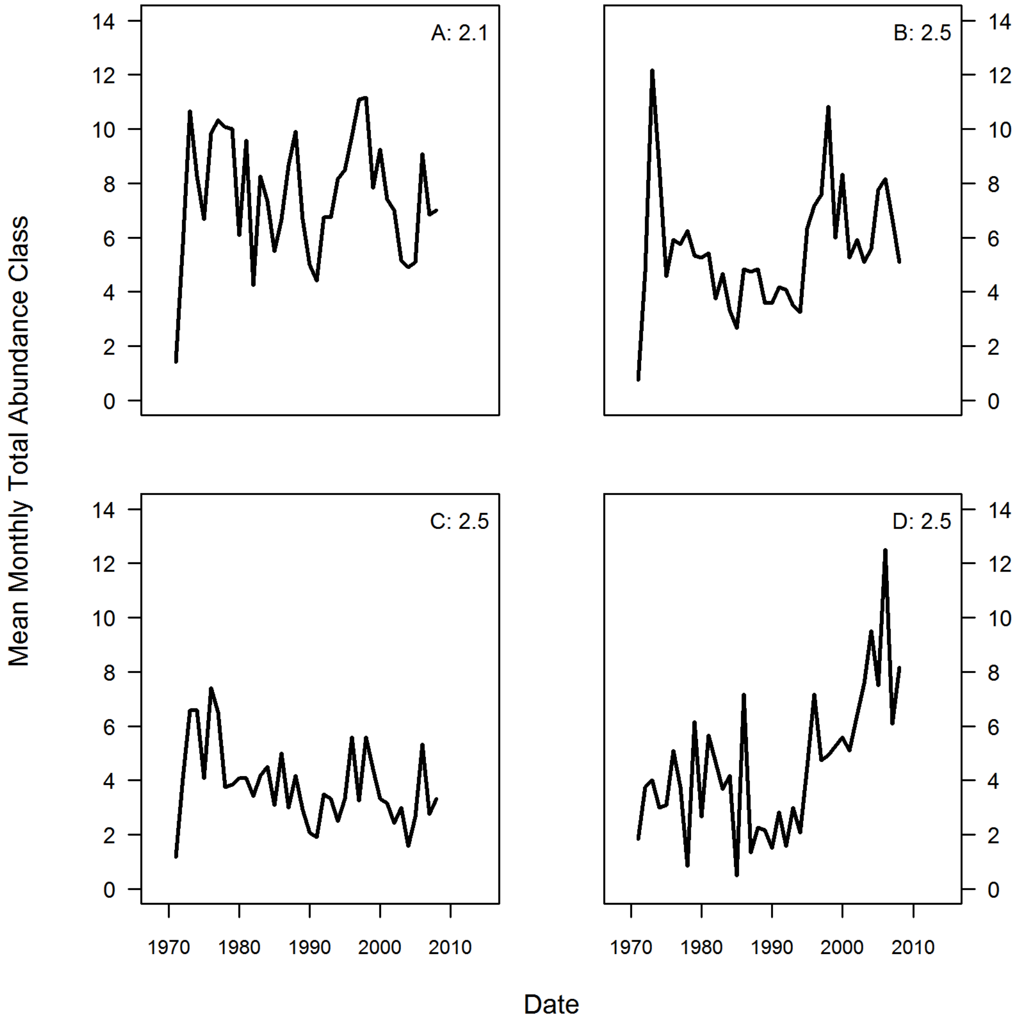


Figure 2.11: Mean annual total abundance class for each phytoplankton group. A: Autumn, B: Summer, C: Winter, D: Spring. Numbers by letters are the number of dominant mode cycles in each time series.

The interannual periodicity in the partitioned time series was too short to be covariant with the long oscillation of the AMO, and did not match the phases of the NAO (which is not cyclical in any case; see chapter 6). Correlations between this mode of variability and the unmodified AMO were moderate. The periodicity of the AMO once its long trend was removed was approximately 11 years. No correlations were found when AMO was detrended. Autumn and winter phytoplankton correlated most at 2 year lags, summer with 0 lags, and spring with 1 year lag (Table 2.8). Periodicity of phytoplankton was between ~14 and 18 years, or approximately 25% of the longest level of periodicity in the AMO.

Group	**0 year lag**	**1 year lag**	**2 year lag**	**3 year lag**
++ (Autumn)	0.09	-0.1	**-0.27**	-0.24
+- (Summer)	**0.32**	0.20	0.04	0.02
-+ (Winter)	-0.21	-0.22	**-0.36**	-0.35
-- (Spring)	0.34	**0.40**	0.31	0.34

Table 2.8: Correlations between normalised detrended phytoplankton groups, and Atlantic Multidecadal Oscillation index, lagged to three years. Values in bold are highest correlations. No correlations observed for summer phytoplankton.

2.3.1.2 *Modelling and forecasting abundance*

To determine if the interannual variability was likely to be periodic and not just the result of autocorrelated production between years, dynamic linear models were applied with separate components to describe seasonal variability, irregular interannual variability, and longer term cyclical variability. The wavelengths in table 2.7 were used as the values for long term periodicity. Models were approximate to the observed data on which they were based (Figure 2.12). To validate the importance of the long term periodic component, the last 5 years of data between 2004 and 2008 were removed from each time series, and the same model applied to this subset and forecast to the end of observed data. Correlations were moderate and significant for three of four time series, with the exception of winter phytoplankton (Table 2.9). Model fits tracked interannual and seasonal variability (Figure 2.13).

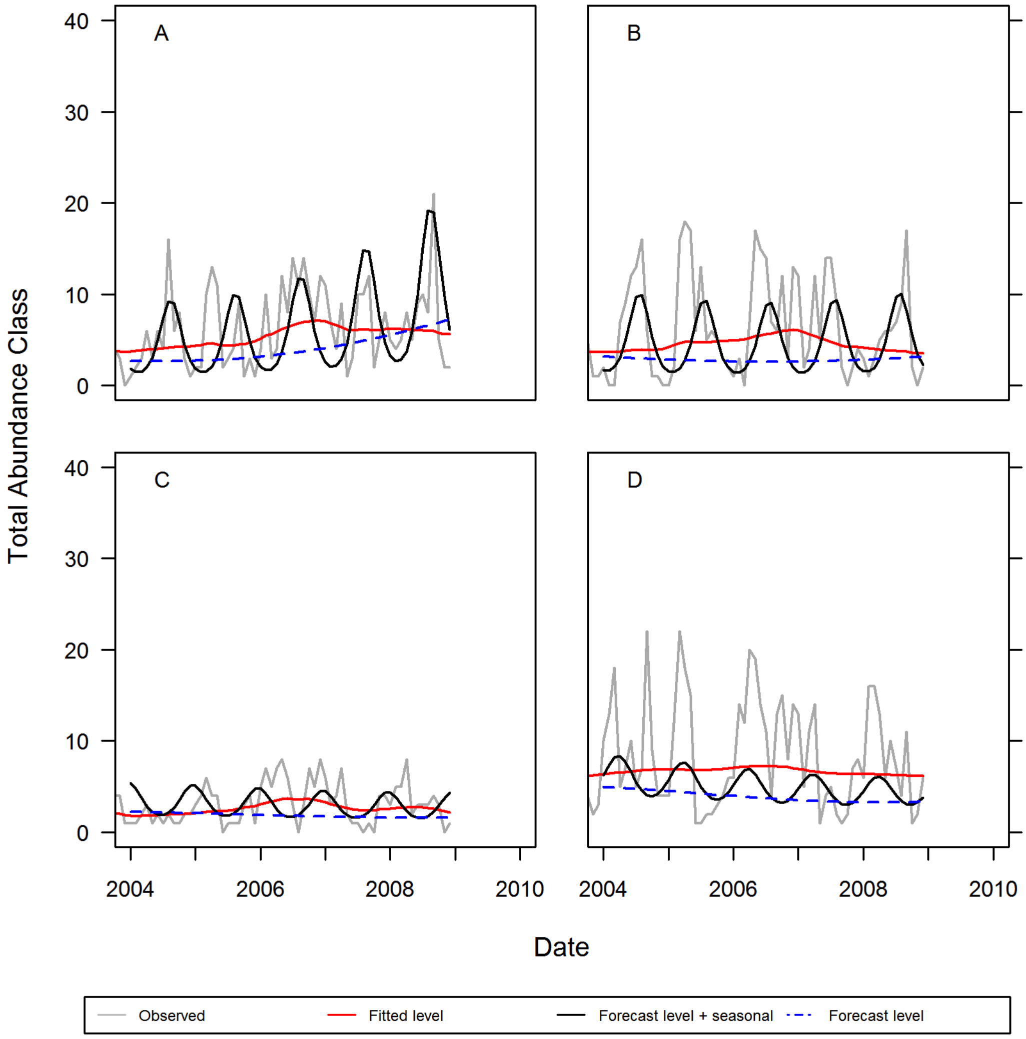


Figure 2.12: Validation forecasts for A: autumn, B: summer, C: winter and D: spring phytoplankton. Blue dashed line is forecast level, black is level with seasonality modelled. Red line is the posthoc level from the non-validation model and grey lines are observed data.

Group	**Spearman ρ**	**p**
++ (Autumn)	0.32	<0.01**
+- (Summer)	0.48	<0.001***
-+ (Winter)	0.21	<0.11^{ns}
-- (Spring)	0.45	<0.001***

Table 2.9. Spearman correlation coefficients for validation forecasts and withheld part of the phytoplankton time series. All groups show positive and significant correlations, indicating seasonality and trends in the models are approximate to observed values.

Forecasts were made into the future to determine if the interannual periodicity in the time series was likely to bring about changes in the abundance class of each group.

This suggested an upward trend in spring and summer phytoplankton, and downward trends in winter and autumn phytoplankton (Figure 2.14). Values are summarised in table 2.10.

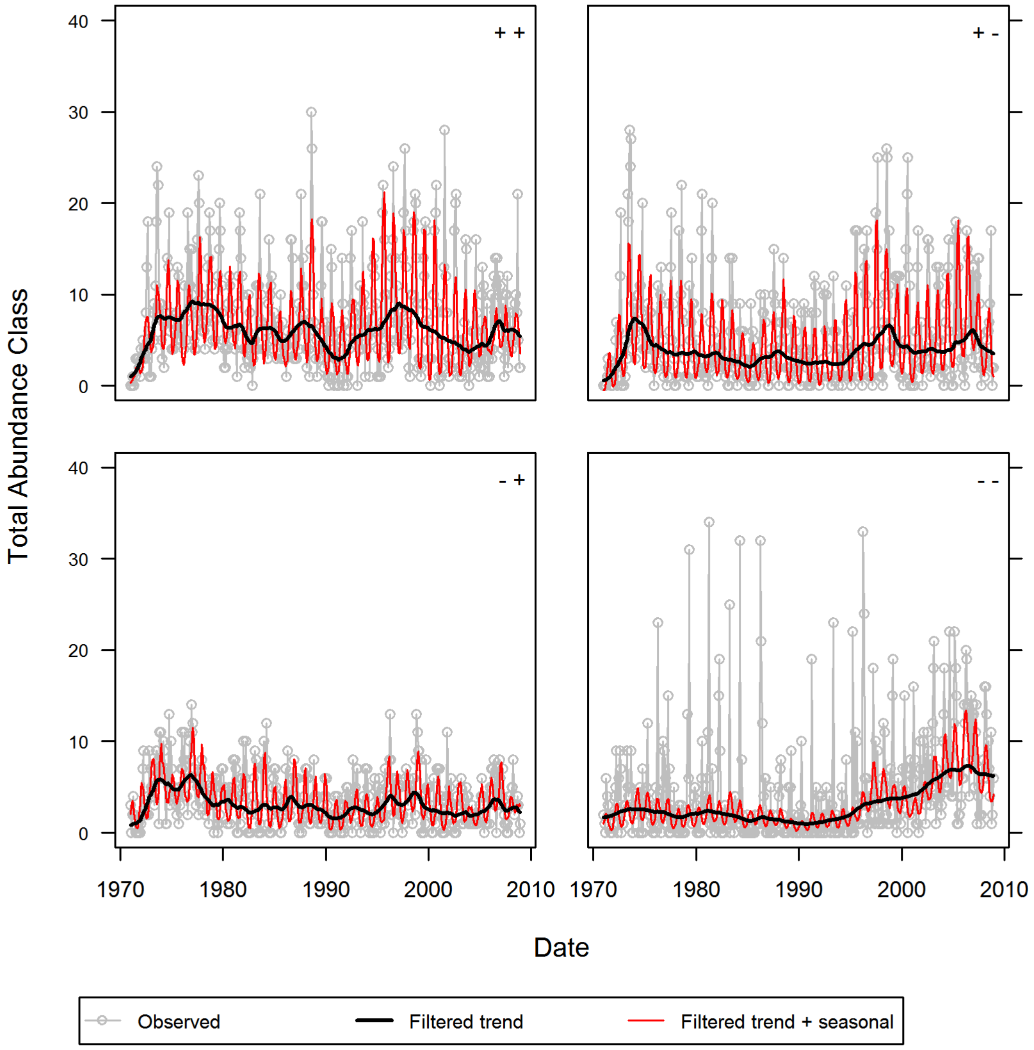


Figure 2.13: Dynamic linear models of: Autumn (++), Summer (+-), Winter (-+) and Spring (--) phytoplankton. Heavy black line is filtered local linear trend and long term periodicity. Red lines impose seasonality on top of this, plotted against observed data.

Group	95-08 Mean	09-13 Mean	% difference	T	p
++ (Autumn)	6.09	5.40	-11.33	-6.01	$<0.001^{***}$
+- (Summer)	4.51	3.39	-24.83	-15.26	$<0.001^{***}$
-+ (Winter)	2.78	1.76	-36.69	-17.20	$<0.001^{***}$
-- (Spring)	4.92	9.53	+93.69	10.84	$<0.001^{***}$

Table 2.10: Difference in mean deseasonalised monthly phytoplankton abundance level between 1995-2008 period and the forecast period to December 2013.

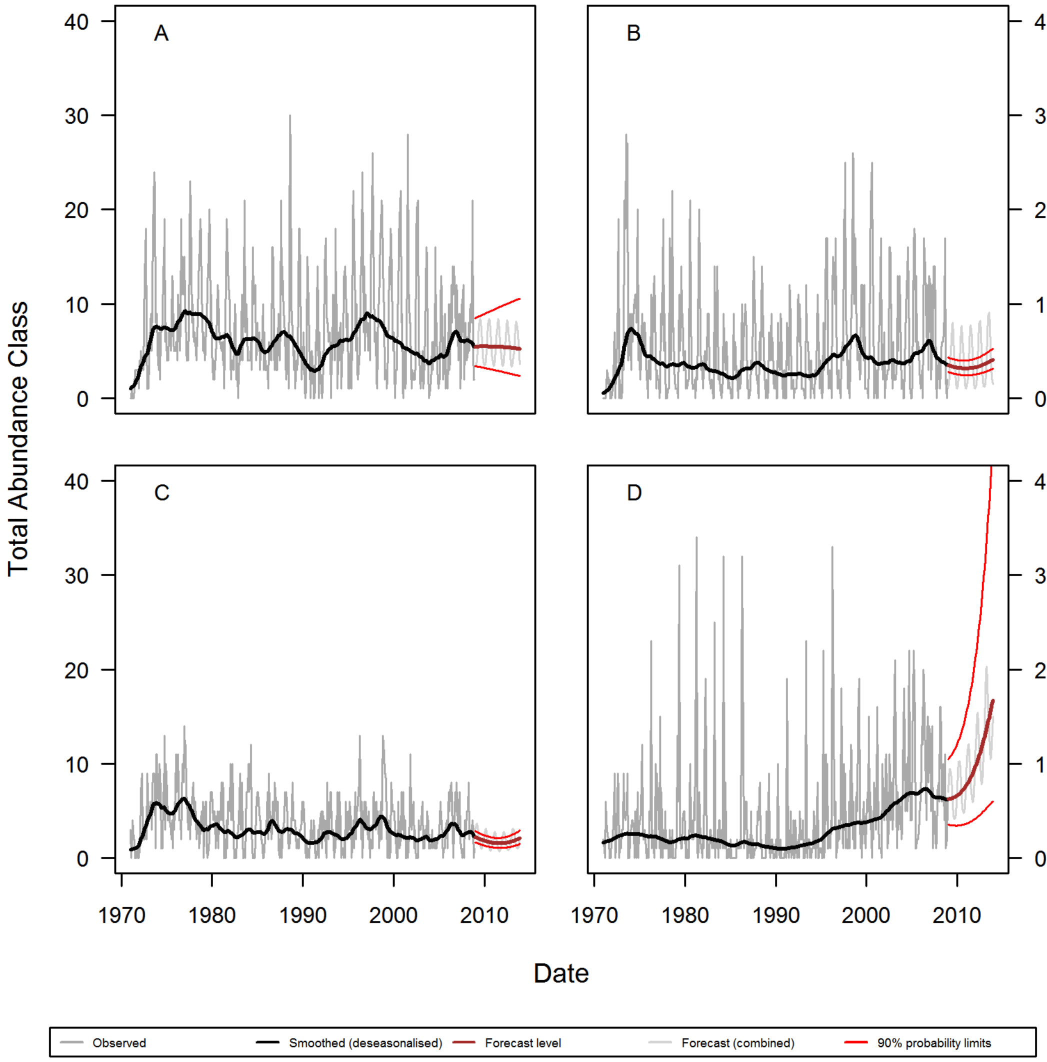


Figure 2.14: Dynamic linear models forecasts of: A: Autumn (++), B: Summer (+-), C: Winter (-+) and D: Spring (--) phytoplankton. Heavy black line is filtered local linear trend and long term periodicity. Heavy brown line is forecast long term periodicity, red lines are 95% probability limits and light grey lines are forecast + seasonality.

To check the sensitivity of the long term variability in the models to short term variability, FFBS plots were made 10 times per time series, each time with 12 months fewer data. This indicated closely aligned estimations of level were repeated in each case, confirming the resilience of the models and the appropriate parameterisation of the long term periodicity and thus accurate placement of the peaks and troughs in the model fits (Figure 2.15).

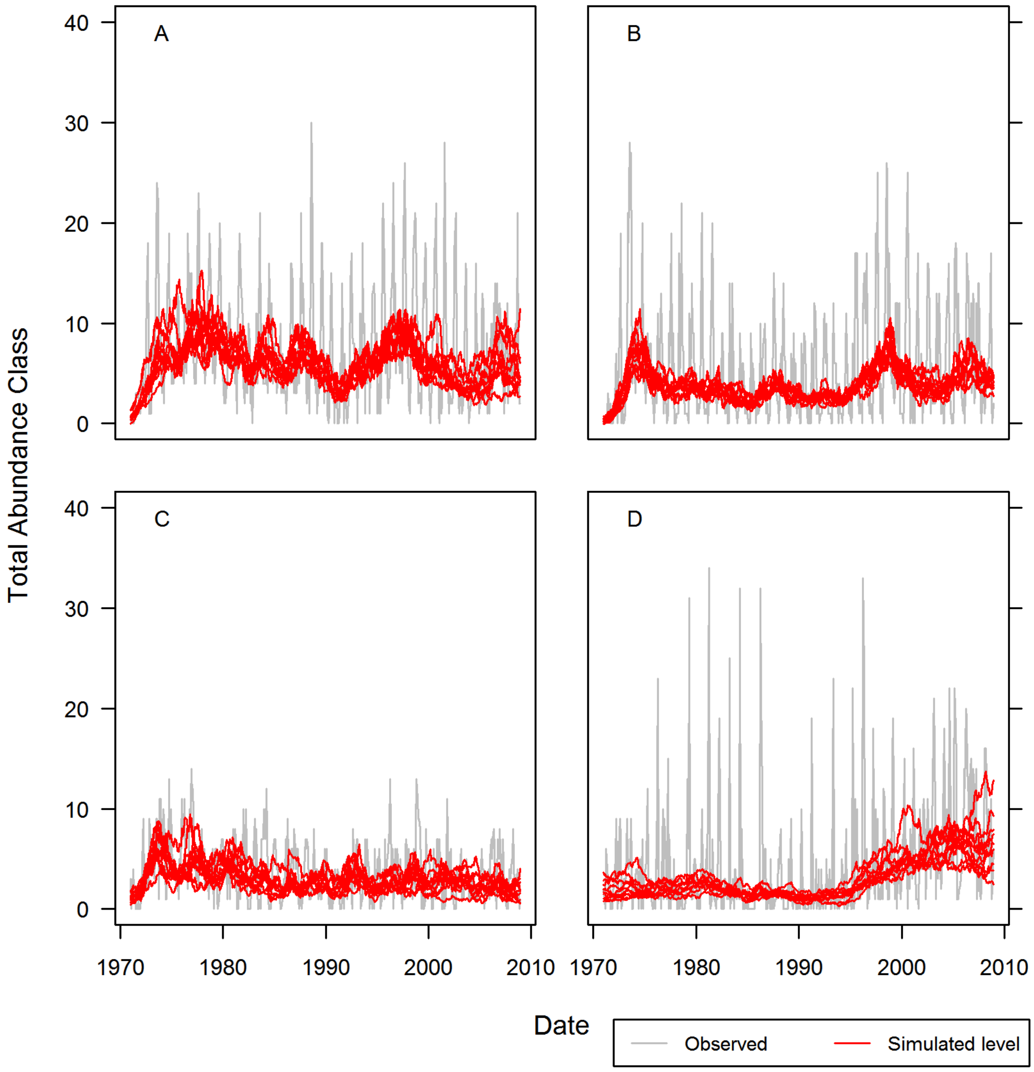


Figure 2.15: FFBS plots of local linear trend + long term periodicity for A: Autumn, Summer, Winter and Spring phytoplankton. Each red line represents 1 run of the model with 12 months fewer data than the previous run.

2.3.2 *Phenological change in abundance of each group*

As established, the phytoplankton communities were strongly seasonally organised according to their weighted average scores against CCA1 and CCA2. Over nearly 40 years of observations there was little evidence of strong trends in the seasonal timing of greater abundance of summer or winter species (Figure 2.16). T-tests of the mean of the seasonal peak are summarised in table 2.11. There was no change in mean peak of winter or summer phytoplankton, but moves earlier observed of approximately 10 days for autumn phytoplankton, and approximately 24 days for spring phytoplankton. Trends were potentially occluded by variation in peak of up to three months.

Figure 2.16: Phenological phytoplankton peak as determined by atan2 of the sine and cosine elements of a local linear trend + seasonal dynamic linear model. A: Autumn, B: Summer, C: Winter, D: Spring.

Group	71-94 Mean	95-08 Mean	Days difference	T	p
++ (Autumn)	8.42	8.08	-10	4.96	$<0.001^{***}$
+- (Summer)	7.24	7.23	-0.3	0.17	0.86^{ns}
-+ (Winter)	1.38	1.33	-1.5	0.59	0.54^{ns}
-- (Spring)	3.88	3.07	-24	10.144	$<0.001^{***}$

Table 2.11: T-test results comparing phytoplankton seasonal peak before and after 1995 breakpoint.

Spatial plots confirmed the peak extraction results, and illustrated seasonal spread of each assemblage through time. Autumn phytoplankton after 1995 were found earlier in the year than the preceding 1990s, similar to the late 1970s. In the 2000s their peak abundance remained centred on August and September, but were more restricted in their presence outside of these months than in the 1990s (Figure 2.17). Summer phytoplankton varied little in the timing of their peak, though the peak was associated with particularly high abundance between 1995 and 2000 (Figure 2.18), with particularly poor abundance evident between 1984 and 1995. Winter phytoplankton (Figure 2.19) was interesting in that spatial plotting indicated for the first 5 years of the time series, this group was actually present in abundance throughout the year and had therefore not been outcompeted by other phytoplankton species during the stratified period of the year as was normal in the rest of the time series. Spring phytoplankton (Figure 2.20) were most variable, as Figure 2.16D suggested. The most notable change was that after 1995 the restricted spring peak changed, with abundance peak earlier in the year and sporadic presence extending into summer, though this appeared restricted after 2005.

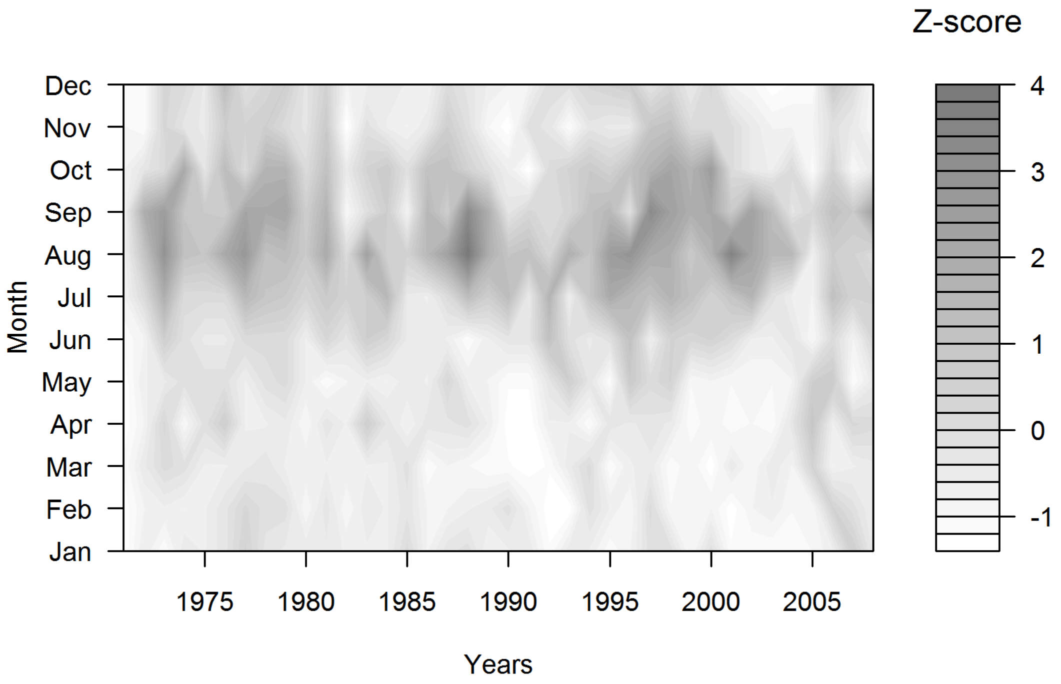


Figure 2.17: Normalised autumn phytoplankton seasonality. Darker areas represent greater abundance. Data are normalised to zero mean and variance 1, scale is standard deviations above the time series mean.

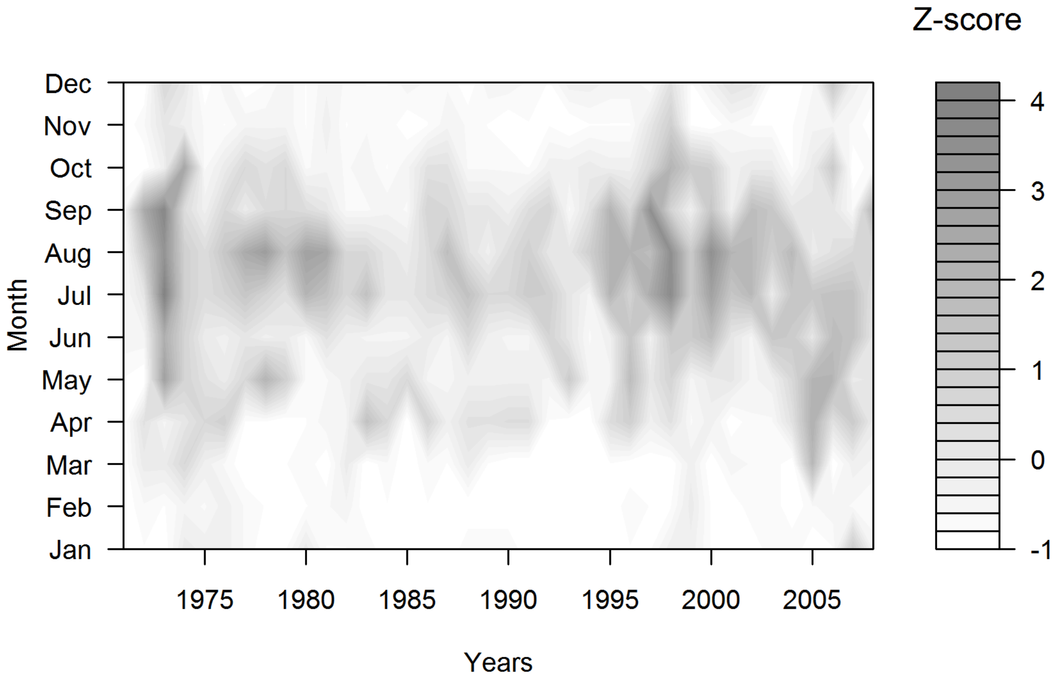


Figure 2.18: Normalised summer phytoplankton seasonality. Darker areas represent greater abundance. Data are normalised to zero mean and variance 1, scale is standard deviations above the time series mean.

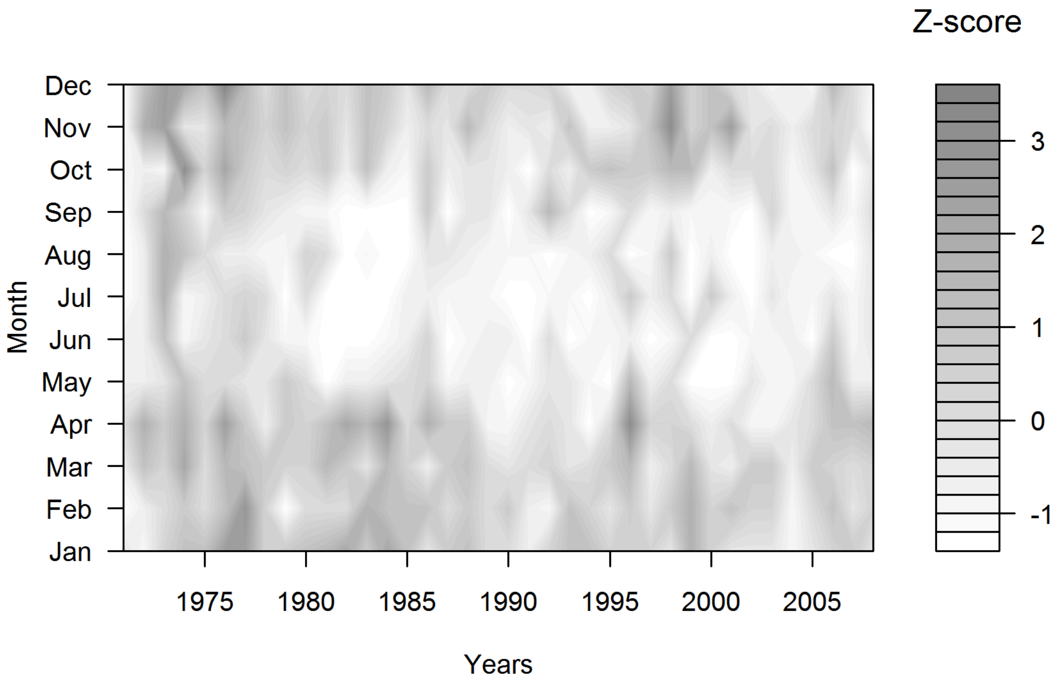


Figure 2.19: Normalised winter phytoplankton seasonality. Darker areas represent greater abundance. Data are normalised to zero mean and variance 1, scale is standard deviations above the time series mean.

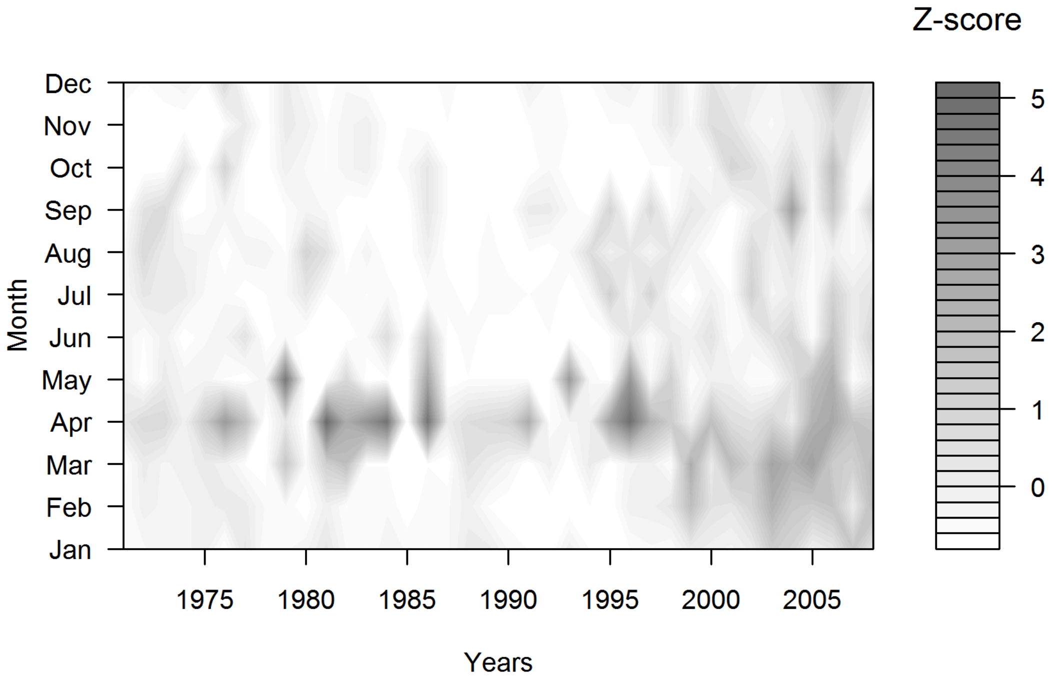


Figure 2.20: Normalised spring phytoplankton seasonality. Darker areas represent greater abundance. Data are normalised to zero mean and variance 1, scale is standard deviations above the time series mean.

The late 1990s and 2000s were characterised by little change in timing of summer, autumn or winter phytoplankton, but a move in spring phytoplankton to be present in anomalous abundance earlier and later in the year.

2.3.3 *CCA linear constraints as predictors of abundance*

Extracting the linear constraint scores, that is the combined effect of all predictive variables as represented by constrained axes, indicated CCA1 had over time become steadily more positive in its effects on species composition. As this axis was most strongly correlated with SST this was expected. CCA2 exhibited a change from a positive effect, to a more negative effect, the change in slope beginning in the 1980s. As CCA2 had a very weak correlation with SST, this indicated the atmospheric predictive variables of wind speed, cloud cover were most representative. The timing of the downward trend in CCA2 was coincident also with the upward trend in AMO (Figure 2.21). Thus, CCA1 was a gradient of variability strongly correlated with local SST variation, while CCA2 was a gradient of variability correlated with weather and long term Atlantic SST variation.

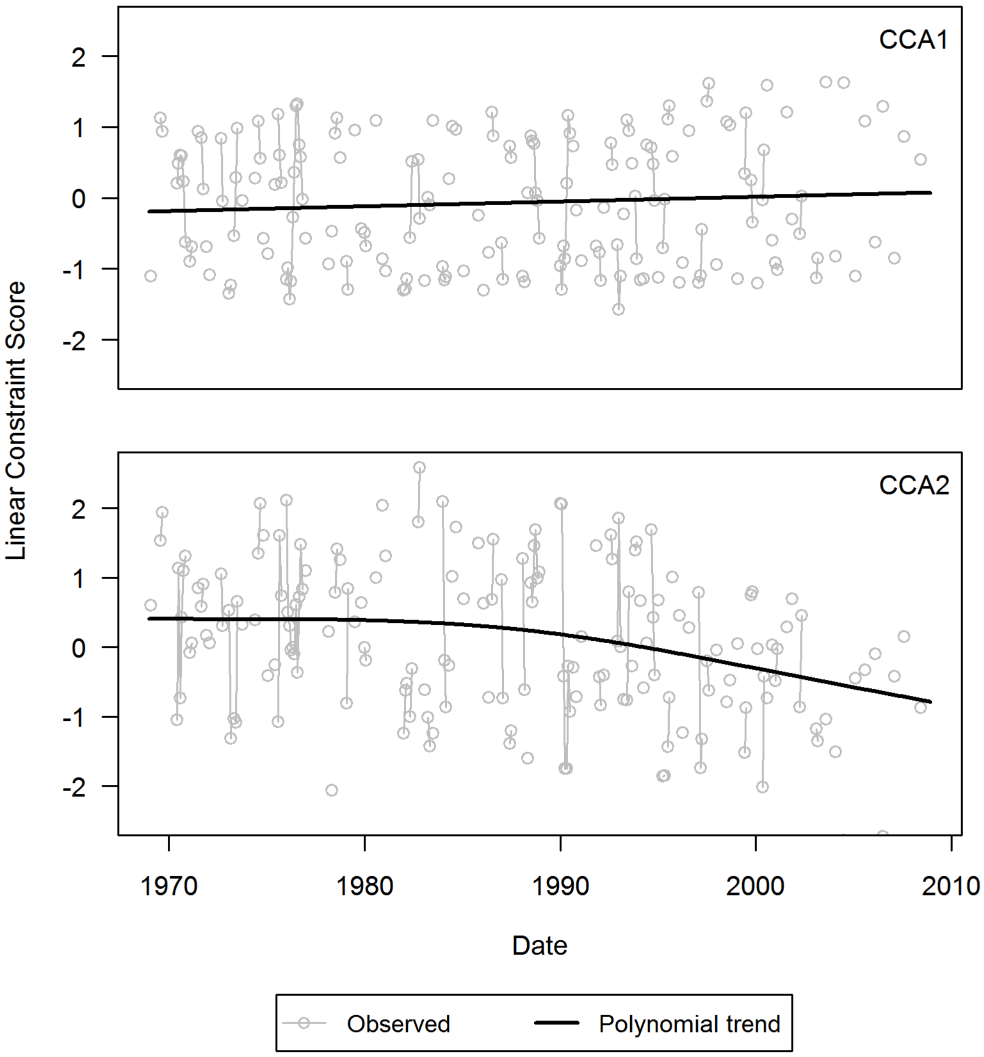


Figure 2.21: CCA analysis linear constraint scores. CCA1 is most strongly correlated with SST, while CCA2 is correlated with a combination of wind speed, cloud cover and AMO anomaly.

A generalised linear model using CCA1 and CCA2 as predictive variables indicated CCA2 to be significant in predicting phytoplankton abundance class, while CCA1 was significant only at α0.1 (Table 2.12, model fit: Figure 2.22). As neither of these variables contained nutrient data (due to these predictive variables being unacceptably sparsely available) it is unsurprising the GLM fit was not precise. Nonetheless with the exception of ammonia, all nutrient data that had been sourced from the European Environment Agency database was correlated with CCA1 (Figure 2.23).

Variable	Intercept	Slope	Standard error	T value	p
CCA1	3.079	0.08	0.049	1.685	0.094$^{\cdot}$
CCA2		-0.08	0.038	-2.207	0.029*

Table 2.12: GLM output of phytoplankton total abundance class versus samples CCA1 and CCA2 linear constraint scores. Intercept, error and slope on log scale.

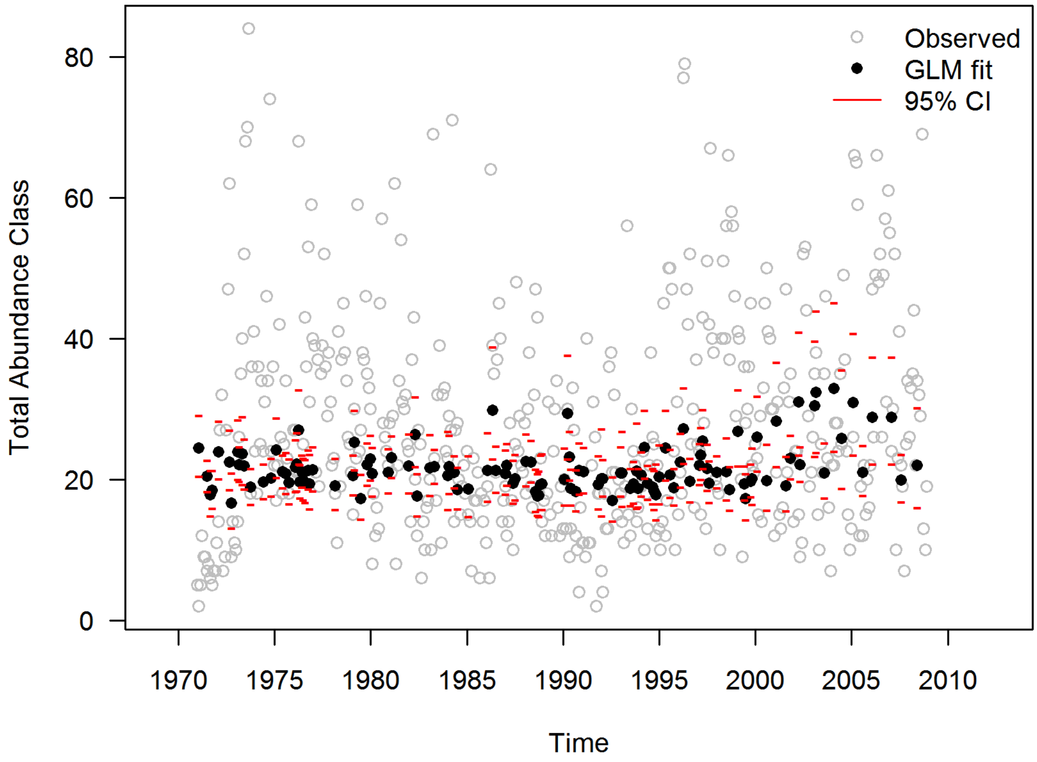


Figure 2.22: GLM model fit using CCA linear constraint values to predict phytoplankton abundance class.

The conclusion of GLM analysis was that increasingly negative CCA2 promoted increased abundance of phytoplankton at the Dove Site. CCA1 was marginally non-significant and thus less important in determining overall abundance of phytoplankton. As after 1990, both CCA1 was increasingly positive and CCA2 was increasingly negative, phytoplankton abundance was maintained at a higher level.

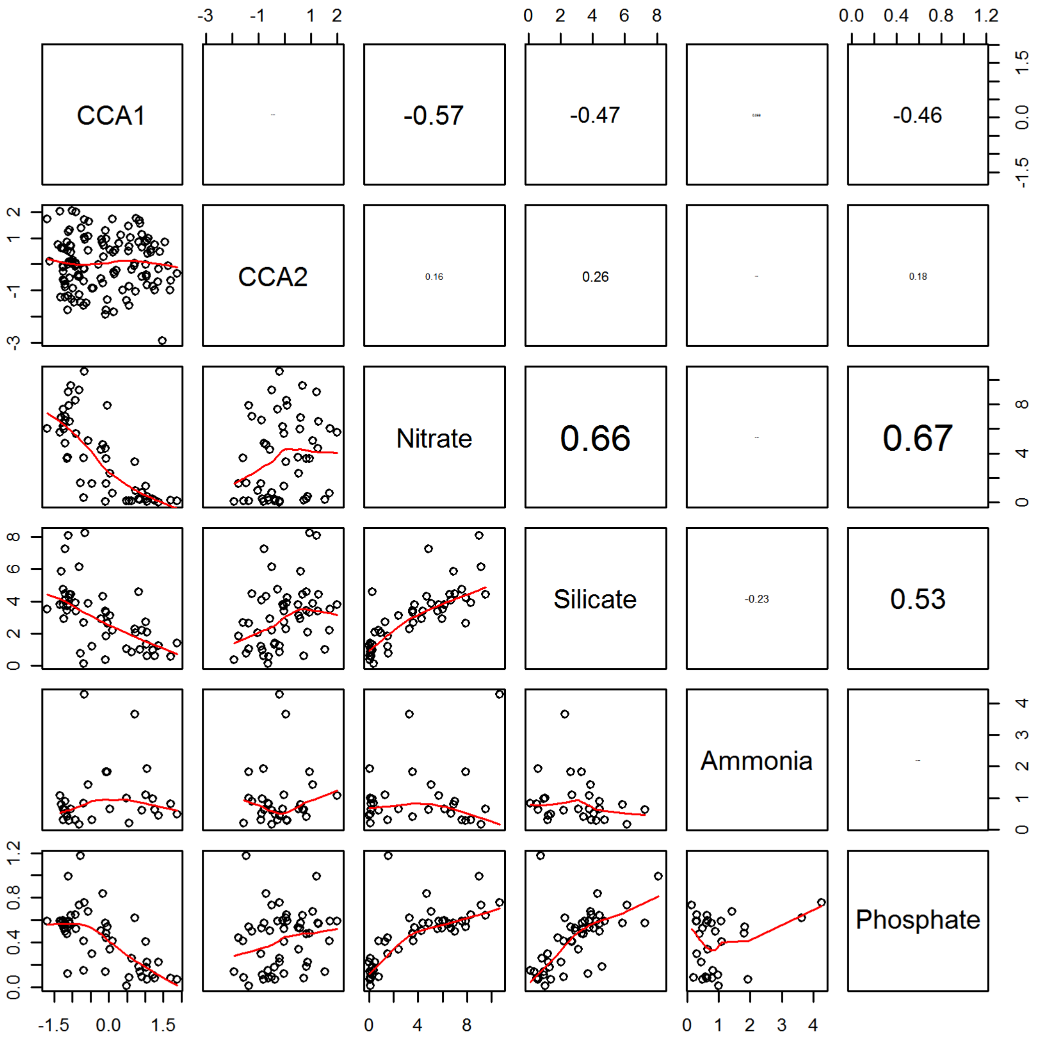


Figure 2.23: Spearman correlation coefficients of CCA sample linear constraint scores and EEA surface nutrient data. Lower panels are plots of one variable against another, upper panels are associated Spearman ρ values with font scaled according to the strength of the correlation. Moderate negative correlations with CCA1 indicate it partly described by proxy seasonal nutrient cycles for three of four nutrients. Positive CCA1 was found mostly in summer, when it would be expected these nutrients would be depleted by the population growth of phytoplankton in the upper mixed layer. CCA2 did not correlate with any of these variables and could be considered not to be collinear with nutrient cycles.

2.4 Discussion

2.4.1 *Changes in phytoplankton assemblage composition caused by changing hydro-meteorological conditions*

The DTS in winter is low abundance, composed mainly of diatoms with low surface area to volume ratios and many chloroplasts, able to increase drag, sunlight capture and survive winter after population growth in autumn. By spring, these forms are outcompeted by small, high surface area to volume, rapidly growing species such as *Chaetoceros*, *Skeletonema*, and *Thalassiosira. Chaetoceros*, *Guinardia* and *Leptocylindrus* dominate in summer, alongside a diverse assemblage of mostly peridinian dinoflagellates that are likely to be predatory on the diatom flora. By autumn, dinoflagellates were increasingly mixotrophic species such as *Ceratium* (Stoecker, 1999) which alongside *Chaetoceros* and rhizosolenoid diatoms were assumed to be taking advantage of the newly available nutrients following deeper stratification. The seasonal pattern of these species was similar to that observed to the north at Stonehaven (Bresnan *et al*, 2009). Like Edwards *et al* (2002), this time series observed a greater increase in dinoflagellate abundance than diatoms after the 1980s. Diatom species richness was much higher than dinoflagellate after the 1980s in the DTS.

Sea surface temperature was the most important predictor of the species composition of a sample in the DTS. Edwards *et al* (2001) identified SST and wind stress as important correlates with phytoplankton community structure. In the case of the DTS, SST is unlikely to have had a direct influence on population growth: the variable CCA1 was moderately and negatively correlated with the sparsely available nutrient concentration data (Figure 2.29). High SST, and so positive CCA1 weighted average score, represented a proxy measure of the presence of a density gradient in the water column, and the loss of dissolved organic nutrients from the upper mixed layer. The second axis of variability in CCA biplots dealt was uncorrelated with nutrient concentrations. Where a low CCA1 score would indicate cold and therefore mixed seas (though it may have been the case stratification through low salinity could have occurred at this time) with high nutrient concentrations, CCA2 was representative of meteorological conditions – particularly wind speed and cloud cover. Wind in particular was not orthogonal with CCA2 or CCA1, indicating an effect on both axes, albeit mostly obscured by SST variability in CCA1. Wind is an important factor in determining deep mixing of nutrients in winter (e.g. Lenhart *et al*, 2004), though in the relatively shallow water around the DTS, it is unlikely that anything less than complete mixing occurs over winter. It is also important in slackening sufficiently to allow stratification to occur (Sharples *et al*, 2006), and this is more likely to explain the longer and earlier productive season, and higher abundance class after 1995.

2.4.2 *Forecast increases in spring phytoplankton and decreases in other groups*

CCA2 was the significant predictor of overall abundance of phytoplankton, while CCA1 was only significant at α0.1. CCA1 increased in a linear fashion over time but the main increase in phytoplankton after 1995 was associated with the negative sign of CCA2. The moderate correlations between nutrients and CCA1 indicate the nutrient regime near to the DTS has been stable, though the sparsity of data made it impossible to know if the SST and nutrient trends diverged enough to mean CCA1 had by the 2000s become a poor proxy, and thus falsely interpreted as a non-significant predictor of abundance. Over the whole North Sea, nutrients have not increased (OSPAR, 2010). The secondary axis CCA2 was most important in affecting interannual change in abundance of spring species, leading to increased contribution of this group to overall abundance.

Dynamic linear model forecasts appeared to suggest decreases relative to the 1995-2008 mean deseasonalised level in summer, autumn and winter species, and substantial increases in spring phytoplankton could be expected in the 5 years subsequent to the study period. As noted in the section below on the evidence in the DTS of regime shift, the periodicity in the DTS did not adequately covary with any predictor data used in this study, and thus the possibility exists that it may not be a real cyclical process, though see consideration of sea ice transport below. Nonetheless, as positive AMO led to increased abundance of spring taxa, the direction if not the absolute value of the prediction was considered to be accurate, provided AMO remained positive in the period 2008-2013. It is likely to be the case that as wind speed had increased over the course of the time series, the greater spring abundance of diatoms occurs as a result of the AMO effect on wind and thus stratification, clarifying water in the upper layer earlier in the year (Pingree *et al*, 1978).

2.4.3 *Wind and cloud regime promotes a longer and earlier growing season*

The evidence for phenological change was mixed. Modest moves earlier in autumn and spring peak abundance were identified in time series with sporadic peaks within a range as wide as 3 months. Winter and summer showed no evidence of a change in peak. The most pronounced shift was that of spring, which as noted above was predicted by gradients of change in wind speed and cloud cover conditions as a consequence of the increasingly positive AMO SST anomaly contribution to CCA2. The figures from T-test analyses suggest the growing season moved earlier by approximately 24 days, and lengthened by approximately 2 weeks as an aggregate of the different degrees of phenological shifts in spring and autumn phytoplankton. Bresnan *et al* (2009) found *Skeletonema* to peak earlier in the 2000s which was reflected in this study in the incorporation of *Skeletonema* into the spring assemblage. *Thalassiosira* at the DTS was mainly found in spring, but in Stonehaven they were found throughout summer in the 2000s. *Chaetoceros* were found throughout summer in the DTS, but mostly in spring at Stonehaven. Salinity anomalies at this site were suggested by Bresnan *et al* (2009) as important in affecting species composition, particularly *Skeletonema-Chaetoceros* dominance, while change in salinity at the DTS was of minor importance in determining species composition, which would suggest any transit of the coastal front at the DTS is not frequent enough to affect composition. Later peaks were observed in in the North Sea PCI following the GSA (Edwards *et al*, 2002), and in the central North Sea after the warm water event (Edward *et al*, 2001). Henson *et al* (2009) found phytoplankton in the open North Atlantic ocean peaked later in positive NAO years and earlier in negative NAO years. The DTS peak moving on aggregate earlier by 2 weeks represents a change in phenology unrelated to the changes affecting the wider North Sea, which suggests its coastal position spares it strong Atlantic influence. The tendency of peak abundance to move later in the southern North Sea (Wiltshire and Manly, 2004) was not observed in this time series. The degree to which phenology has changed is similar to that observed in other time series, but the fact not all assemblages showed a significant change in peak timing would indicate the effect of the change to spring and autumn species has not led to major reorganisation of the phytoplankton as a whole.

2.4.4 *DTS position likely shoreward of frontal zone for part of the year*

The evidence of a change in abundance mediated by a change in the weather, representing a change in the energy circulating in the sea instead of transferring to the atmosphere would appear to discount any substantial alteration in residual circulation in the vicinity of the DTS. Inshore and offshore SST and wind speed time series were so strongly positively correlated that reductions in AIC of the CCA model afforded by using the offshore time series were essentially meaningless. This was not the case for cloud cover and salinity, the inshore and offshore variants being weakly correlated. However, it was not the case that both variants were offshore, as AIC had determined for SST and wind speed. AIC selected salinity that was inshore, and cloud cover that was offshore. It should be noted that salinity was correlated with higher dimensions of the CCA that were not investigated due to the difficulty of interpretation. Furthermore, offshore salinity was well below 35.45, so not representative of the high salinity open North Sea (e.g. Skjoldal, 2006), due to the variable nature of freshwater influence in the area (Pingree and Griffiths, 1978).

There is a seasonal frontal zone between regions of the coastal water that are tidally dominated towards the shore, and the offshore region that is more strongly stratified. It is difficult to be definite about where the DTS site is in relation to this frontal zone, there are no directly measured oceanographic data to accompany the plankton and the monthly scale probably smooths the tidal cycle to an unsatisfactory degree. The abrupt move earlier in abundance of spring phytoplankton in the after 1995 period could therefore represent movement, or sharper relief, of the front, sustained since this time. Inshore salinity was on average 34.42, which would place the DTS on the shoreward side of the front (Skjoldal, 2006). Without direct measurements of oceanography at the site this remains speculation. Tidal amplitude is important in determining frontal zone position (Hill, 2005), which would mean a future study of the date on which sampling took place relative to the tidal cycle may prove illuminating. Future sampling of the DTS should include directly measured oceanographic parameters and available remotely sensed data, such as AVHRR thermal fronts.

2.4.5 ***A persistent shift in phytoplankton abundance – for how long?***

Breakpoint analysis determined two dates at which the slope of knot to knot regression models of abundance versus time changed in a manner which minimised residual sum of squares. That is what breakpoint analysis does – it does not look for upward or downward shifts in the level of a time series. As such its interpretation requires care. The 1995 breakpoint was the only one that appeared to coincide with a rapid change in abundance of phytoplankton. The 1984 breakpoint had much wider confidence intervals and did not appear to be coincident with any abrupt change in abundance. While the interval around 1984 covered the the beginning of the NAO related change to phytoplankton biomass in the North Atlantic (Beaugrand and Reid, 2003), the breakpoint date was so wide, and the direction of change opposite, that this was probably a coincidence. The major shift in the DTS occurred at the time of the shift with the weakest support, identified by Weijerman *et al* (2005) and Reid *et al* (2001). The 95% confidence intervals for the 1995 break covered the anomalously negative winter NAO in 1995/6, when prevailing wind direction to the north of the British Isles meant North Sea circulation was disrupted, and the open sea became continentally, rather than Atlantic influenced (Pingree, 2005; Lenhart *et al*, 2004). This event appears to have resulted in greater phytoplankton abundance after 1995. Model studies suggested enhanced wind-driven mixing in winter 1996 in the northern North Sea promoted greater nutrient availability and higher net primary production (Pätsch *et al*, 2002; Lenhart *et al*, 2004), though at the coastal location of the DTS the relatively shallow depth probably means there would have been negligible increase in nutrients due to stronger winter winds. More probably, a change in degree and onset of stratification was the reason for the post 1995 change in abundance of phytoplankton at the DTS.

Dynamic linear model forecasts were made using models containing an approximately 14 to 18 year interannual harmonic component. This is much shorter than the dominant ~80 year periodicity of the AMO, related to the Gleissberg solar cycle (Braun *et al*, 2005), but longer than the approximately 11 year periodicity of the AMO with this long trend subtracted, which covaries with the sunspot cycle (Miclaus and Dima, 2011). This, and the confusing range of lags at which AMO correlated best with seasonal species assemblage time series, suggests the periodicity in the phytoplankton models was unrelated to solar cycles. The NAO was considered as an alternative, but it was subordinate in determining species composition to the AMO. The Fram Strait Sea Ice Export (FSSIE) time series has a 14 year periodicity that is coincident with the GSA passage around Greenland in 1968 and 1982, and partly correlated with the winter NAO index (Schmith and Hansen, 2003). Sea Ice export is linked to variability in the AMO

(Dima and Lohmann, 2007), which is less positive when mixing distributes heat through the water column, as it did in 1994 (Robson *et al*, 2012b). In the North Atlantic, SST is moderated by sea ice transport from the Arctic via the Fram Strait at a lag of 5 years, and sea ice transport is moderated by wind stress due to the sea level pressure gradient in winter between Greenland and northern Europe (Miclaus and Dima, 2011). Sea ice cools SST until energy flux between sea and air decreases sea level pressure differences and thus wind speed, reducing sea ice transport, leading to solar warming of the sea. The mid 1990s was coincident with a 14 year minimum in FSSIE (Miclaus and Dima, 2011), suggesting, as a possiblility, the origin of the periodicity in phytoplankton at the DTS may lie in this Atlantic-Arctic interaction, and the particular effects local to the DTS of SST, wind and cloud cover on the onset and duration of stratification, leading to earlier peak abundance of spring and autumn phytoplankton. One must bear in mind there was no equivalent opposite effect of phytoplankton as a whole in the DTS in the late 1970s during the GSA transit (or zooplankton: see Bonnet and Frid, 2004). The major difference however was in spring phytoplankton which were sparse in the 1970s and 1980s and abundant in the 1990s and 2000s. The chlorophyll dynamics of spring and autumn blooms would require investigation to determine the trends in biomass at the DTS with reference to cyclical AMO variation, but this is sadly not possible.

DeYoung *et al* (2004) list criteria that are required to accept a change as a regime shift. They must occur over a short time, persist in a quasi-stable state post change, occur at large spatial scales, be observable in different trophic levels, and be related to a change in climate. Notwithstanding the fact a change in phytoplankton is not a change in an ecosystem so cannot be considered in and of itself a regime shift, it is likely to be the case that the 14 year periodicity in the DTS is a response to a long term cycle related to sea ice export, and therefore future changes to the timing and degree of abundance of phytoplankton will depend upon the meteorology prevalent at the site, as a result of air-sea fluxes associated with this cycle. It is well known that Arctic ice cover in declined between 2008 to 2012 to the lowest extent in the 1979 to 2012 satellite record, coincident with warming in the Icelandic Low (NSIDC, 2012). The time series to 2008 should have reached the high point of the ~14 year cycle, so sustained high abundance beyond 2008 may reflect a change in the phytoplankton-atmosphere-ocean feedback governing the site. The move earlier in spring and autumn phytoplankton may already be indicative of such a change, though solar related cycles would need to be taken into account.

The fact peaks and troughs in the DTS phytoplankton did not match with those in the CPR suggests the coastal location of the DTS is key to the difference in its patterns. The timing of the late 1980s warm water event is not marked in the DTS by any particular spike in phytoplankton abundance class. The ICES salinity data indicate between 1979 and 1985, inshore salinity was often lower than the long term mean. This was coincident with a decline in abundance of phytoplankton, but certainly not a minimum in phytoplankton abundance, which came shortly after 1990. The strongest response of North Sea phytoplankton abundance and phenology was in the central North Sea (Edwards *et al*, 2001). The central North Sea on the eastern edge is also the region with the weakest wind driven currents and the least reached part in terms of direct Atlantic ocean inflow (Stephens *et al*, 1998), which may explain the lack of a signal coincident with increased inflow observed for the open North Sea by McQuatters-Gollop *et al* (2011). Sea circulation can be disregarded as a likely explanation of the change observed in the DTS phytoplankton. Future study of the nutrient and stratification regime at the DTS relative to FSSIE periodicity will likely determine if the rapid change in spring phytoplankton phenology and abundance after 1995 is indeed representative of a quasi-stable change related to climate. It is suspected as it is part of the variability in the AMO, that eventually the factors that in the 2000s promoted higher phytoplankton abundance will weaken and lead to a different state of the community.

2.4.6 *Conclusion*

The DTS is a coastal phytoplankton time series that has an unresolved relationship with local oceanography at the time of sampling as a consequence of having no directly measured physicochemical data taken alongside biological samples. It has been inferred that species composition changes through the year according to the development of a thermocline to arrest sinking, and the availability of nutrients, as is normal for a temperate marine plankton environment. Spring phytoplankton has undergone an increase in abundance, and a move earlier in peak abundance after 1995, a date within a narrow range identified as the point at which total phytoplankton abundance increased rapidly and remained at this higher level. This change has been inferred to represent a changed wind regime of weaker winds in spring leading to earlier stratification which has lasted for longer, leading to earlier peaks in spring and autumn phytoplankton. Models of the time series of phytoplankton incorporated a 14-18 year periodicity which may be a response to the 14 year periodicity in sea ice export through the Fram strait, which occurs as a result of air-sea flux feedback. Record low sea ice extent in the Arctic presents an ideal opportunity to test the theory that sea ice export ultimately regulates the stability regime at the DTS, at the 1995-2008 state of the 60-100 year AMO anomaly. The location of the DTS relative to the offshore front is important in understanding the reason for the timing of the spring bloom, which will require future sampling to be undertaken alongside CTD profiles.

Chapter 3: Long Term Oceanographic, Meteorological and Biological Variability and Their Effects on Zooplankton at the Dove Time Series.

3.1 Introduction

Warming sea and changing weather have been demonstrated to have a major effect upon zooplankton in the North Sea. Colebrook (1982) reported widespread declines in abundance of several zooplankton species in the CPR time series, and found declining copepod abundance to be strongly correlated with the diminishing frequency of westerly winds (Colebrook, 1985), the implication being that declining westerlies had a weaker mixing effect which in some way harmed transport of overwintering zooplankton (Colebrook *et al*, 1984), later confirmed by Heath *et al* (1999). Lindley *et al* (1995) highlighted the decline in calanoid copepods was accompanied by an increase in echinoderm larvae, as benthic echinoderm abundance increased. This was observable from the 1980s in the western and central North Sea (Lindley and Batten, 2002). Kirby *et al* (2008) further suggested positive effects of warming seas on some planktonic larvae had a positive feedback effect on their benthic adult phases, resulting in reorganisation of both pelagic and benthic ecosystems. Biogeographical shifts northward of up to 10° in latitude of warm temperate zooplankton species were observed in northeast Atlantic Ocean CPR samples after the mid 1980s (Beaugrand and Reid, 2003). These shifts were correlated strongly with the phase of the NAO and were interpreted to be a biological signal of changing climate and oceanography in the region. Edwards *et al* (2002) detected a low in copepod abundance in 1979 caused by the movement of the Great Salinity Anomaly through the North Sea. *Calanus hyperboreus* was observed in the North Sea, when this is normally an Arctic species. Reid *et al* (2002) linked increasing winds in the warmer period beginning the mid 1980s (so named as a regime shift – Reid *et al*, 2001) to stronger Atlantic inflow to the North Sea. This water was warmer, and faunistically more southern in composition than in the earlier part of the CPR dataset, reflected in an increase in the warm temperate *Calanus helgolandicus* relative to abundance of the boreal *Calanus finmarchicus,* advected from the Faroe-Shetland Channel (Heath *et al*, 1999). As seas warmed and westerly wind strength increased, rather than reversing the general decline as suggested by Colebrook *et al* (1984), across the North Sea biomass declined (Pitois and Fox, 2006), suggesting the control mechanism in place in up to the 1980s had subsequently become less important as a regulator of abundance.

The southern North Sea receives oceanic inflow via the English Channel, which did not exhibit interannual variations related to change in the oceanography of the Channel (Eloire *et al*, 2010). In both the case of the northeast Atlantic northward shift in copepod fauna (Beaugrand *et al*, 2002) and L4 in the English Channel (Eloire *et al*, 2010), species richness did increase. Biomass of zooplankton is greater in the southern North Sea (Pitois and Fox, 2006), perhaps as a result of the different nutrient and hydrodynamic regime in the area, which is seasonally separated from the northern North Sea (Turrell, 1992). In the southern North Sea, the Helgoland Roads time series has revealed temperature related changes in community composition and phenology, but no long term trend in the abundance of the dominant small calanoid copepod group (Greve *et al*, 2004).

Before the late 1980s warm water event, Aebischer *et al* (1990) observed in the northwest North Sea that trends in abundance of phytoplankton, zooplankton, herring and kittiwake chicks appeared to be responding to declining frequency of westerly weather, with very short lags in transmission of the signal upwards in the trophic chain. The changes in advection resulting in biogeographical shifts described earlier then lead to the consideration of the mid 1980s warming event to be a 'regime shift' (Reid *et al*, 2001). Beaugrand (2004) considered this to be strongly related to change in large scale sea circulation and the effect on local oceanographic and meteorological conditions, with a positive NAO key to the wind regime at this scale and its effects via Ekman transport on oceanic input to the North Sea. Weijerman *et al* (2005) agreed with the conclusion of Beaugrand (2004) that the regime shift of the mid 1980s was as a result of the NAO phase and its effect on wind driven sea circulation from Atlantic to North Sea, winter mixing and stratification. These publications lead to widespread use of the term 'regime shift' (e.g. Alheit *et al*, 2005; Daskalov *et al*, 2007; McQuatters-Gollop and Vermaat, 2011; Möllmann *et al*, 2008, Peterson and Schwing, 2003) leading to scrutiny of what is precisely meant by the term, citing difficulty in comparing the causes of purported regime shifts in different systems, identified with different criteria (Lees *et al*, 2006; DeYoung *et al*, 2004). Heath *et al* (1999) criticised the lack of clarity in explaining the underlying mechanism of the NAO-plankton relationship in Fromentin and Planque (1996) and Stephens *et al* (1998), citing the lack of a change in *C. finmarchicus* advection extent in the negative NAO year 1996, instead suggesting longer term decline in transport was a result of long term declines in deep water advection, not wind driven surface advection. Further criticism of the regime shift 'switch' concept came from Spencer *et al* (2011), who questioned whether in the UK case, regime shift really was an apposite term for what could be misidentified as such using the typical step-change detection methods (e.g. Rodionov, 2004; Weijerman *et al*, 2005) on time series with underlying trends, suggesting instead state of the art state space or dynamic linear time series models could better describe temporal variability. This leads to an interest in the role of long term variation in plankton dynamics, and what it may signify as an ultimate mechanism of observed changes.

The role of ocean climate variation in properties of the plankton at the DTS has been studied by a number of authors. Early work by Frank Evans indicated strong local climate effects on copepod size and thus suggested local scale replenishment of the Dove copepod community (see Evans, 1977; Evans and Diaz, 1978; Evans, 1981). Clark (2003) determined an inverse relationship between zooplankton abundance and the latitude of the Gulf Stream North Wall which was caused by the enhanced abundance of *Sagitta elegans* when the Gulf Stream was further north, after earlier work on the DTS by Roff *et al* (1988) and Nicholas and Frid (1999) had established interannual correlations between predators and prey, and Evans and Edwards (1993) found higher chaetognath abundance in the 1980s compared to the 1970s. Frid and Huliselan (1996) noted a correlation between GSNW and zooplankton abundance in the Dove Time Series, similar to the conclusions of Stephens (1998) who studied CPR records for the entire North Sea. Clark and Frid (2001) found coincident changes in NAO, GSNW, local meteorology and plankton from the DTS and CPR, though the authors acknowledged that the noisy nature of their results indicated the pathways from climate change to biological response were not necessarily straightforward. Evans and Edwards (1993) and Bonnet and Frid (2004) detected anomalous spikes in abundance of copepod species that were coincident with the dates of transit of the GSA, and late 1980s warm water event. It is clear that there is some link between the wider variability in ocean climate across the North Atlantic and the zooplankton at the DTS, but the complexity of this relationship compared for example to the CPR would point towards the coastal location being an important aspect of the time series. In the case of Stonehaven, which has been monitored at weekly scale since 1997, there has not been a long term decline in copepod abundance as observed in the CPR (Valdes *et al*, 2005). Both of these stations are relatively close to the coast, and discrepancy between the CPR, which smooths inshore-offshore differences in hydrometeorology, highlights the importance of the geographic context of each time series. That is not to say a coastal influence is definitely at work, but it must be ruled out in order to compare inshore and offshore time series.

As noted in chapter 1, previous DTS authors (Evans and Edwards, 1993, Clark and Frid 2003, Bonnet and Frid, 2004) have used a combination of vertical whole water column (WP2) samples and larger mesh samples towed horizontally (WP3) and combined per m^3 calculated from one or the other dependent on the organism. As there is likely to be transient stratification at the site, there is a likelihood of interference in abundance estimates of those plankton sampled by the WP3. For this reason they were not included in this analysis, which reserved only those taxa sampled with the vertical WP2 net.

3.1.1 ***Aims***

Against the context of a warming trend over the course of the 20th and 21st centuries, CPR data suggests changes have occurred in the biomass, species composition and time of peak abundance of zooplankton. Studies at the DTS point to both responsiveness to basin scale change, and to the importance of local hydro-meteorological variability. With the benefit of a further decade of monitoring at the site, the aim was to further resolve the important predictors of variability in the zooplankton community, measured as composition of the assemblages, overall abundance, and any changes in timing of peak abundance. To investigate this in the DTS, four hypotheses were considered:

1. Changing oceanographic and meteorological conditions have had no effect on zooplankton assemblage composition.

2. Changing oceanographic and meteorological conditions have had no effect on zooplankton abundance.
3. Changing oceanographic and meteorological conditions have had no effect on timing of zooplankton peak abundance.
4. There will be no difference in goodness of fit of multivariate models of zooplankton assemblage composition using either inshore or offshore predictor variables.

3.2 Methods

3.2.1 *Field sampling*

Samples were collected with WP2 nets on the R.V. *Bernicia* in the method of Evans and Edwards (1993), preserved in approximately 10% formaldehyde in seawater. The WP2 net is a medium plankton net with a mesh size of 200µm and mouth diameter of 57cm (UNESCO, 1968). The sample site as mentioned in Chapter 2 is 54m depth, and four vertical hauls from 50m of sunk cable to surface were combined to represent plankton collected from four repeat hauls (Evans and Edwards, 1993). Accurate distance sampled was determined with a TSK flow meter (Tsurumi Seiki Co., Japan). Before analysis, samples were rinsed on a filter gently with fresh water to flush out residual formaldehyde. WP3 nets were used to enumerate some zooplankton species by Evans and Edwards (1993) and this method was followed for succeeding authors. This is a coarser (1mm) mesh net with a wider (1.13m) mouth diameter and is sampled horizontally as opposed to vertically. In this study zooplankton sampled by WP3 nets were *not* included in analysis with respect to the established time series.

3.2.2 *Laboratory analysis and use of FlowCAM*

In this study, only zooplankton sampled by the WP2 net were analysed. The dataset was complete up to the end of 1996, and in this study, samples from 1997 to 2008 were enumerated. Each sample was gently mixed by inverting several times.

100ml of the sample was taken and loaded into a Folsom plankton splitter. The Folsom sample was split until estimated visually to be of a suitable density for subsequent analysis in the FlowCAM image analyser (Flow cytometer and microscope, Fluid Imaging Technologies, Yarmouth, Maine, USA). The Folsom fraction was then placed in a small beaker and further diluted, typically to 50ml. This was partly to allow enough material for any false starts caused by blockages or incorrect settings and partly to dilute the formosaline the sample had been in previously to safe working exposure levels. The FlowCAM was flushed with fresh water in preparation for the sample and the relevant objective focused between the planes of the FlowCAM chamber to ensure consistent image capture. The pump was always run at 7.8ml min^{-1} after preliminary investigation of the most appropriate speed for optimum image capture of zooplankton samples. 20ml of sample was added gently to the FlowCAM system and periodically mixed by pipette in the loading funnel during runs to keep the sample homogeneous. Samples were run for a mean time of 348 (±113 S.D.) seconds. The sample run time and flow rate were used to calculate run volume. The total count of all zooplankton in the master sample was calculated as follows:

$$Z_P = \frac{Z_F \times \left(\frac{V_R}{V_S}\right) \times \left(\frac{V_P}{V_F}\right)}{F_F} / F_D \tag{3.1}$$

where Z_P is the zooplankton in the master sample, Z_F is the zooplankton count in the FlowCAM output, V_R is the FlowCAM full run volume, V_S is the volume of sample added to the blank FlowCAM volume, V_P is the volume the Folsom Fraction was made up to, V_F is the volume of the Folsom fraction, F_F is the Folsom Fraction as a proportion of 1 and F_D is the fraction of the master sample the 100ml loaded into the Folsom splitter represented. From this sample volume, abundance per m^3 was calculated by dividing by the total volume sampled as determined by the TSK flowmeter reading. Where TSK readings were absent, the ideal volume of 49.26m^3 ($\pi \times 0.28^2 \times 200$) was substituted.

Zooplankton samples needed pre-filtering on a 1mm mesh before passing through FlowCAM in order to remove larger taxa represented in samples such as fish larvae, chaetognaths, larger adult copepods, jellyfish and other groups too large to be passed through the 1mm by 10mm flow cell. The portion of the sample retained by the 1mm mesh was kept in 70% EtOH and analysed using a dissecting microscope manually separate to the sub-1mm sized fraction of the sample that was prepared for analysis using FlowCAM. Per m^3 counts were combined from results of both FlowCAM and manual procedures. FlowCAM output was tagged image file format (TIFF) files that were split according to the image recognition software into fragments of the full TIFF images per organism imaged. FlowCAM's automatic image recognition algorithms performed reasonably well in preliminary investigation for taxa of particular size and shape (such as *Oithona* spp.). However it was determined to be faster and more accurate to review images manually and classify them using taxonomic knowledge rather than complex morphometric and colour information recorded by FlowCAM. For the purpose of analysing the entire time series, taxa historically represented by the WP3 net were removed entirely from the dataset.

3.2.3 *Modelling and term selection*

The zooplankton record was much less rich than the phytoplankton record (see Chapter 2) for the methodological reasons established in Section 3.1. Nonetheless determining the sensitivities of species necessitated a very similar signal extraction process as was undertaken in Chapter 2. The following analyses were conducted to identify periods in the DTS that were numerically and qualitatively distinct from neighbouring periods, in an attempt to identify candidate community shift events, and to describe variation in species with common responses to changes in their drivers.

An autoregressive integrated moving average (ARIMA) model was diagnosed with autocorrelation (ACF) and partial autocorrelation (PACF) functions to describe cyclical patterns in the data and interannual trends respectively. These were used to construct an initial ARIMA model of interannual variation in mean phytoplankton abundance class across all taxa. To explore the ARIMA model of mean zooplankton abundance (now largely excised of seasonal variation) for distinct shifts, linear breakpoint analysis was applied (Bai and Perron, 2003; Zeileis *et al*, 2002; Zeileis *et al*, 2003). The process is summarised in Chapter 2.

The relationship between abundance and environment and biological predictors was examined using constrained correspondence analysis (CCA; Oksanen *et al*, 2010, Legendre and Legendre, 1998). Model selection was accomplished with the 'ordistep' function, which used minimised Akaike Information Criterion as its selection statistic. Weighted average species scores on each axis were used to combine abundance class of species into one of four groups for time series analysis. Thus the collective abundance class of taxa with common affinities to the CCA axes (and thus the linear combination of the effect input predictors) could be constructed and the time series structure and behaviour described, and forecast a modest period into the future. Peak abundance was determined in the same way as in Chapter 2, using state space models to describe irregular and structured interannual variability, and the seasonal cycle (Petris, 2010).

Throughout this chapter there are points at which subsets of variables are chosen for analysis of one feature in particular, aside from the signal extraction and forecasting outlined in the previous section. Where this has been done for a multivariate analysis, this was accomplished primarily through minimising AIC, with further refinement by removing confounding variables that could not independently explain more inertia than was common to all predictors. Univariate analysis depended on extracted linear constraint time series from CCA analysis, so no term selection protocols were applied.

3.3 Results

3.3.1 *Time series structure and lack of breakpoint features in abundance*

The time series of zooplankton was stable over time, with no conspicuous changes in the slope of the time series. As a consequence, breakpoint analysis conducted on an ARIMA model fit found no point at which RSS and BIC was minimised by introducing a knot in the breakpoint model (Figure 3.1). Exceptionally low abundance was observed in January 1996, and exceptionally high abundance in July 2004. The top 10 low abundance years were found throughout the time series, while the top 10 high abundance year were almost all found in the 2000s (Table 3.1).

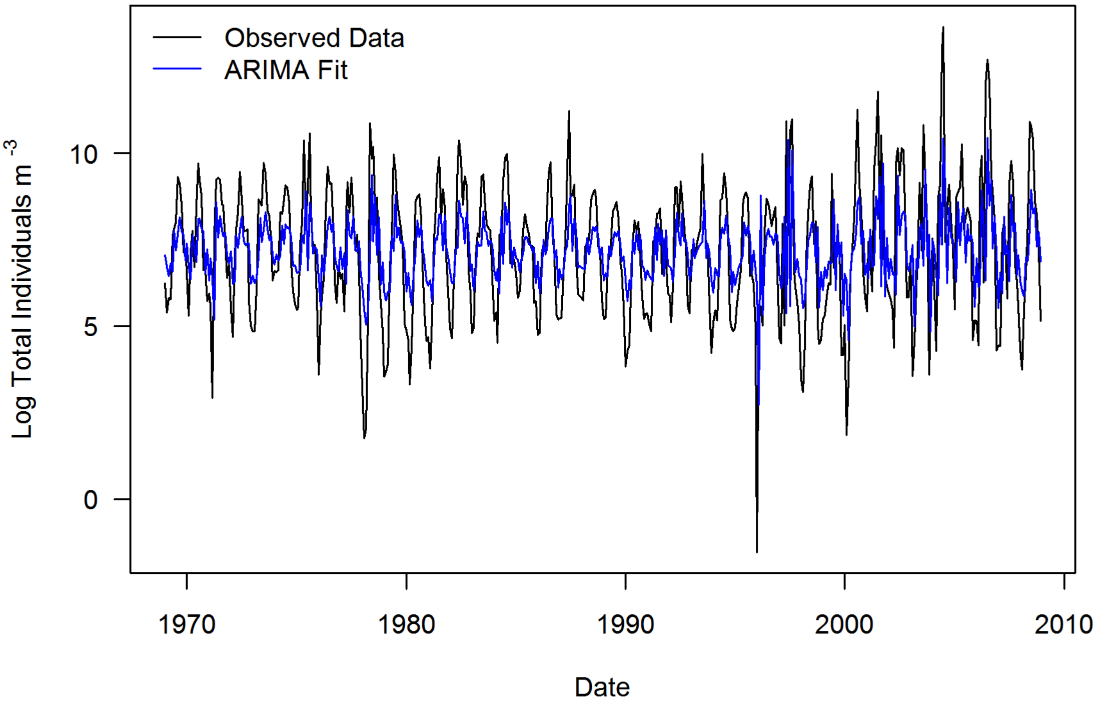


Figure 3.1: Mesozooplankton time series, with overlaid ARIMA model fit. No breakpoints were determined to significantly lower RSS or BIC.

Therefore, while breakpoint analysis did not further minimise residual sum of squares or Bayesian information criterion, there was apparently heterogeneously distributed instances of extremely high abundance through the time series. The ratio of the maximum value to minimum value was determined, which revealed that after 1995 the mean changed from 4.91 to 7.16. Of the top five ratio values, four were found after 1995 (Figure 3.2).

Rank	Rank 1 = Lowest	Rank 1 = Highest
1	January 1996	July 2004
2	February 1978	June 2004
3	February 2000	July 2006
4	March 1978	August 2006
5	March 1971	June 2006
6	February 1998	July 2001
7	January 1978	August 2000
8	March 1980	June 1987
9	January 1998	August 1997
10	March 2000	May 1997

Table 3.1: Ranked lowest and highest mesozooplankton abundance samples.

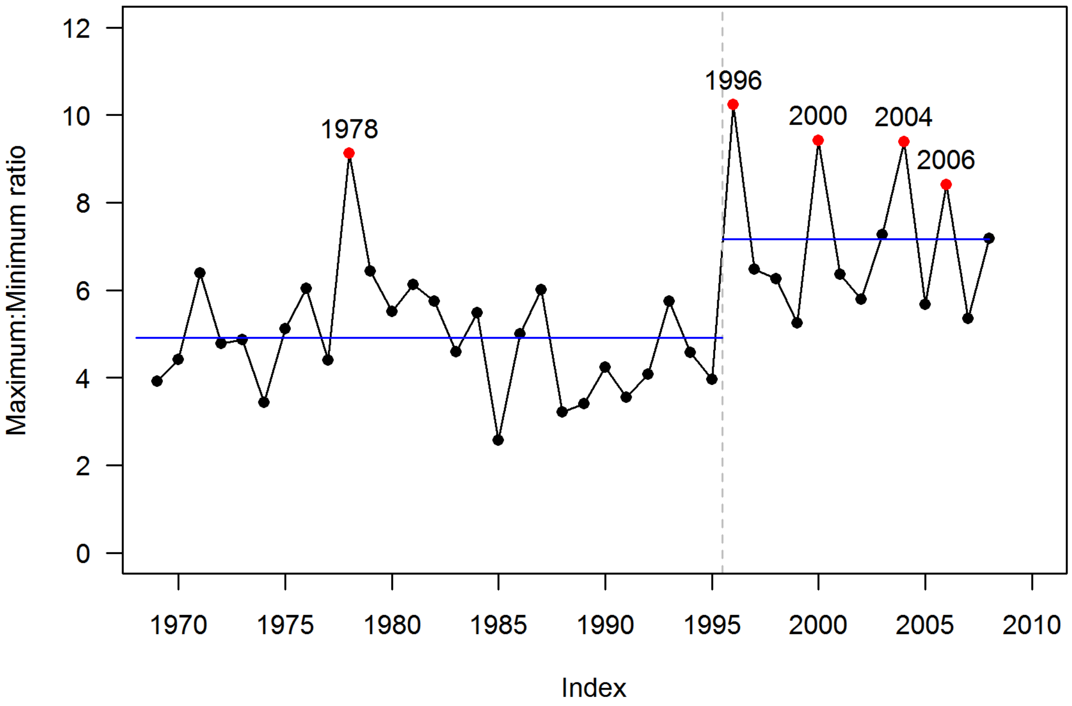


Figure 3.2: Annual mesozooplankton maximum:minimum abundance ratio. Blue line is mean before and after June 1995 (grey dashed line). Red points are top 5 highest ratios.

3.3.2 *Abundance and community composition*

CCA analysis indicated CCA1 (47.52% of constrained inertia) was correlated strongly with SST and Wind Speed. The axis thus represented a gradient of sea state. CCA2 (19.36% of constrained inertia) was most strongly correlated with the AMO and with Phytoplankton abundance. The axis represented a gradient of AMO mediated phytoplankton abundance. North-South wind direction and NAO index were also important, but their correlations with the first two axes were lower than other predictors (Figure 3.3). Predictors were chosen by minimising AIC, and their correlations are summarised in table 3.2.

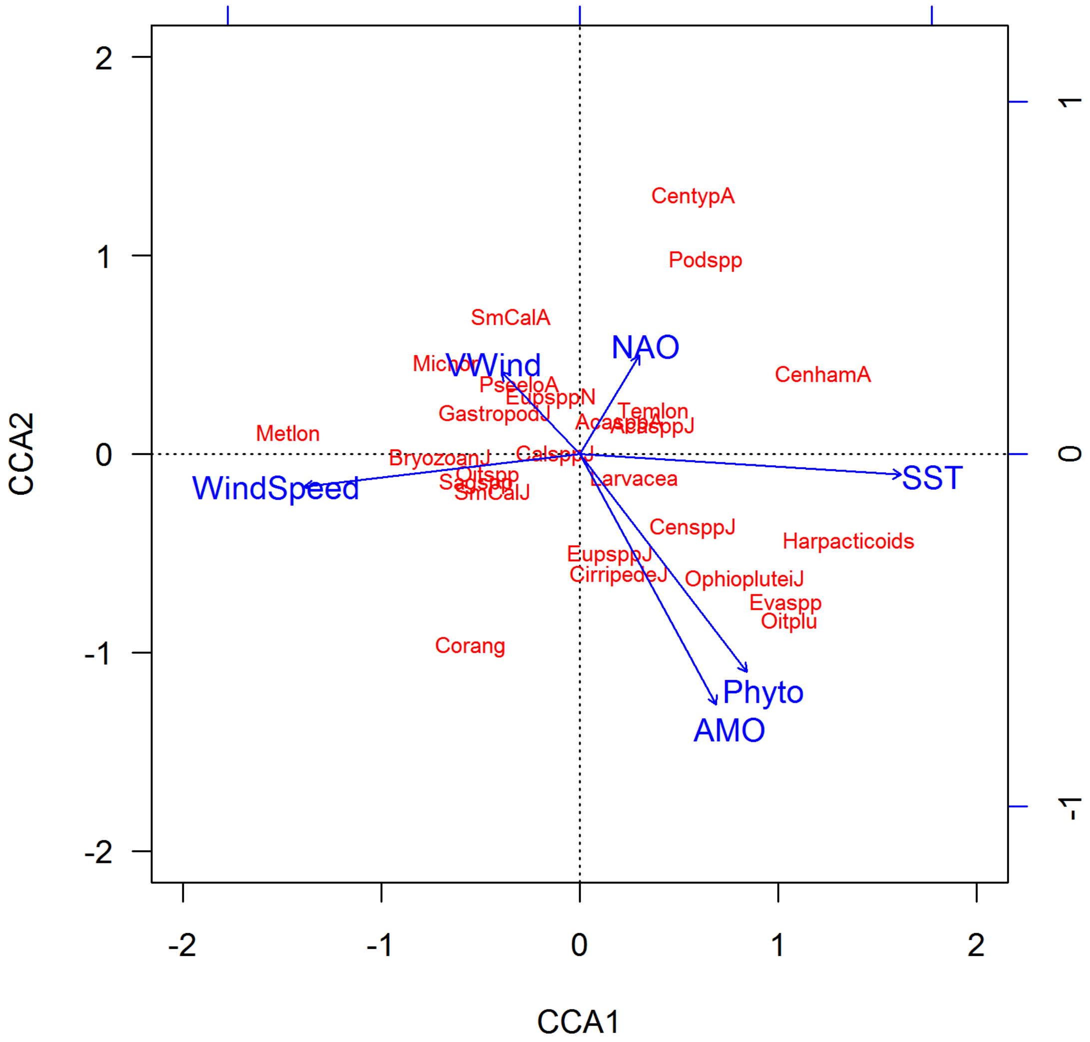


Figure 3.3: CCA analysis of mesozooplankton community composition. SST and Wind Speed correlated most strongly with CCA1, while the AMO anomaly and phytoplankton abundance correlated most strongly with CCA2.

Variable	CCA1 correlation	CCA2 correlation
SST (offshore)	0.91	-0.05
NAO	0.17	0.27
AMO	0.38	-0.71
Wind Speed (offshore)	-0.78	-0.09
V-Wind (offshore)	-0.22	0.23
Phytoplankton abundance	0.47	-0.61

Table 3.2: Correlation coefficients of input predictors with CCA eigenvectors.

Species scores against axes thus divided the zooplankton into groups that favoured conditions contingent on the AMO anomaly and its effect on phytoplankton. Zooplankton with positive scores on both axes were found more often in higher abundance when the sea was warm, wind was calm and more negative AMO lead to lower phytoplankton abundance. When zooplankton scored positively only on CCA1, they were more abundant when warm and calm seas coincided with a more positive AMO. When zooplankton that scored positively on CCA2 only, SST was cool, wind speed was higher and AMO led to high phytoplankton abundance. When zooplankton scored negatively on both axes, SST was low, wind was high, AMO was more negative and phytoplankton were less abundant. These differences are summarised in table 3.3.

Sign combination	**SST**	**AMO**	**Wind Speed**	**Phytoplankton**	**Abundance proportion**
CCA1+ CCA2+	Warm	Negative	Low	Low	0.235 (± 0.199)
CCA1+ CCA2-	Warm	Positive	Low	High	0.107 (± 0.129)
CCA1- CCA2+	Cool	Negative	High	Low	0.089 (± 0.084)
CCA1- CCA2-	Cool	Positive	High	High	0.591 (± 0.216)

Table 3.3: Interpretation of conditions under each quadrant of CCA1 and 2 biplot in figure 3.3. NAO and V-Wind correlated with higher dimension axes and are not shown.

The species so divided are detailed in Table 3.4. The first group (++) was mostly composed of medium sized calanoid copepods. *Acartia* spp. was numerically dominant. This was the second most dominant fraction, constituting approximately 24 (±20)% of total abundance. The second group (+-) had a large proportion of abundant non-copepod zooplankton. Appendicularians and *Evadne* spp. were the most abundant representatives of this group, in addition to several larval zooplankton. This group was approximately 10 (±13)% of total abundance. The third group (-+) was numerically dominated by *Pseudocalanus elongatus* stage CVI copepodites and also contained several larval forms, such as bryozoan, gastropod and euphausiid larvae. Group -+ as a whole contributed approximately 9 (±8)% to total abundance. The fourth group (--) included *Calanus* spp. juveniles, *Sagitta* spp. and several other copepods, notably *Oithona* spp. This was the most abundant group as a result of the inclusion of *Oithona* spp. and small calanoid CI-V copepodites, constituting approximately 59 (±21)% of abundance. While phytoplankton were quite distinctly seasonally ordered by CCA partitioning, this was not the case for zooplankton, which all reached peak abundance between July and August (Figure 3.4).

Group	**Designation**	**Species**
CCA1+ CCA2+	*'Acartia'* group	*Acartia* spp. CVI, *Acartia* spp. CI-V, *Centropages* hamatus CVI, *Centropages* typicus CVI, *Podon* spp., *Temora longicornis* CI-VI
CCA1+ CCA2-	'Appendicularian' group	*Centropages* spp. CI-V, *Euphausiid* calyptopi, *Evadne* spp., Appendicularians, *Oithona plumifera*, Cirripede nauplii and cyprids, Harpacticoids, Ophioplutei
CCA1- CCA2+	*'Pseudocalanus'* group	Euphausiid nauplii, *Microsetella norvegica*, Small calanoid copepod CVI, *Pseudocalanus elongatus* CVI, Bryozoan cyphonautes larvae, Gastropod juveniles
CCA1- CCA2-	*'Oithona'* group	*Calanus* spp. CI-V, *Sagitta* spp., *Corycaeus anglicus*, *Metridia lucens*, *Oithona* spp., *Oncaea* spp. CVI, Small calanoids CI-V

Table 3.4: Mesozooplankton species assemblages as identified in CCA.

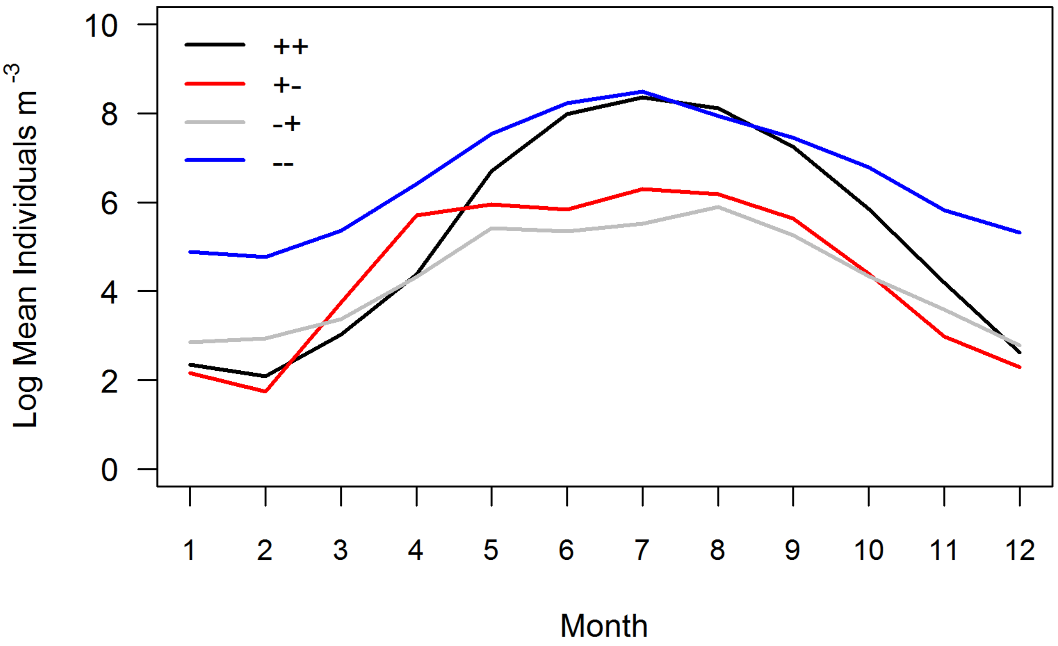


Figure 3.4: Average annual abundance of each mesozooplankton CCA group. ++: 'Acartia' group, +-: 'Appendicularian' group, -+: 'Pseudocalanus' group, --: 'Oithona' group.

The two axes of variability determined by the CCA analysis indicated CCA1 had a shallow and long oscillation, while CCA2 varied considerably with a move from being mostly positive to the mid 1990s and then becoming negative after this point (Figure 3.6). A generalised linear model was applied to total zooplankton abundance using these linear constraints as predictors. This revealed CCA1 to be the significant predictor of zooplankton abundance, and CCA2 to be insignificant (Table 3.5). Though variables were log transformed, the numerical dominance of the *Acartia* and *Oithona* groups meant their affinity to CCA1 may have obscured the effect of CCA2, which was a more variable gradient. The GLM model fit was closely approximate to observed values (Figure 3.5).

Variable	Intercept	Slope	Standard error	T value	p
CCA1	7.77	1.46	0.07	20.11	$<0.001^{***}$
CCA2		-0.03	0.05	-0.71	0.477^{ns}

Table 3.5: GLM output of total mesozooplankton abundance versus samples CCA1 and CCA2 linear constraint scores. Intercept, error and slope on log scale.

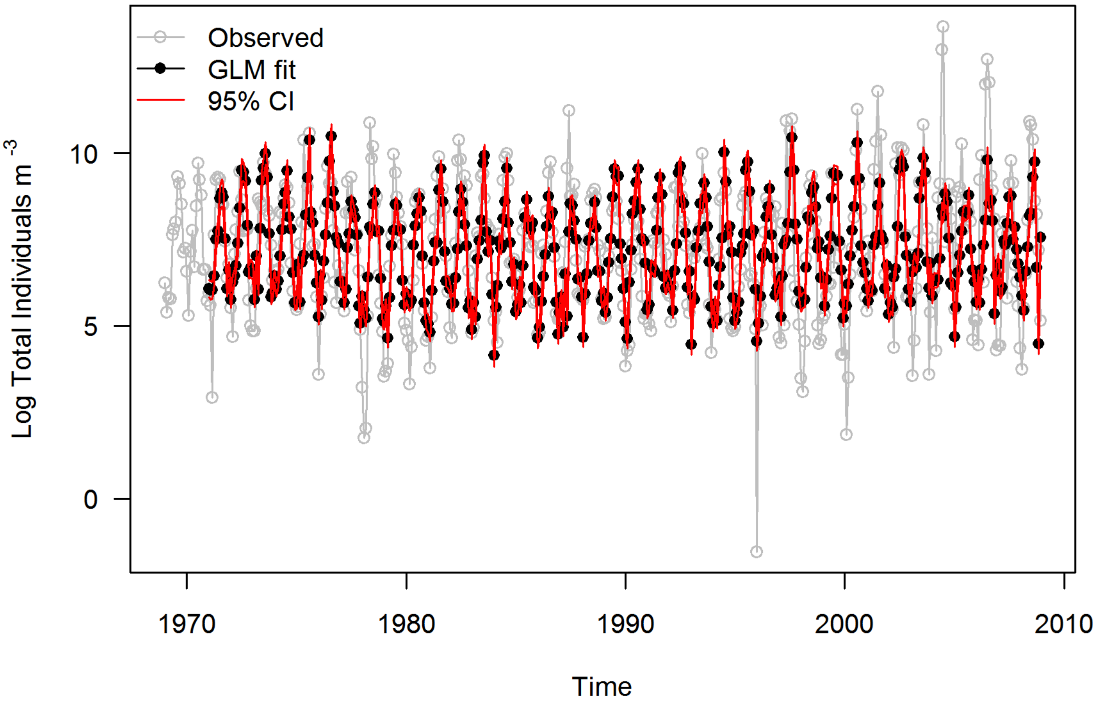


Figure 3.5: GLM model fit of mesozooplankton abundance as a function of CCA1 and CCA2. The first two years are not hindcast as no phytoplankton data were available, which was a minor contributory variable in the CCA model.

The GLM of abundance predicted by CCA linear constraints was a close fit to observed values, with the exception of very high or low values. To investigate this element of the zooplankton time series, a second GLM was created, to look at the effects of CCA linear constraints on the ratio of annual maximum to annual minimum abundance. This indicated that CCA2 was the significant predictor of this ratio (Table 3.6). Thus two effects were in evidence. Firstly, overall abundance of zooplankton was determined according to SST and associated lower wind speed. Secondly, extremely high abundance leading to large maximum:minimum ratio was determined by positive AMO anomaly and higher phytoplankton abundance. As CCA2 had moved negative (correlating negatively with AMO) after 1995, the change in ratio after 1995 was not coincidental.

Variable	**Intercept**	**Slope**	**Standard error**	**T value**	**p**
CCA1	5.71	-0.11	1.41	-0.07	0.94^{ns}
CCA2		-0.81	0.28	-2.90	0.006^{**}

Table 3.6: GLM output of annual maximum:minimum ratio of zooplankton abundance versus annual mean CCA1 and CCA2 linear constraint scores. Intercept, error and slope on log scale.

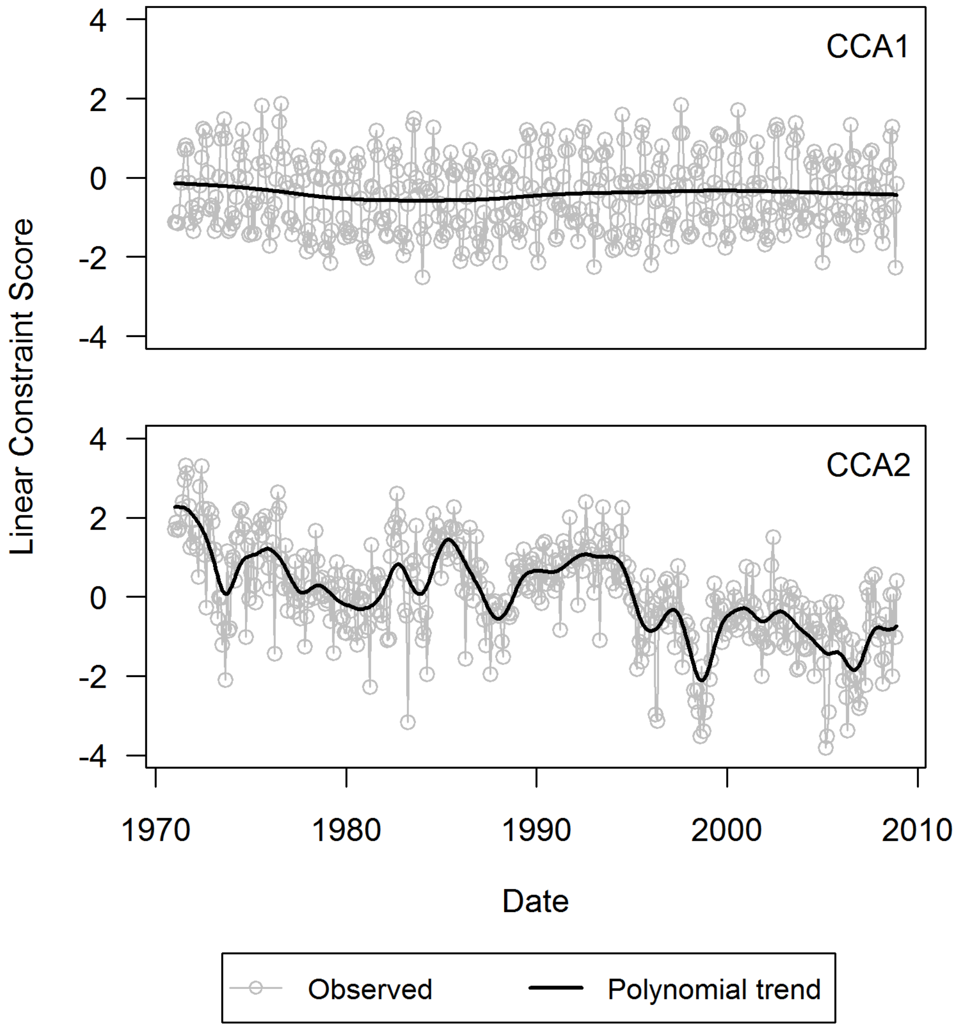


Figure 3.6: Time series of CCA linear constraint scores extracted from zooplankton CCA model.

Detrended annual mean abundance was variable, appearing to reach low abundance around 1990 (Figure 3.7). Periodograms were indicative of a dominant oscillation at approximately 0.4 * time series length (Figure 3.8). Particular wavelengths are summarised in table 3.7.

Group	Peak Frequency	Number of periods	Wavelength (Years)
++	0.425	2.35	17
+-	0.5	2	20
-+	0.35	2.85	14
--	0.45	2.22	18

Table 3.7: Spectral analysis of time series of mesozooplankton species summed according to CCA axis scores. Wavelength determined as time series * peak frequency.

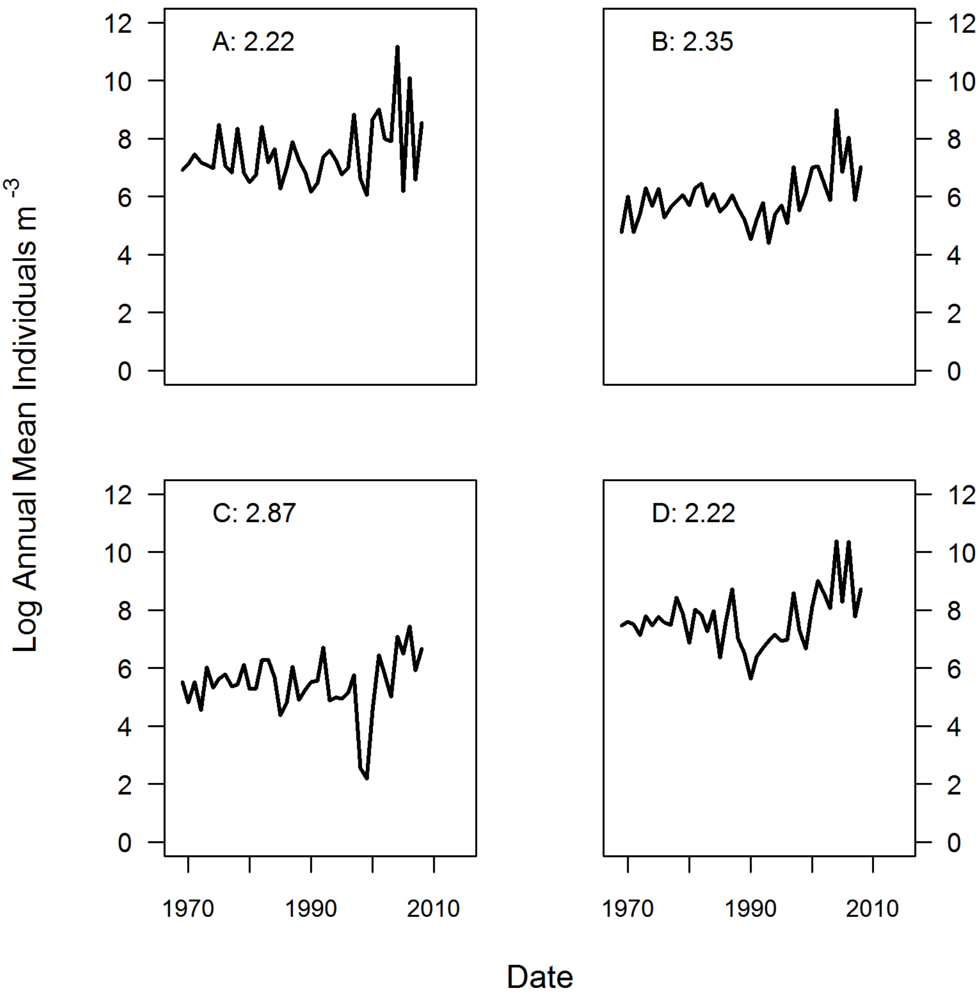


Figure 3.7: Annual mean zooplankton abundance for A: *Acartia* group, B: Appendicularian group, C: *Pseudocalanus* group, D: *Oithona* group. Values indicate the number of peaks of the dominant oscillation identified by periodograms.

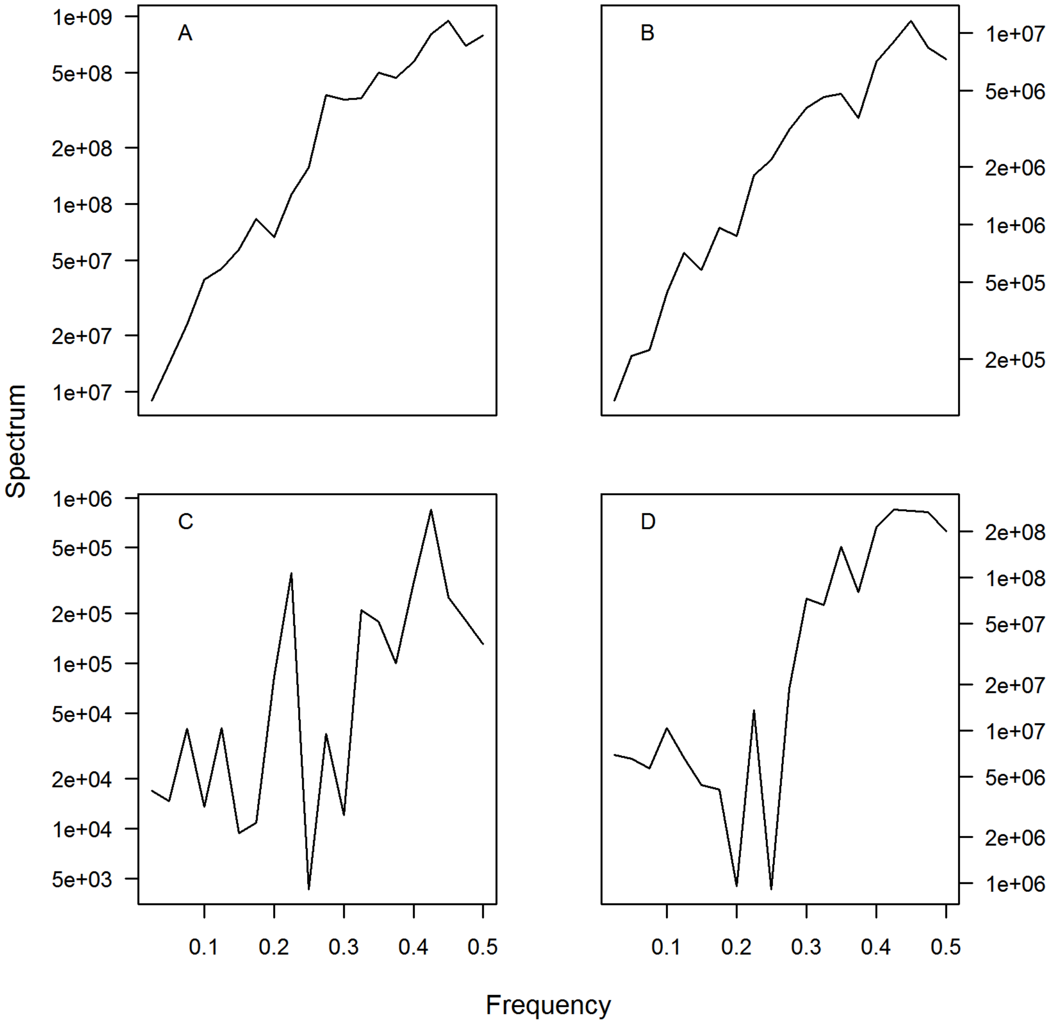


Figure 3.8: Spectral density of detrended annual mean abundance for A: *Acartia* group, B: Appendicularian group, C: *Pseudocalanus* group, D: *Oithona* group.

Dynamic linear models were constructed for each time series, with local linear trend polynomial components combined with trigonometric components using these periodicities to describe long term change in each group of zooplankton. This indicated relatively stable abundance of *Acartia* group, increasing abundance of the appendicularian group, stable abundance of *Pseudocalanus* group excepting a sharp drop in abundance around 1999, and stable abundance of *Oithona* group, with enhanced abundance in the 2000s (Figure 3.9).

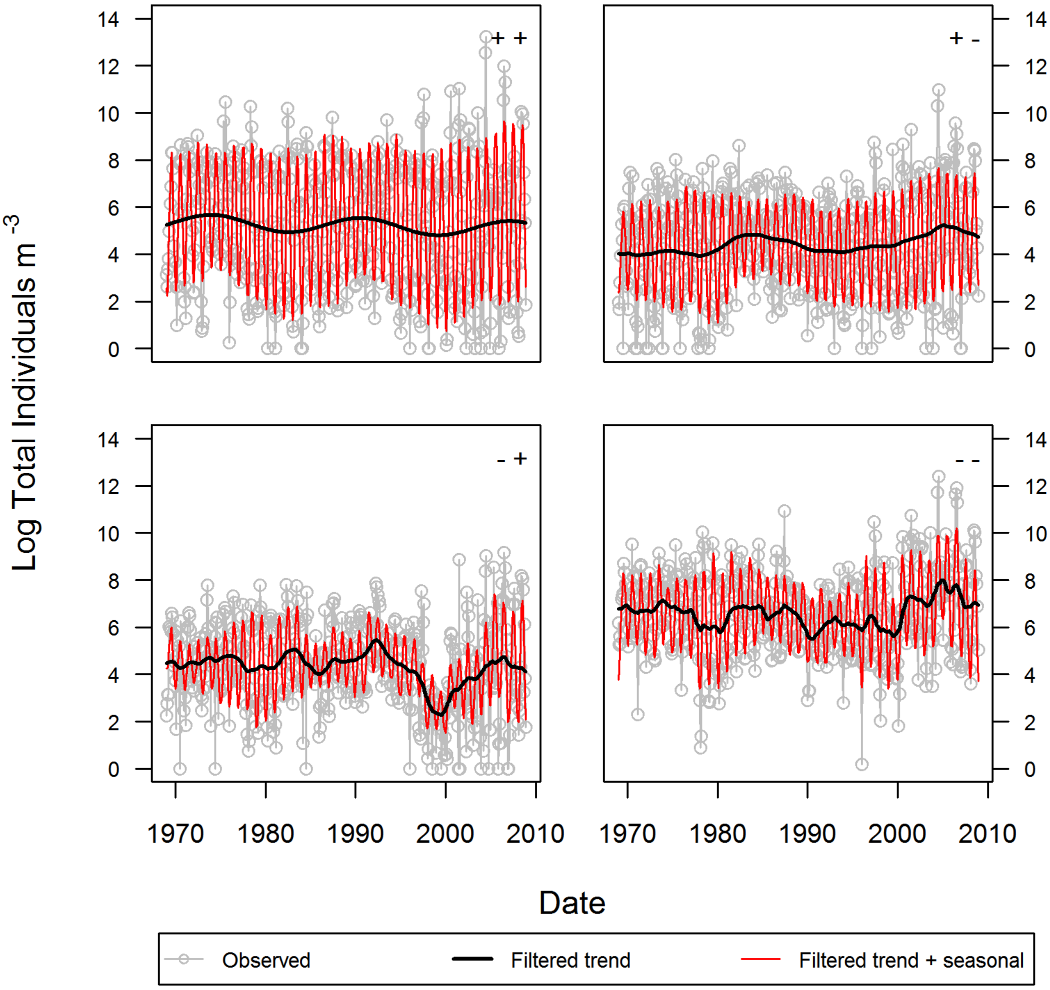


Figure 3.9: Dynamic linear models describing interannual (black) and seasonal (red) variability in: *Acartia* (++) group, Appendicularian (+-) group, *Pseudocalanus* (-+) group and *Oithona* (--) group.

In order to forecast these models forwards in time, they were re-run against 5 years fewer data, and validation forecasts compared to the observed data. This indicated quite close approximation of modelled to observed data, though abundances were underestimated in all cases (Figure 3.10). Correlations were moderate to high in all groups (Table 3.8).

Group	Spearman ρ	p
++	0.72	$<0.001^{***}$
+-	0.74	$<0.001^{***}$
-+	0.63	$<0.001^{***}$
--	0.69	$<0.001^{***}$

Table 3.8. Spearman correlation coefficients for validation forecasts and withheld part of the zooplankton time series. All groups show positive and significant correlations, indicating seasonality and trends in the models are approximate to observed values.

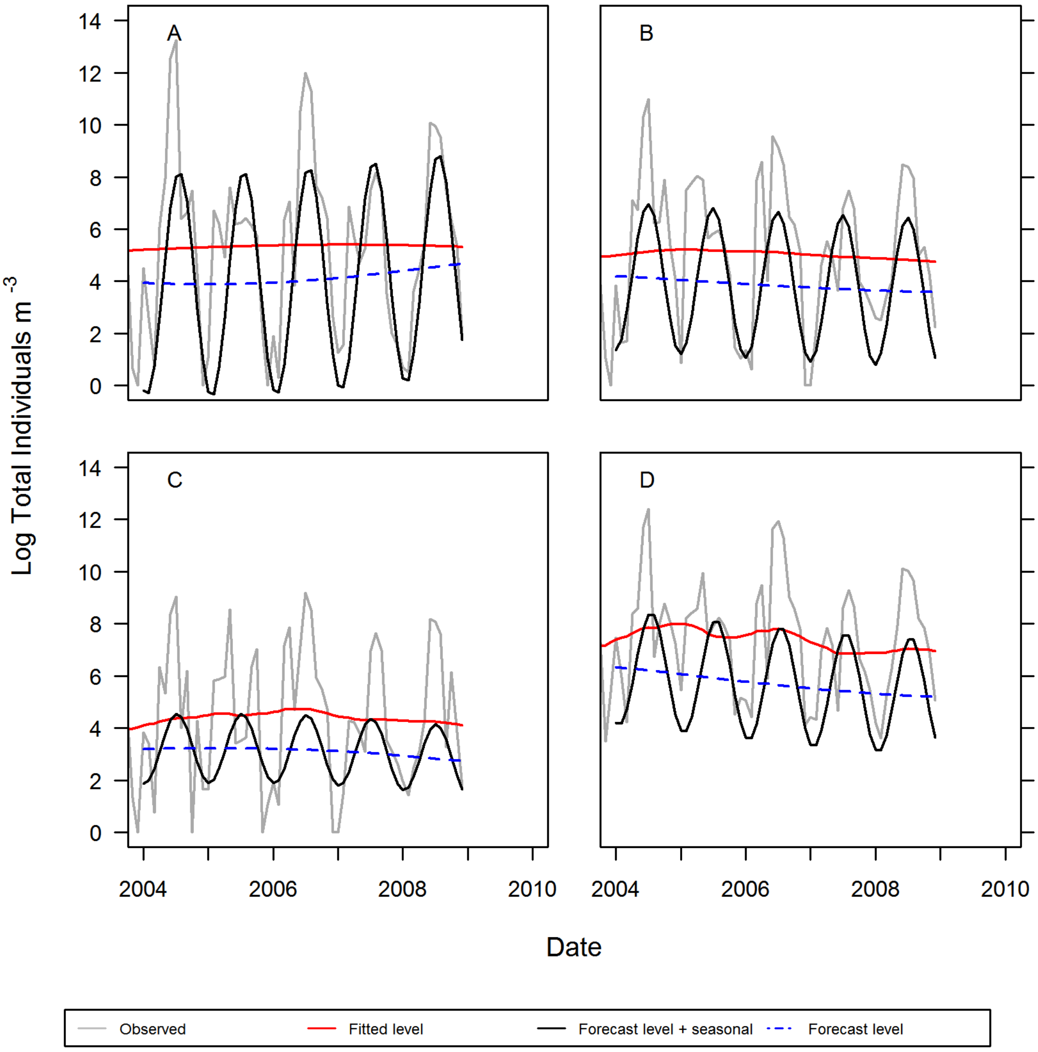


Figure 3.10: Validation forecasts against A: *Acartia* group, B: Appendicularian group, C: *Pseudocalanus* group, D: *Oithona* group. Red line is post hoc model fit against full time series, blue dashed line is validation forecast against time series minus 5 years, and black line is forecast + seasonality.

FFBS sensitivity analysis, 10 iterations of the model fit on 1 year fewer data per iteration indicated model fits to be conservative (Figure 3.11). On this basis, model forecasts were made for the five year period 2009 to 2013.

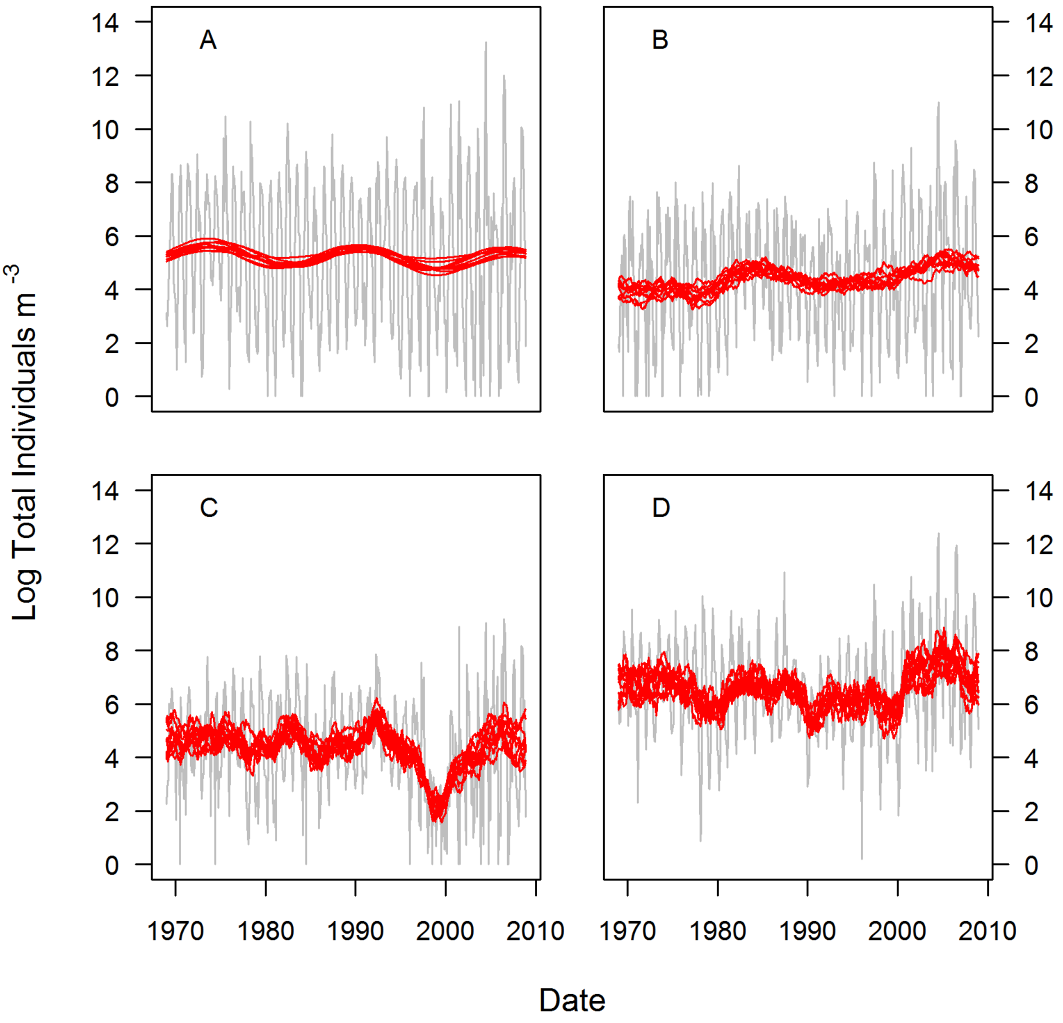


Figure 3.11: FFBS stress tests of model fits. Each line indicates a model run with year less data than the preceding run, up to 10 years of data removed. A: *Acartia* group, B: Appendicularian group, C: *Pseudocalanus* group, D: *Oithona* group.

Forecasts coincided with downward trajectories begun in each group case in 2006 (Figure 3.12). This resulted in estimations of deseasonalised abundance for each group which were lower than the long term mean, with the exception of the appendicularian group (Table 3.10). As noted in validations, abundance was underestimated by the model, so the downward swings in abundance may have themselves been excessive. Considering each group as a proportion of total mean level revealed the period 2009-2013 was expected to be composed of relatively fewer representatives of the *Pseudocalanus* and *Oithona* groups, and relatively greater numbers of the *Acartia* and appendicularian groups, when compared to the long term mean (Table 3.9).

Group	69-08 Mean	09-13 Mean	% Difference	% of 69-08 Total	% of 08-13 Total	T	p
++	208.51	151.41	-27.38	19.85	25.44	-11.09	<0.001***
+-	75.81	75.86	-0.07	7.21	12.74	-0.02	0.982ns
-+	73.69	17.11	-76.78	7.01	2.87	-16.11	<0.001***
--	692.28	350.72	-49.33	65.91	58.93	-8.89	<0.001***

Table 3.9: T-test results comparing forecast abundance of each mesozooplankton group compared to the long term mean. Seasonal variation not included in these figures, due to underestimation of seasonality by the dynamic linear models.

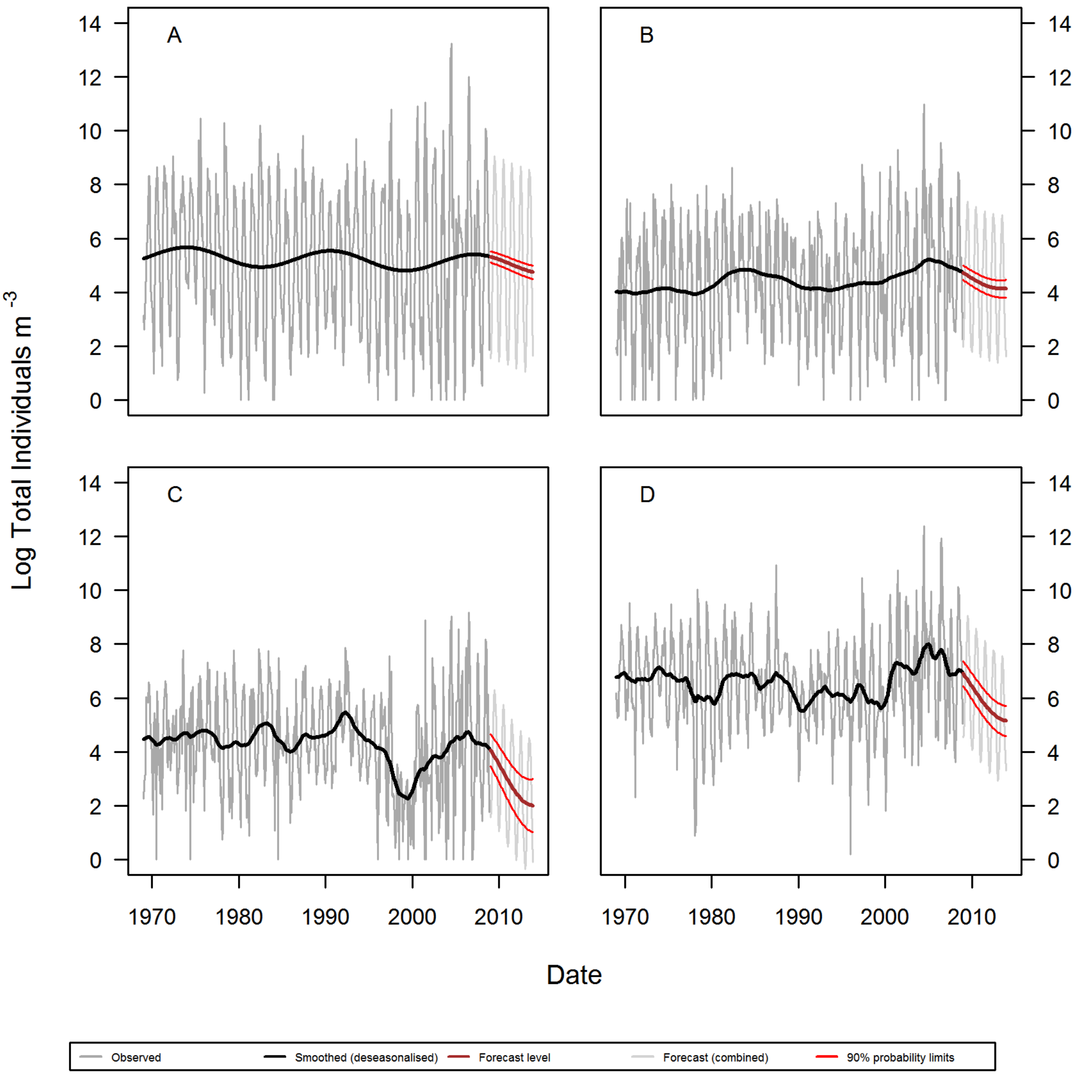


Figure 3.12: DLM forecasts of zooplankton abundance. Black line: deseasonalised abundance. Dark grey: observed data. Light grey: forecast. Brown: deseasonalised forecast. Red: 95% confidence intervals. A: *Acartia* group, B: Appendicularian group, C: *Pseudocalanus* group, D: *Oithona* group.

Species composition was strongly organised by CCA1, representing combined variation of mainly SST, Wind, AMO and phytoplankton. DTS zooplankton samples were mostly various copepod species which varied in abundance according to the sign of CCA1: the genera *Acartia*, *Centropages* and *Temora* in high abundance in summer (positive CCA1) and low abundance in winter (negative CCA1), uncontroversial given the importance of temperature in regulating growth. The genera *Oithona*, *Metridia*, *Calanus* and small calanoid juveniles moderately abundant in winter and spring, as well as highly abundant in summer. Considered collectively, CCA1 was the significant factor in zooplankton abundance. Subordinate in abundance were groups dominated by *P. elongatus* which appeared to have suffered a short period of lower than average abundance in the late 1990s and early 2000s, and a predominantly non-copepod assemblage, dominated by appendicularians and ophioplutei. Increasingly positive AMO anomaly favoured growth of this appendicularian group. Forecasts indicated against the backdrop of declining abundance generally, that the warmer water appendicularian group and the *Acartia* group were expected to become proportionately more abundant than the colder water *Pseudocalanus* and *Oithona* groups.

CCA2 represented AMO and phytoplankton variability uncorrelated with SST/Wind gradients and had the effect of increasing the peak to trough ratio of zooplankton abundance in a given year. Five years had exceptionally high ratios. Of these, in 1978, small calanoid CI-V copepodites were numerically dominant. In 1996, 2000 and 2004, *Acartia* spp. was numerically dominant. In 2006, *Oithona* spp. was numerically dominant. Abundance generally had increased as a result of warming seas, while species composition had altered as a result of the AMO anomaly and its associated effects upon phytoplankton abundance. The null hypotheses of no effect of oceanographic, meteorological or biological variables on zooplankton were therefore rejected.

3.3.3 *Change in phenology of abundance peaks*

Dynamic linear model seasonality was extracted for each of the zooplankton groups. Peak extraction indicated between year peak varied by approximately 2 months, in all cases the peak was centred between June and August. The second group had one anomalous peak in December (Figure 3.13). As there was no breakpoint identified, there was no reference point against which to compare peak abundance before and after, a GLM versus time was modelled on the peak for each group and the trends are summarised in Table 3.10. Mean peak varied between 1969 and 2008 by between 5 days later and 12 days earlier. Variability around mean peak was considerable, suggesting though trends were statistically significant, the timing of peak abundance was determined more by factors extrinsic to the model than they were as a function of time.

Spatial plots confirmed the consistency of the peak abundance range. Figures 3.14 and 3.15 illustrated little variation in peak abundance for groups 1 and 2. In 2004-6 abundance was higher in spring than normal – the very high abundances recorded at this time presenting as darker patches on the spatial plots between June and August. Figure 3.16 indicated the drop in abundance if group 3 observed in DLM plots began in 1996 and continued into the early 2000s. The late 1970s to early 1980s were a period of weaker abundance in spring. This late 1970s to early 1980s weak spot in spring was also observable in group 4 (Figure 3.17). After 2000 this group more frequently was more abundant than the long term mean, again with higher abundance earlier in the year around 2004-6.

Response	**Intercept**	**Slope**	**Peak advance Year^{-1}**	**Standard error**	**T value**	**p**
Acartia group	7.43	-0.0004	+3.21 hours	0.0001	-3.68	<0.001***
Appendicularian group	6.58	0.0004	-3.21 hours	0.0002	2.332	0.02*
Pseudocalanus group	7.28	-0.0008	+6.42 hours	0.0001	-6.509	<0.001***
Oithona group	7.35	-0.0009	+7.22 hours	0.0001	-6.388	<0.001***

Table 3.10: GLM output of seasonal peak versus time for each mesozooplankton group.

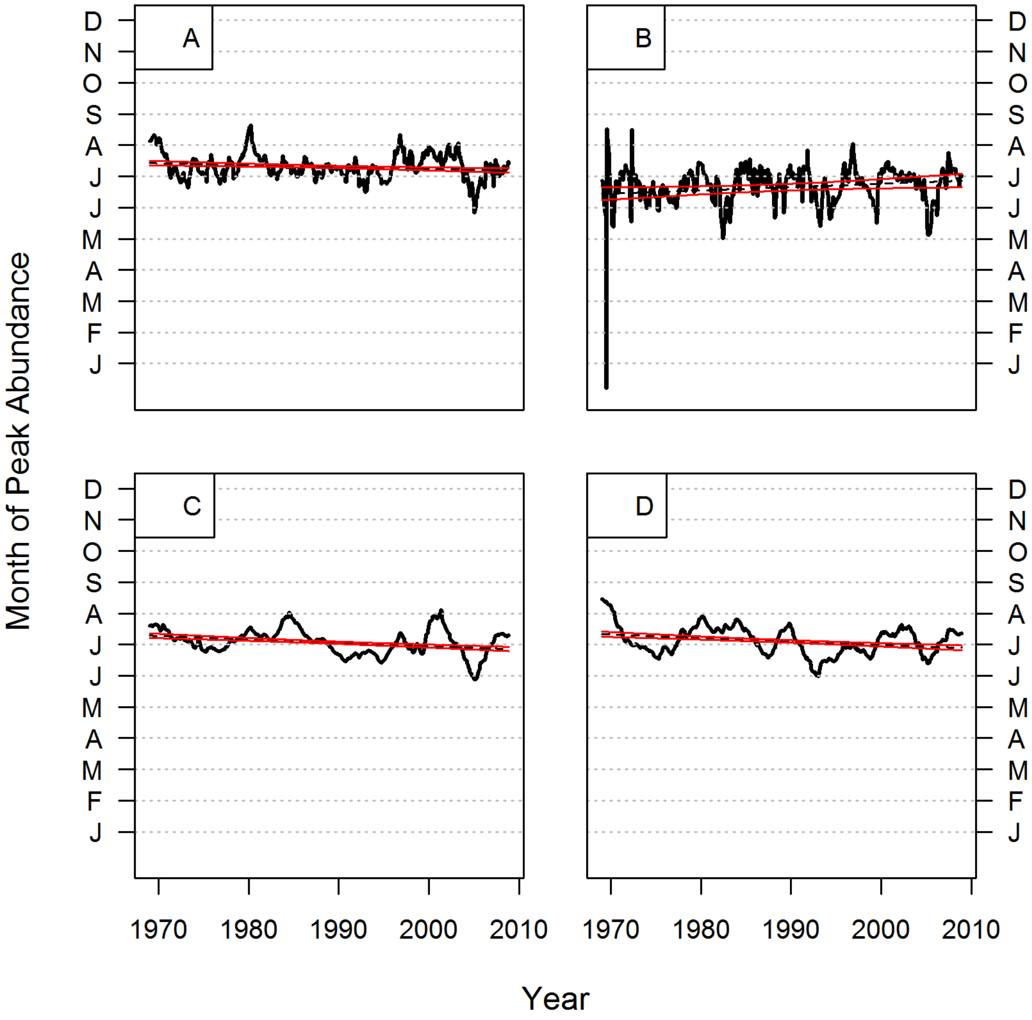


Figure 3.13: Phenology of each mesozooplankton group. A: '*Acartia*' group, B: Appendicularian group, C: '*Pseudocalanus*' group, D: '*Oithona*' group. Dashed line: GLM model fit. Red line: 95% confidence intervals. See Table 3.11 for GLM coefficients.

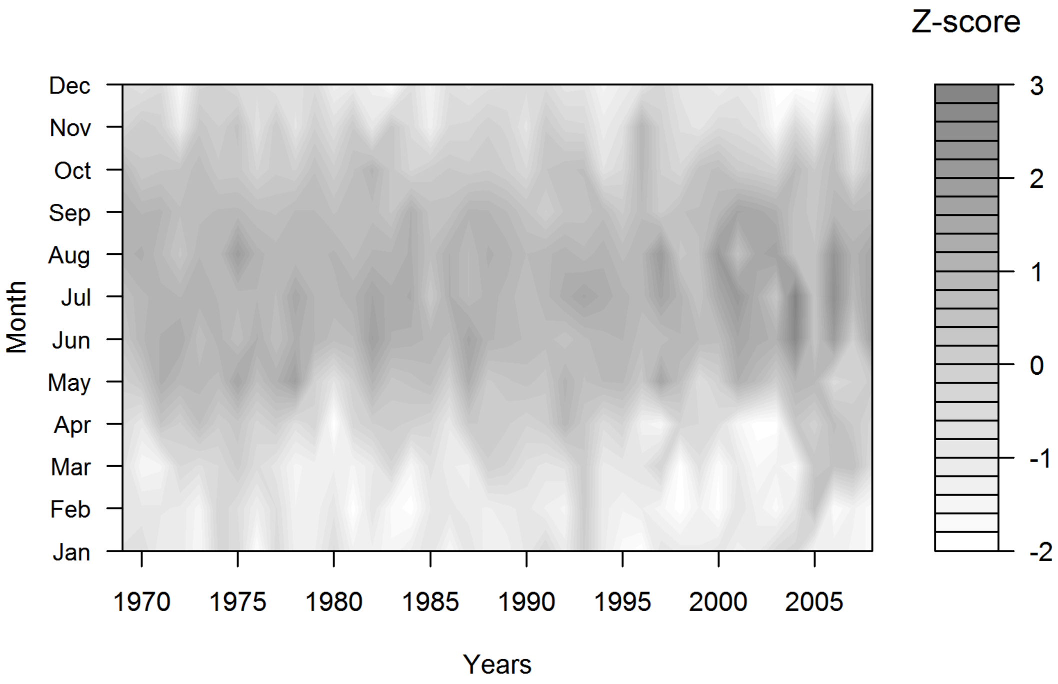


Figure 3.14: Spatial plot of *Acartia* group normalised abundance.

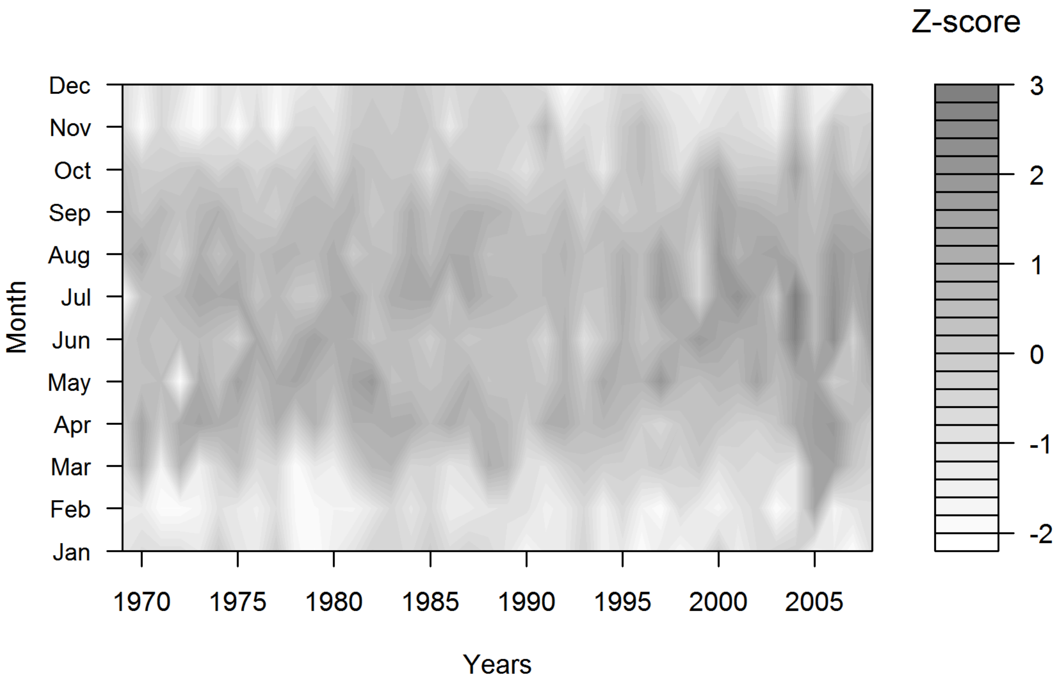


Figure 3.15: Spatial plot of appendicularian group normalised abundance.

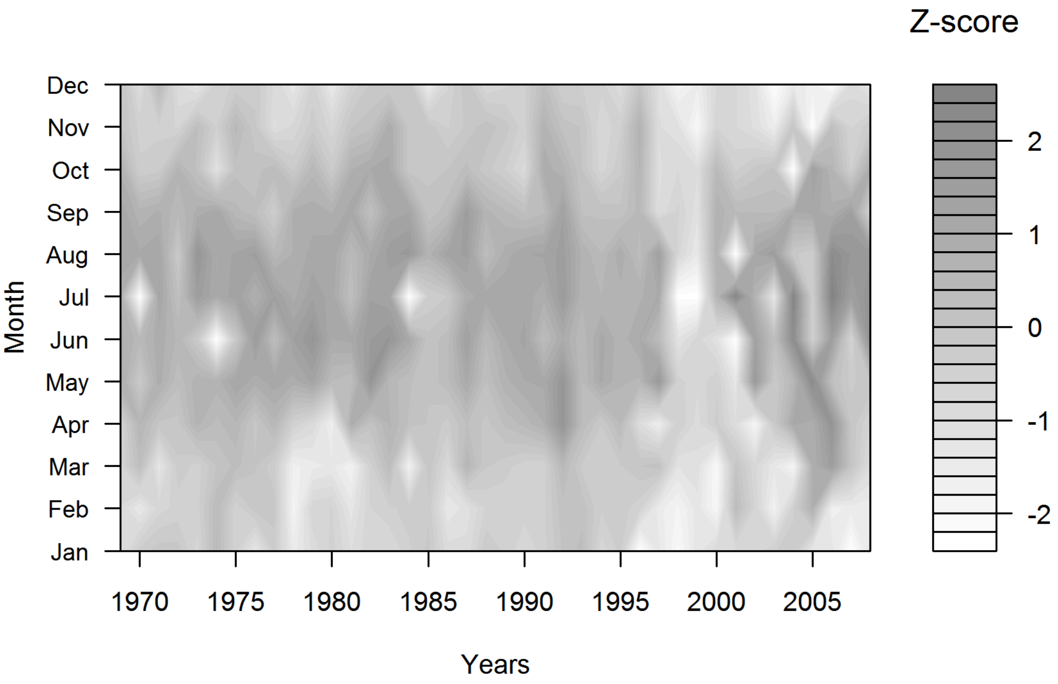


Figure 3.16: Spatial plot of *Pseudocalanus* group normalised abundance.

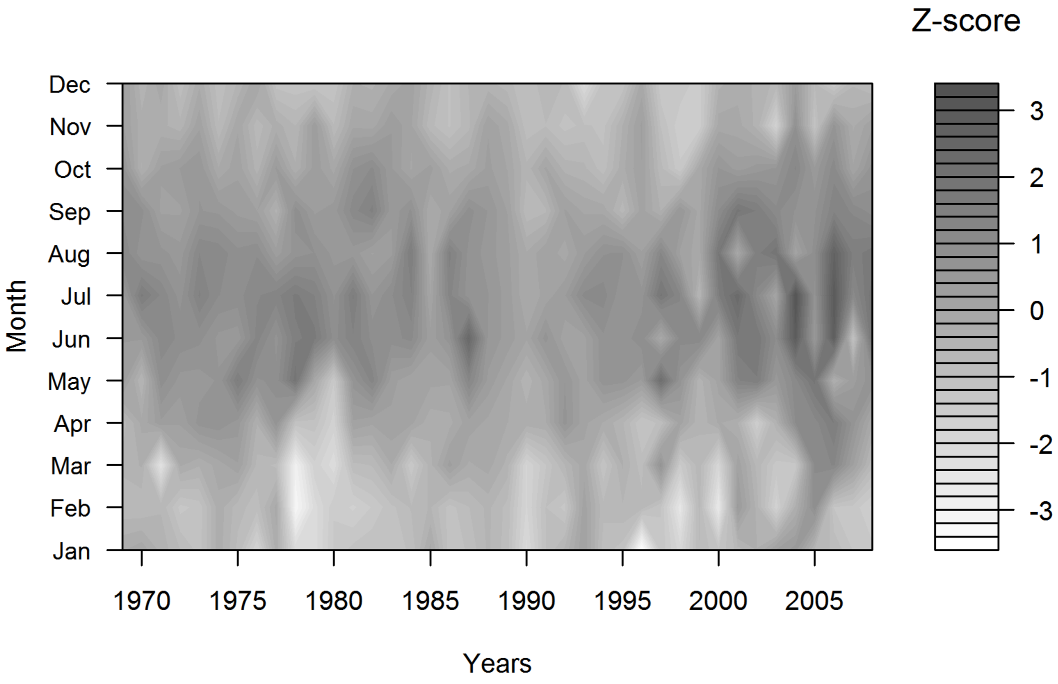


Figure 3.17: Spatial plot of *Oithona* group normalised abundance.

The groups determined by CCA biplot scores did not appear to vary strongly in time, which supported the null hypothesis of no effect of oceanographic, meteorological or biological variables on phenology.

3.4 Discussion

Zooplankton abundance did not appear to undergo a step change in total abundance. Rather, abundance increased as a response to steady increase in CCA1, which was predominantly descriptive of the combined status of SST and wind speed. This sets the DTS zooplankton time series apart from the central North Sea CPR time series, in which a sustained increased zooplankton abundance was evident, after 1989 (Beaugrand and Reid, 2003). The GSA was not coincident with a change in total abundance in the late 1970s. Nor was the step change in abundance observed in DTS phytoplankton reflected in a similar change in total zooplankton abundance after 1995.

The NAO, interpreted as the reason for regime shift in the North Sea as supported by plankton data from CPR studies (e.g. Ji *et al*, 2010; Alheit *et al*, 2005; Edwards *et al* 2002), was important in determining zooplankton community composition, but its variation was most strongly correlated with higher dimension axes of the CCA model. Rather, the AMO, which had been demonstrated in chapter 2 to be of key importance in determining phytoplankton abundance was the more important basin scale oceanographic index. The NAO is variously effective at describing SST across the North Atlantic, while the AMO is a more resilient predictor across wide areas (McGinty *et al*, 2012). The CCA model suggested the AMO worked in two ways – firstly by directly signifying warmer SST near to the DTS, with the resultant effects on zooplankton metabolism and population growth. Warming in the North Sea and North Atlantic has favoured *Acartia, Centropages* and *Temora* growth (Beaugrand *et al*, 2003; Fauchald *et al*, 2011) and allowed *Acartia* to dominate over *Pseudocalanus* in the Baltic Sea (though this was also related to salinity: Alheit *et al*, 2005; Möllmann and Koster, 2002). The beneficial effect of SST on these inshore temperate groups found elsewhere is supported in this study. The second effect of the AMO was by promoting conditions favouring greater phytoplankton abundance, there was more food available for zooplankton to graze upon. This appears to have lead to a step-change in the intensity of zooplankton swarms, if not overall zooplankton abundance.

Earlier spring abundance of phytoplankton should logically have lead to increased abundance of the fast growing copepod, *Pseudocalanus elongatus* (Klein Breteler *et al*, 1995). However the species has greater affinity for colder water, and in the context of the warming North Sea, *Pseudocalanus elongatus* has declined in abundance (Fauchald *et al*, 2011). Wet weather reduces salinity and harms population growth of *Pseudocalanus elongatus* (Möllmann *et al*, 2008), but outside of the Baltic Sea this is unlikely to have had a major effect on abundance, particularly as low salinity values near to the DTS site were in the 1980s, when decreased *Pseudocalanus elongatus* abundance occurred in the early 2000s. At equivalent suitable food conditions *Pseudocalanus elongatus* can reach maturity faster than *Acartia clausi* or *Temora longicornis* in cold (5ºC) water (Klein Breteler *et al*, 1995) and warmer temperature negatively affects *Pseudocalanus elongatus* growth (Isla *et al,* 2008). Warming sea may therefore have slowed growth of *Pseudocalanus elongatus* sufficiently to explain the *overall* decline in abundance of the *'Pseudocalanus'* group, but there was no rapid warming in 1999 to 2005 that would explain the large drop in abundance observed between these years.

Peak abundance of *Pseudocalanus elongatus* moved later at the same time as abundance dipped in the early 2000s. Initially the abundance of early cohorts in 1999-2000 was low, and the later cohorts higher. By 2005 earlier cohorts were more abundant and thus peak abundance shifted earlier by virtue of being more abundant than later cohorts. Klein Breteler *et al* (1995) suggested that the affinity of *Pseudocalanus elongatus* to cold water meant it was well placed to use its wax ester reserves (Kattner and Hagen, 2009) deposited over winter to reproduce earlier in the year than other small copepods. This is certainly in evidence in the DTS, but at the time when spring phytoplankton peak moved suddenly earlier, there was actually much lower abundance of *Pseudocalanus elongatus* and no obvious beneficiary to fill the gap left by lower than normal abundance at this time of year, due to low water temperature. The other highly abundance small calanoid, *Acartia clausi,* feeds on a wide range of prey functional groups and the genus can more readily adapt to different food regimes (Kleppel *et al*, 1991, Kleppel, 1993; Tiselius, 1989) favouring microflagellates over diatoms and appears to have been temperature limited at this time of year.

Food availability appeared not to be a reason for declining abundance given what is known about the lifecycle of *Pseudocalanus elongatus.* The AMO was related to increased wind driven mixing, and wind induced turbulence undoes vertical organisation of zooplankton (Wroblewski and Richman, 1987), inhibits filter feeding activity (Costello *et al*, 1990), and causes foraging efficiency to drop (Alcaraz, 1997). However diatoms require some stability to grow, so there could not be such turbulence as to reduce abundance to ~20% of the long term mean for two years. Nor could grazing by pelagic fish larvae be a cause as fish larvae abundance was eliminated as an important term in CCA analysis. If as was suggested from Chapter 2 that the DTS was shoreward of a coastal front, the coincident timing of the change in the abundance of the '*Pseudocalanus*' group and spring phytoplankton abundance might be a common response to a change in the position of this front relative to the DTS. Gowen *et al* (1998) found *Pseudocalanus elongatus* in the Irish Sea to have a spring peak in stratified water, a summer peak in mixed waters, and that advection from stratified to mixed zone occurred. A sharp drop in *Pseudocalanus elongatus* abundance associated with a shift later in peak therefore may therefore signify a dynamic cross-front advection process that was interrupted by wind driven current changes in the late 1990s to early 2000s, possibly with its origin in the disruption of normal circulation of the North Sea in 1996 (Pingree, 2005). However, this occurred at a time of high diatom abundance so this would not explain the low abundance observed; if *Pseudocalanus* were transported across a front, so was abundant food.

This therefore suggested some sort of response in the DTS zooplankton coincident with a major hydrographic event, namely the 1996 negative NAO event. The AMO correlated second CCA axis was not important in predicting zooplankton abundance, but presumably as this axis represented the previously described AMO-lead change in phytoplankton abundance, this had to have some effect. It appeared to be the case that this effect was not associated with overall abundance, but with extreme peaks in abundance, in most cases of *Acartia clausi*. Most of the highest abundances found were in the 2000s and it was determined that negative CCA2 (positive AMO and high phytoplankton abundance) lead to a higher ratio of maximum to minimum abundance in a year. These peaks in abundance occurred in later summer, 2-3 months after spring phytoplankton abundance peaked. *Acartia* is probably temperature limited in spring, meaning these copepods were feeding on the successor phytoplankton species growing in summer. The drop in abundance of early spring grazers may also promote greater abundance of microzooplankton grazers, both of which favour the growth of omnivorous copepods such as *Acartia* and *Oithona spp* (Dutz and Peters, 2008), to very high levels. Tintinnids reach high biomass in the western central region relative to other parts of the North Sea (Cordeiro *et al*, 1986), so these are credible food sources. Additionally, if the dynamics of frontal zone formation and advection of plankton have altered in the 1990s and 2000s, this may indicate a reason for such high spikes in abundance. It cannot be stressed enough that CTD profiles are essential to resolving this question in future, as well as estimates of microzooplankton abundance, which may be adequately sampled by the 63µm net. Microzooplankton has not been looked at in any detail in the DTS.

Oithona spp., dominant in the group negatively correlated with SST by virtue of its more homogeneous seasonal distribution due to its omnivorous diet (Lischka and Hagen, 2007), also reacted positively to the phase of the AMO. Gissel Nielsen and Sabatini (1996) and Castellani *et al* (2005) determined *Oithona* to be most reproductively successful when feeding on microzooplankton rather than phytoplankton. Microzooplankton is strongly dependent on phytoplankton for food, and feeds more rapidly as the sea warms through the year (Aberle *et al*, 2007). Greater abundance of phytoplankton in warmer seas therefore likely resulted in increased abundance of tintinnids, rotifers, ciliates and other microzooplankton which could feed *Oithona* spp. Microzooplankton have increased in abundance in the northeast Atlantic to a greater degree than the North Sea (Hinder *et al*, 2012), though this time series begins only after the mid 1990s. This would be an excellent further study with the fine mesh dataset of the DTS.

Species composition has remained dominated by copepods, but it would appear a group dominated instead by non-copepods like appendicularians, ophioplutei and the cladoceran *Evadne* spp. has benefited most from the phase of the AMO and has increased in abundance, with forecasts suggesting it was expected to move from approximately 7% of total zooplankton abundance to 12%. *Oikopleura dioica* grows rapidly when temperature and food density is high compared to cooler and more sparsely available food (Lombard *et al*, 2009), and Thompson *et al* (2010) found warmer and acidified conditions to be generally beneficial to *Oikopleura* population growth in mesocosm experiments. It would appear that the positive effect of AMO on phytoplankton, coincident with a generally warmer, if not more acidic, sea near to the DTS has so benefited appendicularians in the DTS. Ophiopluteus abundance did not contribute to any rapid spike in abundance of the 'appendicularian' group. The opportunistic response of *Ophiura albida* to benthic disruption observed in the southern North Sea after the cold winter of 1995/6 (Neumann *et al*, 2009) was not discernible in the time series of ophiopluteus larvae. Ophiuroid larvae are not able to capitalise on rapid changes in food supply due to their low metabolic rate (Whitehill and Moran, 2012), and the response observed in the DTS would seem to suggest no particularly beneficial circumstances presented themselves for this group.

Dynamic linear model forecasts of all four groups appeared to suggest a general downturn in abundance could be expected for the period 2009 to 2013, however validations appeared to underestimate abundance consistently, and the periodicity determined from periodograms was much less distinct than had been the case for phytoplankton. This suggests the periodicity related to moderate scale oscillations in AMO found in phytoplankton does not transmit clearly through to zooplankton. While Aebischer *et al* (1990) suggested synchronous trophic responses had their basis in changing weather, this apparently does not hold quite so true in the DTS. The influence of SST on abundance, which showed no periodicity shorter than the length of the time series was much more important than that of the AMO signals more easily seen in the phytoplankton data.

Most long term phenological change was earlier, in agreement with the results of CPR study suggesting moves of approximately 10 days earlier (e.g. Edwards and Richardson, 2004; Mackas *et al*, 2012). The exception to this was the appendicularian dominated group. *Oikopleura dioica* and *Fritillaria borealis* in the southern North Sea have begun to peak earlier in the year, and this has a strong relationship with warming SST (Greve, 2001, Greve *et al*, 2004). The seas have warmed at the DTS site by approximately 1ºC in the 2000s (Figure A7.1), so according to these southern North Sea examples, it should follow that appendicularians peak earlier as a result, though they did not do so. Appendicularians filter smaller food particles than do copepods (Thompson *et al*, 2010), which would suggest a role for the seasonal distribution of bacteria and microflagellates in the pattern observed in the DTS that regrettably cannot be further resolved with the net samples that were available for this study, though presumably if there is a trend later in peak abundance of the 'appendicularian' group, there is likely to be a trend later in their prey. *Evadne* spp. was the second most abundant taxon in this group. *Evadne nordmanni* is the main species of the genus found in the North Sea according to the CPR (Lindley and Batten, 2002) and feeds upon larger sized microzooplankton and predatory dinoflagellates (Bainbridge, 1958; Katechakis and Stibor, 2004). There was no particular phenological trend for *Protoperidinium*, the most abundant heterotrophic dinoflagellate in DTS phytoplankton, which would go some way to explaining the lack of a strong trend to peak earlier in this constituent of the 'appendicularian' group, as observed in the CPR. Relative to the high level of variability in peak between years, on the order of 2 months, the trends of 5-14 days from 1969 to 2008 were quite minor in magnitude, and probably of little ecological importance compared to the shorter term variability in peak abundance. Certainly the SST related moves earlier of up to 5 weeks in peak abundance of southern North Sea copepods (Schlüter, 2010) were not in evidence in the DTS.

3.4.1 *Conclusions*

Total abundance has increased gradually over the course of the time series and a linear constraint with a major SST component has had a strong predictive effect. Abundance of two groups of zooplankton, one numerically dominated by *Pseudocalanus elongatus,* and one by warm temperate copepods of the genera *Acartia, Temora* and *Centropages* had static or declining abundance over the long term. Two other groups, one dominated by *Oithona* spp. and another by appendicularians, had increased abundance. The positive phase of the AMO in the 1990s onwards favoured these two groups which mostly have non-herbivorous feeding preferences, indicating change to diatom and dinoflagellate abundance and species composition has potentially had a further effect on the availability of their prey.

The ratio of minimum to maximum abundance has undergone a step-change upwards after 1995, that has been predicted by a linear constraint with strong correlations with the AMO-mediated increase in phytoplankton. Maximum abundance occurs 2-3 months after the phytoplankton spring bloom, indicating greater importance of summer phytoplankton in this phenomenon. The rapid decline and recovery of the

'*Pseudocalanus*' group at a time when diatom abundance was higher earlier in the year may have represented a coincident change in horizontal advection of copepodites across the offshore front of the Northumberland coast, though this cannot be substantiated with the data here analysed. Future study would benefit from the incorporation of a CTD profile in order to confirm or refute this hypothesis.

Long term phenological change has been quite modest, though shorter term variation in peaks between years have varied considerably. Earlier peaks in zooplankton corresponded to earlier peak in the spring bloom, though the appendicularian group had the opposite trend, for reasons that are not fully understood. Evidence for major reorganisation of the zooplankton at the DTS is limited, and the major factors affecting abundance and species composition appeared to be seasonal weather variation, alongside a change in phytoplankton abundance as a result of changed weather. The neritic dominated mesozooplankton at the DTS would appear to be quite resilient to changing oceanographic and meteorological conditions. A future study on the development and extent of the frontal zone and its effects on these elements of zooplankton at the DTS is strongly recommended.

Chapter 4. Oceanographic, Meteorological and Biological Change and their Effects on a New Ichthyoplankton Dove Time Series

4.1 Introduction

The North Sea and surrounding areas contain a diverse assemblage of fish larvae in the plankton that has undergone major changes in abundance and composition at the decadal scale. Russell (1973) presented evidence of rapid shifts from a high abundance ichthyoplankton community in the English Channel in the 1920s to a low abundance community in the 1940s, 1950s and 1960s before a resurgence to 1920s levels in the 1970s. The high abundance of ichthyoplankton generally coincided with high abundance of typically rare (in the English Channel) species, for example *Scomber scombrus* in 1926, *Trachurus trachurus* in 1927, and *Buglossidium luteum* in 1971 and *Melanogrammus aeglefinus* in 1972, as well as a shift in balance from herring to sardines. This was a periodic change in geographic range of fish according to changing conditions, named the Russell Cycle (Cushing, 1995b). SST described by the longest signal in the Atlantic Multidecadal Oscillation is a significant explanatory variable in this cycle in the English Channel, which appears to be based on habitat switching by adults (Edwards *et al*, 2013). In the DTS, fish larvae are sampled by the large mesh WP3 net, though there has until now not been an attempt to describe the taxonomic composition of this element of the plankton, or what factors affect community composition and abundance. Boehlert and Mundy (1988) described the important factors for coastal ichthyoplankton as they migrate to nursery areas: as newly hatched larvae, their distribution is governed by Ekman transport, counter-currents and eddies. Their vertical movement is motivated by phototaxis, thermotaxis and moderated by diel vertical migration of their own prey. As they grow older, feeding and movement activity becomes associated with tides and chemical cues associated with the water of nursery areas, often estuaries. Clearly prey and hydro-meteorological factors exert influence on the survival of fish larvae.

Temperature optima are important in regulating growth of larvae, and therefore key to mediating survival of larvae in the plankton, entry to the foodweb at a suitable time to graze preferred prey (and avoiding periods of high predator abundance) and ultimately through optimal development and recruitment, the abundance of adult fish. Malzahn and Boersma (2007) found cumulative dominance plots of fish larvae contributions to annual abundance flattened by the time of the summer SST peak, which indicated SST dynamics were influential in population growth of larvae: colder winter SST delayed the occurrence of larvae at Helgoland Roads. The importance of SST in promoting larval population growth was further underlined by Genner *et al* (2010), who found that an increase of 1.5°C in December SST in Plymouth waters delayed peak abundance of larvae of spring spawning fish by up to 20 days, and a 3.5°C change in March SST brought forward peak of summer spawning larvae, also by up to 20 days. Greve *et al* (2005) presented earlier middle season times for ten German Bight species ranging from 1 to 10 weeks with increasing winter SST. Gallego *et al* (1999) found faster growth in *M. aeglefinus* larvae later in spring than earlier, attributable to warmer SST and compounded by higher plankton abundance. Sole spawn earlier when SST is warmer (Teal *et al*, 2008). These examples from both south and north North Sea as well as the English Channel indicate SST to be an important factor in determining the timing of peak abundance, which ultimately determines when the majority of surviving larvae recruit to the juvenile population. Warming seas has resulted in sacrifice of range in the North Sea of cod and plaice as adults migrate to deeper water (Dulvy *et al*, 2008), which will alter spawning patterns and may also affect larval recruitment. The collapses of herring and mackerel spawning sites and nurseries was caused by failure of the newest cohort to meet an older one and shoal to learn migration routes. The collapse of the sprat population in the western central North Sea was caused by failure of winter spawning populations to reach spawning grounds (Petitgas and Alheit, 2010). These phenological (and consequently geographical) shifts can have major ecological impacts in the North Sea.

Larval survival depends upon suitable food. Food selectivity is exhibited by most fish larvae to a degree. Lebour (1918) presented a qualitative summary of the gut contents of 41 fish species and *Amphioxus lanceolatus* (possibly feeding on *Coscinodiscus* spp.) sampled in the sea near Plymouth. She recognised that generally the most abundant copepods were most commonly found in the stomachs of simultaneously sampled fish larvae, but noted targeting of copepod species that did not rank highest among species present as well as prey switching to dominant copepods when target species abundance fell below an unknown critical level, or with ontogeny. Plaice *Pleuronectes platessa* (Dickey-Collas and Geffen, 1992) and lesser sandeels *Ammodytes marinus* (Cushing, 1983) feed upon appendicularians in preference to copepods. This is now recognised to be a combination of obtaining optimal fatty acids for growth, niche development to avoid competition between species, and ontogenetic prey switching to optimise growth (Demain *et al*, 2011). In the DTS, as there has been a gradual increase in zooplankton as SST has risen, it would be reasonable to assume that this has resulted in an increase in abundance of fish larvae surviving to be sampled. Beaugrand and Kirby (2010) and Olsen *et al* (2010) demonstrated a strong plankton effect on North Sea cod, that is not observed in Icelandic cod, through the abundance of the preferred prey species *Calanus finmarchicus* and *Pseudocalanus elongatus*. In this case, the timing of spawning by the adult population was crucial to the survival of their offspring, with poor survival in larvae that hatch when these copepods are not in high abundance, leading to poor recruitment to the adult stock (Durant *et al*, 2005). There are consequences of the diet of copepods too, suggesting signals may transfer between trophic levels quite rapidly. For example, St John and Lund (1996) found juvenile cod feeding during a diatom based food web to be of better condition than later juveniles feeding in a flagellate based food web, which suggests keen sensitivity to the nutritional quality of individual prey. Herring (*Clupea harengus*) lay demersal eggs and thus larvae hatch close to the location of spawning, which are located where there has historically been high zooplankton abundance (Dickey-Collas *et al*, 2010). It was therefore expected that zooplankton abundance would be an extremely important factor in larval abundance in the DTS, as it would be likely that larvae present in the samples were there as a result of proximate adult spawning.

While abundant food for larvae is obviously important, there are reasons why being present when zooplankton abundance is at its highest may not be the optimal strategy for larval survival (Sameoto, 1984), such as those mentioned earlier, and co-occurring predators increasing mortality rates above growth (Buckley *et al*, 2010). Different species of fish that have pelagic larvae can influence each others population dynamics. For example adult cod eat adult herring, adult herring eat larval cod, larval herring and larval cod eat zooplankton. The relative ontogenetic dynamics of the two species can influence adult population dynamics and ultimately exploitable biomass for fisheries (Speirs *et al*, 2010). Changes in the balance of the adult populations of these two species in the North Sea have resulted in depressed recruitment of cod (Fauchald, 2010). These authors therefore demonstrate the fine balance created by the level of pressure on these commercially important species. Recruitment to the adult population is negatively affected by inappropriate plankton food, a hydro-meteorologically mediated process, but when high zooplankton biomass is present, so are predators, leaving a tight window for certain species on the margin of the productive season to grow and enter the adult population before mortality exceeds growth and the smaller larval population diminishes the pool of potential recruits.

Wind has a major effect on water column stability and thus primary production, but in fish larvae it can have a direct effect on grazing success. Larvae tend to inhabit the upper mixed layer which is a turbulent environment. Wind stress increasing turbulence accelerates encounter rates between fish larvae and other particles. Model results validated by field data revealed first feeding cod larvae encounters with *Calanus* spp. nauplii increased by a factor of 7 when wind speed increased from 2m s^{-1} to 10m s^{-1} (Sundby, 1997). Wind can have a negative effect too: northern anchovy, *Engraulis mordax* has less variable recruitment when conditions are calm (Peterman and Bradford, 1987). Pepin *et al* (1995) found wind stress to influence daily abundance estimates in a study off the Newfoundland coast by up to 75%, with equally positive and negative effects, depending on direction and strength. These vertical and horizontal mixing and transport effects in these short term studies may translate into a wind mediated trend in species composition, according to the varying capability of species to adapt to changing wind conditions.

As described in Chapter 1, positive North Atlantic Oscillation index signifies stronger westerly winds and thus influences mixing layer depth and so primary productivity. By the same stroke in negative phase, the combination of environmental variables represented by the NAO can influence lower order production and thus negatively affect fish larval recruitment (Cushing, 1995a). This type of atmospheric index interaction with fish larvae has been observed elsewhere, though without consistent effect; Hsieh (2005) demonstrated fish larvae in the CALCOFI time series did not have a common relationship with Pacific climate indices, with more oceanic species correlating with variation in the Pacific Decadal Oscillation (PDO) than did coastal species. Auth *et al* (2011) showed these CALCOFI responses in addition to varying between species, were variably non-linear. In their atlas of fish larvae for the North Atlantic (Edwards *et al*, 2011) determined southward movement in abundance of clupeids, sandeels, whiting and northward movement in abundance of cod, between periods 1948-1985 and 1985-2006, the two periods of the 'regime shift' promoted by SAHFOS (e.g. Burkill and Reid, 2010). Durif *et al* (2010) detected negative correlations with SST and NAO for *Anguilla anguilla* larval recruitment at 11-12 year lags. Arnott and Ruxton (2002) found positive phase NAO to have a negative effect on *Ammodytes marinus* recruitment, due to warmer temperatures during the larval development period. The Atlantic Multidecadal Oscillation (AMO) is a major descriptor of SST variation across the northeast Atlantic and correlated strongly with sardine egg abundance in the English Channel (Edwards *et al*, 2013). The potential for either index to describe quasi-cyclical variation in fish larvae abundance in the DTS was therefore of interest, as this would indicate a cyclical ocean-atmosphere basis for the dynamics of this economically important trophic group in the plankton.

The DTS ichthyoplankton represent a significant but almost unstudied fraction of the DTS. Previous work has referred to fish larvae found in the samples simply as 'fish'. Exploring this section of the plankton in greater detail means the range of issues affecting fish larvae outlined above over many years of research can better be compared to the trends revealed in this study. The changing fortunes of groups vulnerable to the range of environmental and biological predictors identified were unknown. Studying this group was all the more important due to the high commercial importance of adult fish, and their importance to the ecology of the central North Sea. A dataset of ichthyoplankton sets the stage for exploration of interactions between trophic levels during a period of climate driven community change, and is a key strength of the Dove Time Series. Aebischer *et al* (1990) found coincident responses to changing weather in North Sea phytoplankton, zooplankton, *Clupea harengus* and the kittiwake, *Rissa tridactyla*. As those authors noted, the reason for the parallel trends was not obvious, as one would expect a degree of lag between trophic levels commensurate with their population growth rates. Frederiksen *et al* (2006) found a rapid response from diatom to seabird and intervening levels mediated by sandeel abundance and recruitment. It has already been demonstrated in the DTS that the phytoplankton and zooplankton respond to change in AMO with changed community composition, greater spring abundance of phytoplankton and more intense summer peaks in zooplankton. It was of interest to understand how a meroplanktonic element of the DTS would respond to changing conditions, and if there was a Russell cycle element to variability in the larvae present in the DTS.

4.1.1 *Study aims*

Ichthyoplankton have not previously been analysed to species level in the DTS and represent a new time series. The main aim of this study was to determine the extent to which larval fish in the DTS to be responded to changes in their environment, looking both at the various hydro-meteorological factors studied in chapters 2 and 3, as well as the abundance of lower trophic level plankton. To investigate this in the DTS, four null hypotheses were considered:

1. Changing hydro-meteorological and food conditions have had no effect on ichthyoplankton assemblage composition.
2. Changing hydro-meteorological and food conditions have had no effect on ichthyoplankton abundance.
3. Changing hydro-meteorological and food conditions have had no effect on timing of ichthyoplankton peak abundance.
4. There will be no difference in goodness of fit of multivariate models of ichthyoplankton assemblage composition using either inshore or offshore predictor variables.

4.2 Methods

4.2.1 *Field sampling*

Ichthyoplankton were sampled in the Dove Time Series using its WP3 net. This is a 1.13 metre width net with a 1mm mesh and 200µmm filtering cod end. The net was towed by *R.V. Bernicia* at approximately 25m depth at 2 knots for approximately 10 minutes. A TSK (Tsurumi Seiki Co. Ltd., Yokama, Japan) flow meter was used to determine the volume trawled relative to an ideal volume of a cylinder 617.73m long (distance travelled in 10 minutes at 2 knots). Species were preserved in approximately 10% formosaline solution, transferred after fixation to 70% EtOH.

4.2.2 *Laboratory analysis*

Fish larvae were identified using Halbeisen (1988), Munk and Nielsen (2005) and fishbase (Froese and Pauly, 2011, www.fishbase.org). The WP3 net had been sampled since 1969, but through sample degradation, desiccation and other losses, a reliable time series was only available from samples from 1978 to 2008. Missing samples between 1978 and 2008 were interpolated using the same approach as described in Chapter 2. While data do exist sporadically in the period 1969-1977 they were because of their fragmented nature not usable in this time series analysis.

4.2.3 *Searching for linear breakpoints, and multivariate statistics to aggregate species according to affinities for predictive variables*

Determining the sensitivities of species necessitated a very similar signal extraction process as was undertaken in Chapters 2 and 3. The following analyses were conducted to identify periods in the DTS that were numerically and qualitatively distinct from neighbouring periods, in an attempt to identify candidate community shift events, and to describe variation in species with common responses to changes in their drivers.

An autoregressive integrated moving average (ARIMA) model was diagnosed with autocorrelation (ACF) and partial autocorrelation (PACF) functions to describe cyclical patterns in the data and interannual trends respectively. These were used to construct an initial ARIMA model of interannual variation in mean phytoplankton abundance class across all taxa. To explore the ARIMA model of mean ichthyoplankton abundance (now largely excised of seasonal variation) for distinct shifts, linear breakpoint analysis was applied (Bai and Perron, 2003; Zeileis *et al*, 2002; Zeileis *et al*, 2003). The process is summarised in Chapter 2.

The relationship between abundance and environmental predictors was examined using constrained correspondence analysis (CCA; Oksanen *et al*, 2010, Legendre and Legendre, 1998). Predictors used in this chapter were the same as those used in Chapter 2, although of course ichthyoplankton abundance as a predictor was substituted with zooplankton abundance. The 'ordistep' function in R package vegan (Oksanen *et al*, 2010) was used to determine best model fit in a stepwise fashion, selecting best fit through AIC minimisation. The responses of ichthyoplankton taxa to CCA eigenvectors were used to determine sensitivity to climate variables correlated with these eigenvectors. High scores represented a tendency to be more common/sparse along a gradient associated with a CCA eigenvector. Thus the collective abundance of taxa with common environmental or biological affinities could be constructed and the time series structure and behaviour described, and forecast a modest period into the future.

4.3 Results

4.3.1 *Time series structure and weak evidence for a breakpoint*

54 types of ichthyoplankton were determined to be present in the DTS time series. 4 genus level identifications were made, 2 indeterminate categories for the larvae of flatfish and larvae, and 50 species level identifications (Table 4.1). Ichthyoplankton abundance had remained relatively static over the course of the time series. Sufficiently dense records existed for DTS ichthyoplankton only from 1978, though intermittent data were present from 1972. These were too sparse for acceptable interpolation and have not been presented in this chapter. Breakpoint analysis on an ARIMA fitted to the time series of total abundance (Figure 4.1) indicated a step in abundance could be detected at July 2002 (Table 4.2). Applying confidence intervals to this model indicated there was essentially a decade in which this break could truly have occurred, which along with non-convergent BIC and RSS (Figure 4.2) would suggest the support for a breakpoint was quite weak.

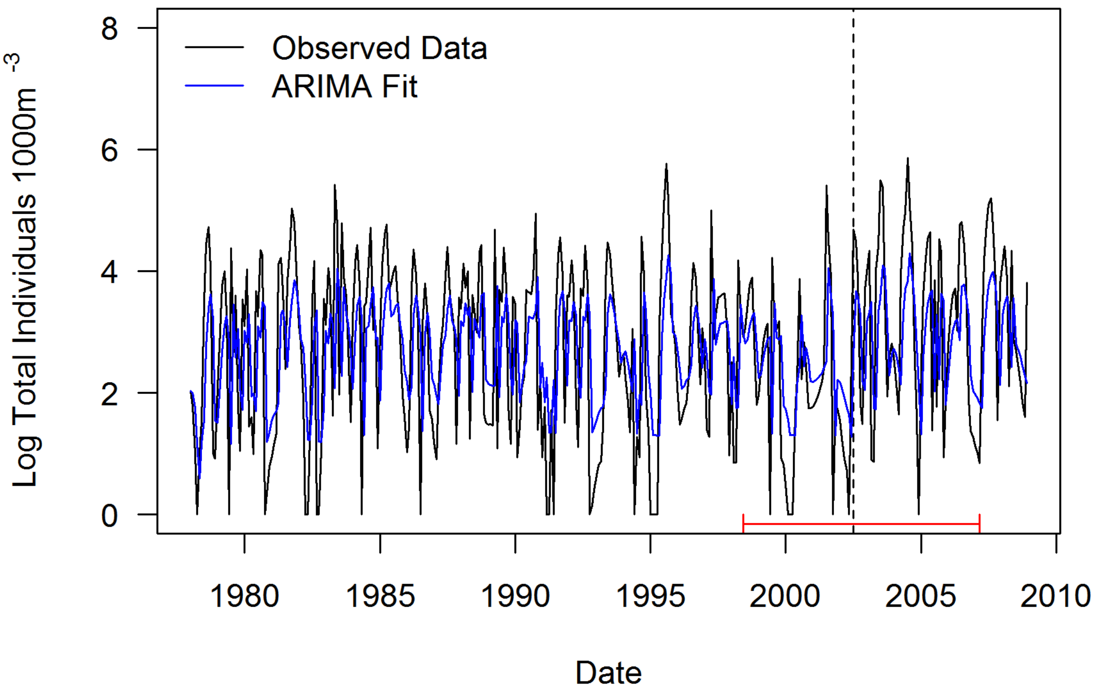


Figure 4.1: Ichthyoplankton time series, with overlaid ARIMA model fit. The breakpoint identified in 2002 coincided with a slightly greater abundance of ichthyoplankton. The 95% confidence intervals are so wide as to suggest this is not a genuine step in abundance.

Scientific Name	Common Name	Scientific Name	Common Name
Agonus cataphractus	Hooknose	*Merlangius merlangus*	Whiting
Ammodytes marinus	Lesser sandeel	*Melanogrammus aeglefinus*	Haddock
Aphia minuta	Transparent goby	*Microstomus kitt*	Lemon sole
Buglossidium luteum	Solenette	*Micrenophrys lilljeborgii*	Norway bullhead
Clupea harengus	Atlantic Herring	*Myoxocephalus scorpius*	Shortspined bullhead
Crystallogobius linearis	Crystal goby	*Pholis gunnellus*	Butterfish
Callionymis lyra	Common dragonet	*Psetta maxima*	Turbot
Ciliata spp.	Rockling	*Pomatoschistus microps*	Common goby
Ctenolabrus rupestris	Goldsinny wrasse	*Pomatoschistus minutus*	Sand goby
Diplecogaster bimaculata	Two-spotted clingfish	*Phrynorhombus norvegicus*	Norwegian topknot
Echiichthys vipera	Lesser weaver	*Pomatoschistus pictus*	Painted goby
Entelurus aequoreus	Snake pipefish	*Pleuronectes platessa*	Plaice
Glyptocephalus cynoglossus	Witch flounder	*Pollachius pollachius*	Pollock
Gobiusculus flavescens	Two-spotted goby	*Pollachius virens*	Saithe
Gadus morhua	Atlantic Cod	*Raniceps raninus*	Tadpole fish
Gymnammodytes semisquamatus	Smooth sandeel	*Sebastes spp.*	Redfish
Hyperoplus immaculatus	Greater sandeel	*Symphodus melops*	Corkwing wrasse
Hyperoplus lanceolatus	Great sandeel	*Sardina pilchardus*	Sardine
Hippoglossoides platessoides	Long rough dab	*Scomber scombrus*	Mackerel
Lumpenus lampretaeformis	Snake blenny	*Sprattus sprattus*	Sprat
Limanda limanda	Dab	*Taurulus bubalis*	Longspined bullhead
Liparis liparis	Common seasnail	*Trisopterus esmarkii*	Norway pout
Liparis montagui	Montagu's seasnail	*Trisopterus minutus*	Poor cod
Lipophrys pholis	Shanny	*Trachurus trachurus*	Horse mackerel

Table 4.1: Species found in the DTS ichthyoplankton time series. Additionally genus level identifications were made for *Ammodytes, Hyperoplus*, as well as categories for indeterminate flatfish and roundfish larvae.

Lower 95% CI	Break Date	Upper 95% CI
June 1998	July 2002	March 2007

Table 4.2: Break date identified by breakpoint analysis of ichthyoplankton on the ARIM A fit, and upper and lower 95% confidence intervals.

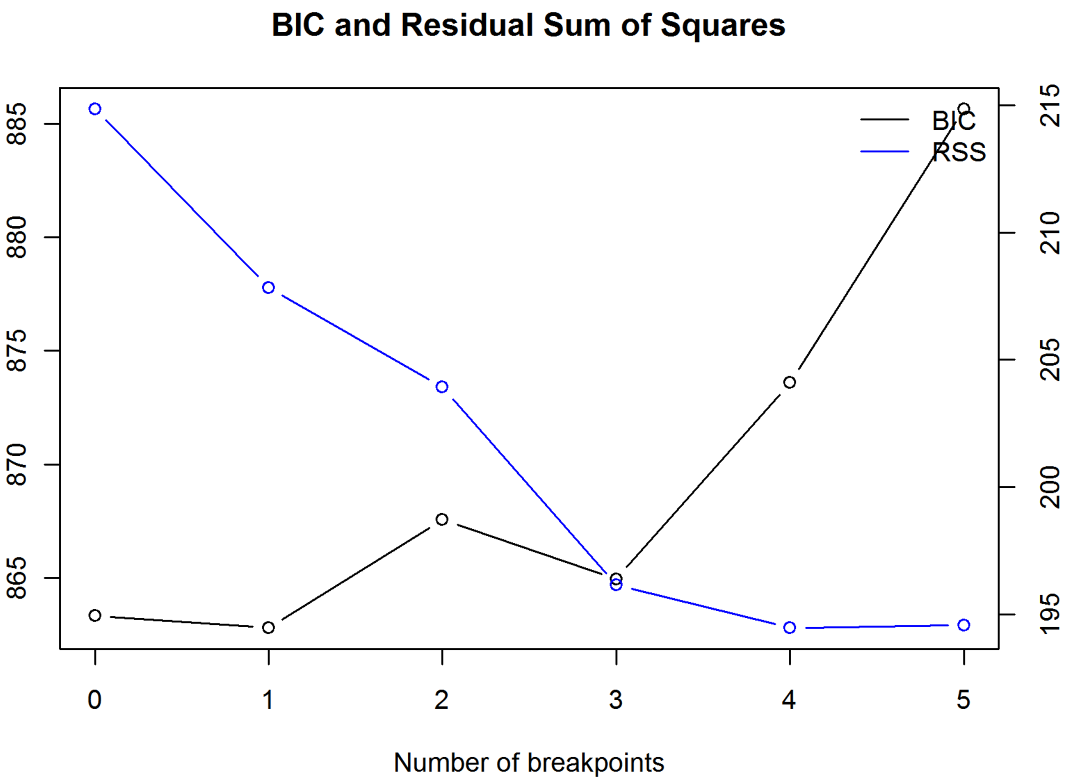


Figure 4.2: Breakpoint analysis diagnostic statistics. Residual Sum of Squares (RSS – right y-axis) is minimised at 4 breakpoints, while Bayesian Information Criterion (BIC – left y-axis) is minimised at 1 breakpoint and overrides RSS. This is indicative of weak evidence for either option, compared to a breakpoint diagnostic where both statistics are convergent.

4.3.2 *Abundance and community composition*

CCA analysis indicated CCA1 (32.12% of constrained inertia) was correlated strongly with SST, and had moderate correlations with the weather variables Cloud Cover and Wind Speed. CCA2 (29.36% of constrained inertia) was strongly correlated with Cloud Cover, V-component of Wind Speed and more moderately correlated with Salinity (Table 4.3). 'Ordistep' model term selection ruled out the importance of either NAO or AMO in larval fish community composition. Zooplankton and phytoplankton abundance also were not included in the best fit model (Figure 4.3)

Variable	CCA1 correlation	CCA2 correlation
SST (inshore)	0.96	-0.05
Salinity (inshore)	0.09	-0.28
Cloud Cover (offshore)	-0.45	-0.64
Wind Speed (offshore)	-0.44	-0.10
V-Wind (offshore)	-0.25	-0.56

Table 4.3: Correlation coefficients of input predictors with CCA eigenvectors.

Weather conditions associated with water column stability and visibility were therefore important. Both primary and secondary CCA axes were nearly equivalent in the proportion of constrained inertia explained by the model, unlike the cases of phytoplankton and zooplankton, which tended to have community composition markedly more strongly ordered by CCA1 than CCA2. This suggested a very much stronger role for Cloud Cover (moderately and negatively correlated against both axes) in fish larva assemblage composition than was the case for lower trophic levels studied. Combinations of conditions are summarised in Table 4.4.

Sign combination	SST	Salinity	Cloud Cover	Wind Speed	V-wind
CCA1+ CCA2+	Warm	Fresher	Clearer	Low	Northerly
CCA1+ CCA2-	Warm	More saline	Cloudier	Low	Southerly
CCA1- CCA2+	Cool	Fresher	Clearer	High	Southerly
CCA1- CCA2-	Cool	More saline	Cloudier	High	Northerly

Table 4.4: Interpretation of conditions under each quadrant of CCA1 and 2 biplot in Figure 4.3.

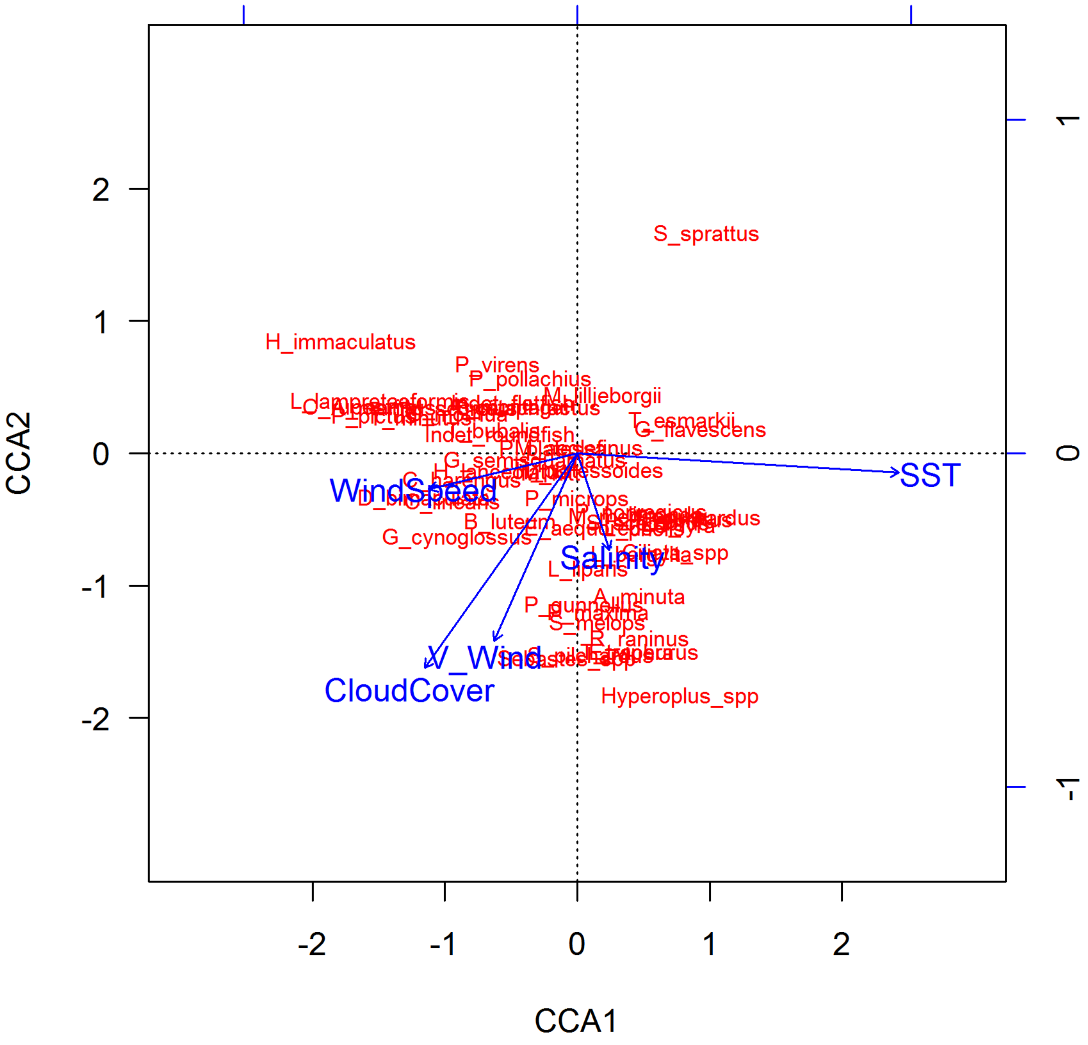


Figure 4.3: CCA analysis of ichthyoplankton community composition. SST correlated most strongly with CCA1, while Cloud Cover correlated most strongly with CCA2.

The species, divided into groups according to their weighted average species scores against each axis are detailed in Table 4.5. Sprats (*Sprattus sprattus*) were numerically dominant in the first (++) group, representing 11.85 (±21.87 S.D.)% of total abundance on average. Dab, *Limanda limanda* and dragonets, *Callionymis lyra*, were both similarly abundant and together dominated the abundance of the second group (+-), which constituted a mean of 34.23 (±32.19 S.D.)% of total abundance. The lesser sandeel, *Ammodytes marinus* was the most abundant member of the third group (-+) which constituted a mean of 25.92 (±32.83 S.D.)% of total abundance. Lemon sole, *Microstomus kitt*, was the most abundant member of the fourth group (--) which constituted a mean of 26.36 (±33.06 S.D.)% of total abundance. Thus the similar contribution to total explainable variance in assemblage composition of both CCA axes translated into quite evenly distributed group of species in terms of abundance contribution.

Group	Designation	Species
CCA1+ CCA2+	'Sprats' group – Summer spawners	*Gobiusculus flavescens, Melanogrammus aeglefinus, Micrenophyris lilljeborgii, Sprattus sprattus, Trisopterus esmarkii*
CCA1+ CCA2-	'Dab/Dragonet' group – Summer spawners	*Aphia minuta, Callionymis lyra, Ciliata* spp., *Entelurus aequoreus, Eutrigla gurnardus, Echiichthys vipera, Hippoglossoides platessoides, Hyperoplus* spp., *Labrus bergylta, Limanda limanda, Liparis liparis, Lipophrys pholis, Merlangius merlangus, Pholis gunnellus, Psetta maxima, Pomatoschistus minutus, Phrynorhombus norvegicus, Raniceps raninus, Symphodus melops, Sardina pilchardus, Scomber scombrus, Trachurus trachurus*
CCA1- CCA2+	'Lesser sandeel' group – Spring spawners	*Agonus cataphractus, Ammodytes marinus, Ctenolabrus rupestris, Gadus morhua, Hyperoplus immaculatus,* Indeterminate roundfish larvae, Indeterminate flatfish larvae, *Lumpenus lampretaeformis, Liparis montagui, Myoxocephalus scorpius, Pomatoschistus pictus, Pleuronectes platessa, Pollachius pollachius, Pollachius virens, Taurulus bubalis, Trisopterus minutus*
CCA1- CCA2-	'Lemon sole' group – Autumn spawners	*Buglossidium luteum, Clupea harengus, Crystallogobius linearis, Diplecogaster bimaculata, Glyptocephalus cynoglossus, Gymnammodytes semisquamatus, Hyperoplus lanceolatus, Microstomus kitt, Pomatoschistus microps, Sebastes* spp.

Table 4.5: Ichthyoplankton species assemblages as identified in CCA. Designation derived from the most abundant members of each group and time of peak abundance.

There was clear seasonal distribution of these groups as a result of the different spawning periods of the adult fish (Figure 4.4). The two groups with positive scores on CCA1 were present in greatest abundance in summer. The 'Sprat' group peaked between July and September and was otherwise in low abundance. The 'Dab/Dragonet' group began to increase in abundance in May but otherwise was similar in time of peak abundance as the 'Sprat' group. The 'Lesser sandeel' group was most abundant in April, with minor peaks in February and August. The 'Lemon sole' group was most abundant in September. Thus it was apparent that the CCA groupings were reflective of the sea and meteorological conditions under which adult spawning occurred, giving rise to seasonal peaks in larvae.

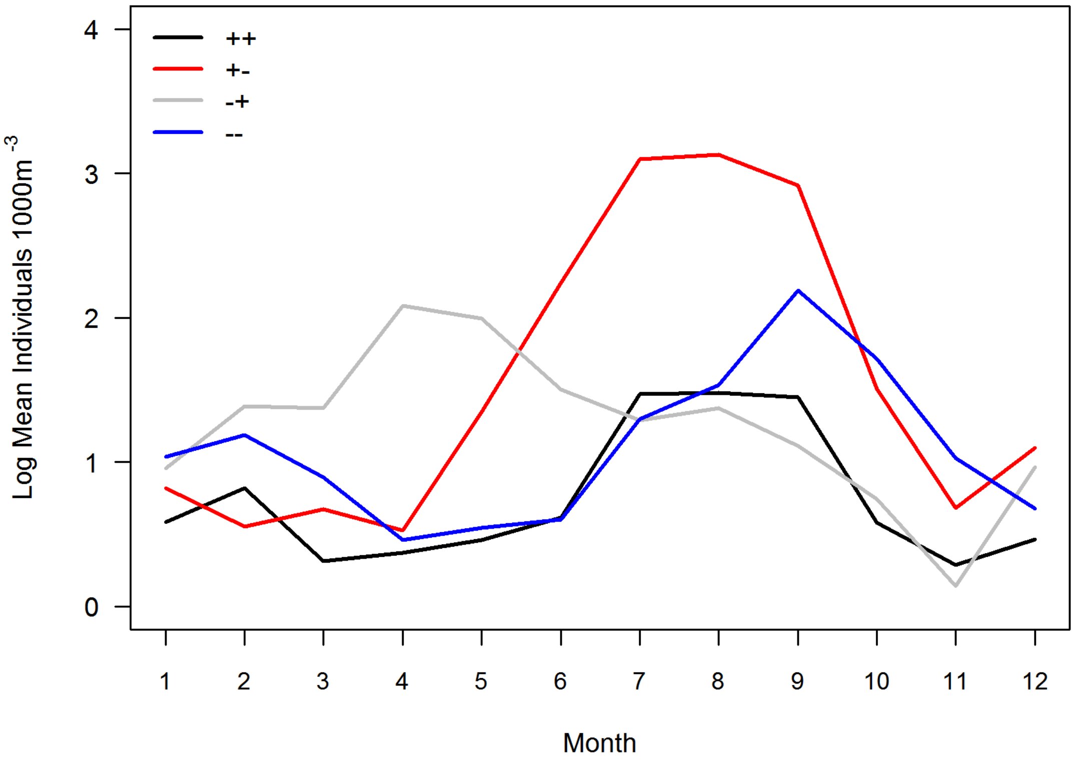


Figure 4.4: Average annual abundance of each CCA ichthyoplankton group. ++: 'Sprat' group, +-: 'Dab/Dragonet' group, -+: 'Lesser sandeel' group, --: 'Lemon sole' group.

The two linear constraint scores determined from the linear combination of effect of model variables in the CCA analysis per sample indicated two time series of linear constraints that had gradual long term trends with little short term fluctuations other than seasonal variation (Figure 4.5). CCA1 had a long term increase with gentle oscillation, while CCA2 was essentially in shallow linear decline. A GLM was applied using CCA1 and 2 as predictors, along with total zooplankton and phytoplankton abundance, and the AMO and Winter NAO indices. AIC minimisation indicated that best fit was achieved by a model with CCA1 and phytoplankton abundance class terms (Table 4.6). This indicated that the ichthyoplankton data in the DTS described the spawning activity of adults, more than it described the trophic interactions of larvae and their zooplankton food.

Variable	Intercept	Slope	Standard error	T value	p
CCA1	2.32	0.513	0.121	4.193	$<0.001^{***}$
Total Phytoplankton abundance class		0.021	0.008	2.493	0.014^{*}

Table 4.6: GLM output of total ichthyoplankton abundance versus samples CCA1 and phytoplankton

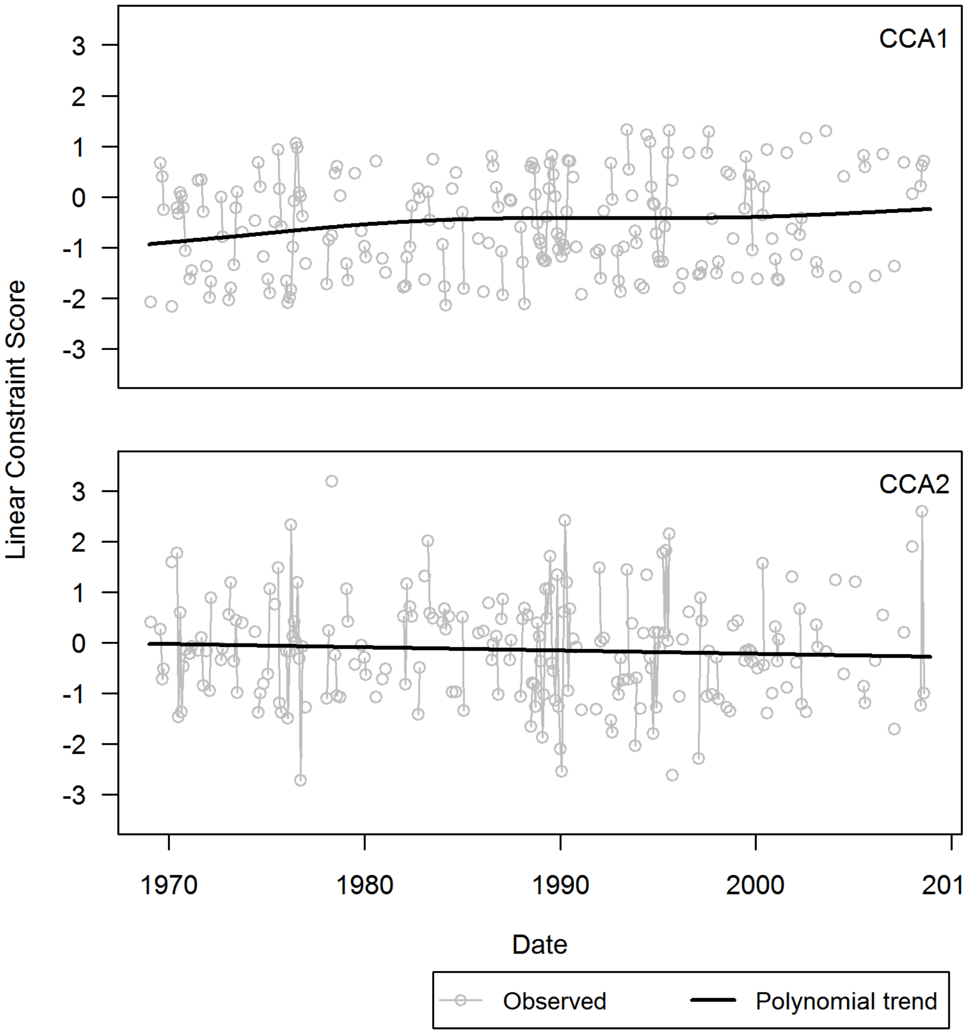


Figure 4.5: Time series of CCA linear constraint scores extracted from ichthyoplankton CCA model. Note as the time series of linear constraints is based upon the environmental input data matrix, it extends backwards in time beyond the start of the ichthyoplankton time series.

The model fit approximated the time series reasonably well, though generally failed to replicate the extent of spikes and troughs in abundance that occurred from time to time (Figure 4.6). This GLM output indicated there was some degree of variability in the ichthyoplankton which appeared to be in some way related to the periodic nature of the phytoplankton and CCA1 predictors. Periodograms were constructed for each CCA group to examine if there was periodicity and at what scale (Figure 4.8). This indicated in each group quite long term periods (Table 4.9), though these were present with considerable interannual noise, with the possible exception of the 'Lesser sandeel' group (Figure 4.9).

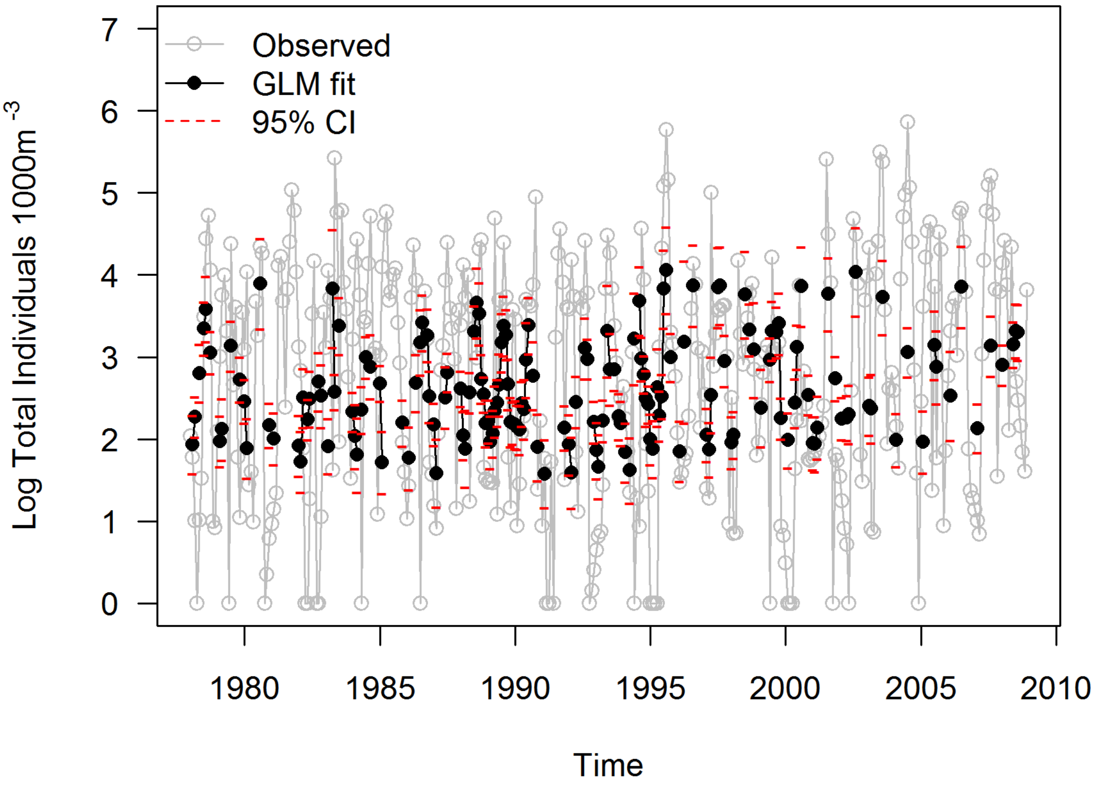


Figure 4.6: GLM model fit of ichthyoplankton abundance as a function of CCA1 and phytoplankton abundance. Natural log scale.

Diversity was variable, with 1992 being the most diverse year, and 1995 being the least diverse (Figure 4.7). Most years had a dominant 1st rank species constituting less than 50% of total annual abundance. Annual mean Shannon diversity index was not strongly predicted by either CCA1 or CCA2, nor were phytoplankton or zooplankton abundance important terms (Table 4.7).

Term	**Slope**	**Standard Error**	**T**	**P**
CCA1	0.277	0.237	1.17	0.252^{ns}
CCA2	0.108	0.196	0.55	0.583^{ns}
Phytoplankton	-0.011	0.126	-0.85	0.400^{ns}
Zooplankton	$-6.419\text{x}10^{-7}$	$4.007\text{x}10^{-6}$	-0.16	0.873^{ns}

Table 4.7: GLM coefficients of Shannon diversity index versus annual mean CCA LC scores and phytoplankton and zooplankton abundance.

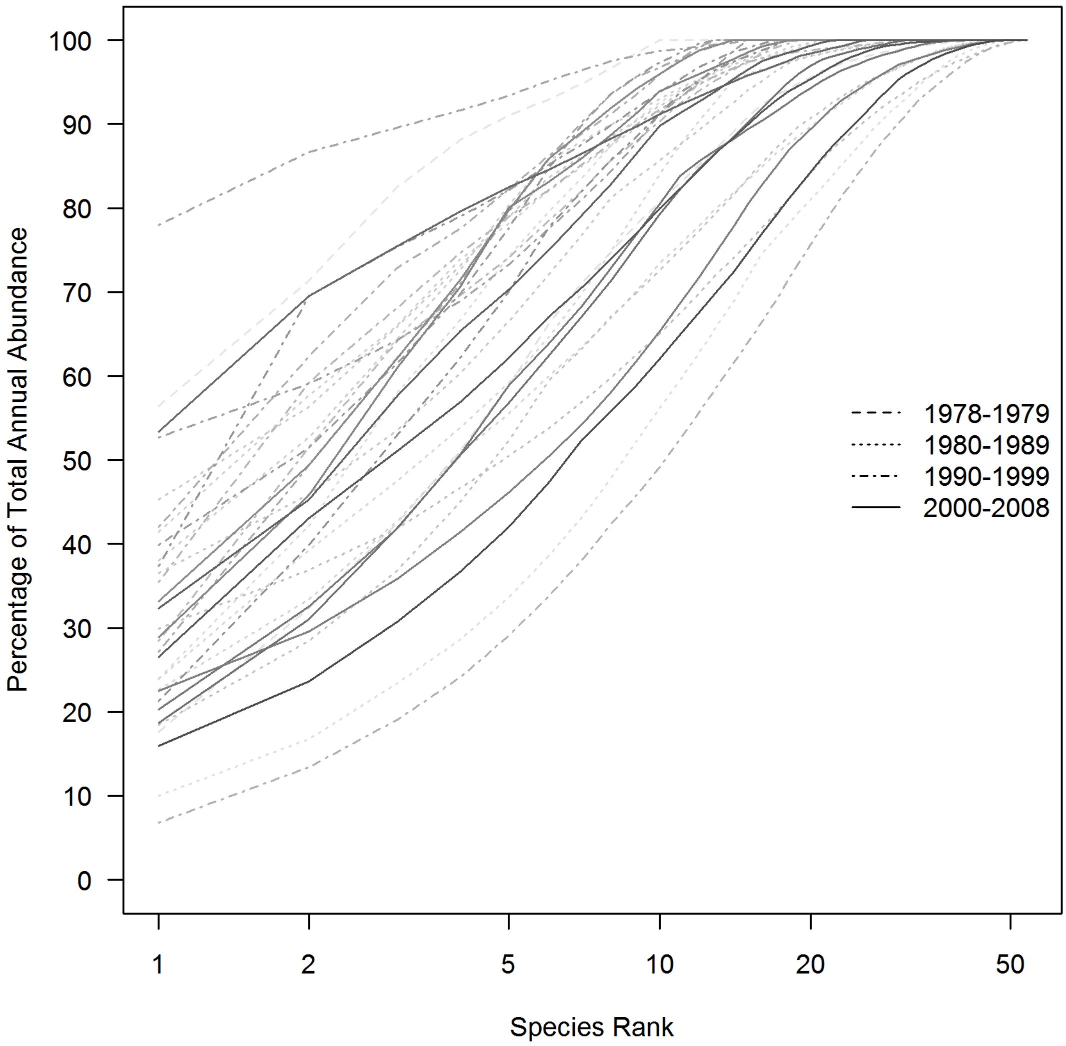


Figure 4.7: Cumulative dominance plot of ichthyoplankton species abundance as a percentage of total abundance. Note log scale of x-axis.

There were two periods of much lower species richness in the DTS ichthyoplankton record, 1984-86 and 1992-2001 (Table 4.8). These periods did not correspond with particularly high or low abundance of either phytoplankton or zooplankton and would suggest therefore that the reason for this change in diversity may have had more to do with the behaviour and distribution of adult fish than the amenability or otherwise of food and hydro-meteorological conditions to larval survival.

Species	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008
C. lyra	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
P. platessa	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•		•	•	•	•	•	•	•	•	•	•	•
M. kitt	•	•	•	•		•	•	•	•	•	•	•	•	•	•	•	•		•	•	•	•	•	•	•	•	•	•	•	•	•
S. sprattus	•	•	•	•	•	•	•		•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•		•	•
E. gurnardus	•	•	•	•	•	•	•		•	•	•	•	•	•	•		•	•	•	•		•	•	•	•	•	•	•	•	•	•
C. linearis	•		•	•		•	•	•	•	•	•	•	•	•	•	•	•		•	•	•	•		•	•	•	•	•	•	•	•
A. marinus		•		•		•	•	•	•	•	•	•	•		•	•	•	•	•	•	•	•	•	•	•	•	•		•	•	•
M. merlangus	•	•	•	•	•	•	•	•		•	•	•	•	•	•	•		•	•				•	•	•	•	•	•	•	•	•
P. norvegicus		•	•	•	•	•	•		•	•	•	•	•	•	•	•			•		•	•	•	•	•	•	•	•	•	•	•
Ciliata. spp	•		•	•		•	•			•	•	•	•		•	•	•	•		•	•	•	•	•	•	•	•	•	•	•	•
L. limanda		•	•	•		•	•	•	•	•	•	•	•	•	•	•				•	•		•	•	•	•	•	•	•	•	•
C. harengus		•	•	•		•	•	•	•	•	•	•	•	•	•		•	•	•	•	•				•	•	•	•		•	•
G. cynoglossus		•	•	•	•	•		•	•	•	•	•	•	•	•		•				•	•		•	•	•	•	•	•	•	•
P. minutus	•	•	•			•	•	•	•	•	•	•	•		•	•						•	•	•	•	•	•	•	•	•	•
S. pilchardus	•	•	•	•	•	•		•	•		•	•			•	•	•	•	•	•	•		•	•	•	•			•		•
L. bergylta		•	•		•	•	•	•		•	•	•		•	•		•	•			•			•	•	•	•		•	•	•
M. aeglefinus		•	•		•	•				•	•	•		•	•		•			•		•	•	•	•	•	•	•	•	•	•
S. scombrus		•	•		•	•			•	•	•	•		•	•			•	•			•		•	•	•	•	•	•	•	•
H. platessoides		•	•		•	•				•	•	•		•	•	•		•							•	•	•	•	•	•	•
L. pholis		•	•	•	•	•	•			•	•	•		•	•			•							•	•	•		•	•	•
M. scorpius		•	•	•	•	•				•	•	•	•	•	•			•	•						•	•	•			•	•
P. pollachius		•	•	•	•	•		•		•		•		•	•							•			•	•	•	•	•	•	•
S. melops		•	•		•	•			•	•	•	•	•	•	•						•	•	•	•		•	•				•
H. lanceolatus		•	•	•	•	•		•		•	•	•		•	•				•						•	•				•	•
M. lilljeborgii		•	•		•	•				•	•	•	•	•	•										•	•		•	•	•	•
R. raninus		•	•	•	•	•	•		•	•	•	•		•	•										•	•	•				•
B. luteum		•	•		•	•				•	•	•		•	•										•	•	•	•		•	•
E. aequoreus		•	•			•				•	•	•		•	•										•	•	•	•	•	•	•
Indet. roundfish			•	•	•	•		•		•	•	•			•										•	•		•	•	•	•
L. montagui		•	•		•	•				•	•	•		•	•					•	•				•	•				•	•
A. cataphractus		•	•			•			•		•	•			•						•				•	•	•	•		•	•
A. minuta		•	•			•	•			•	•	•		•	•									•	•	•				•	•
G. flavescens		•	•		•	•	•			•	•	•		•	•										•	•				•	•
G. morhua		•	•		•	•				•	•	•		•	•										•	•	•			•	•
L. lampretaeformis		•	•		•	•		•		•	•	•		•	•										•	•				•	•
L. liparis		•	•		•	•				•	•	•		•	•			•							•	•				•	•
P. maxima		•	•		•	•				•	•	•		•	•							•			•	•				•	•
P. microps		•	•		•	•				•	•	•		•	•							•			•	•				•	•
P. virens		•	•		•	•	•			•	•	•		•	•					•					•		•				•
P. gunnellus			•			•		•			•	•			•		•		•						•	•		•	•		•
P. pictus		•	•		•	•				•	•	•		•	•										•	•				•	•
T. minutus		•	•		•	•				•	•	•		•	•										•		•			•	•
D. bimaculata		•	•		•	•				•	•	•	•	•	•							•			•						
Hyperoplus spp		•	•	•		•				•	•	•		•	•										•					•	•
T. bubalis			•	•		•			•		•	•	•		•						•					•		•			•
E. vipera		•	•		•	•				•	•	•		•	•										•						•
H. immaculatus		•	•			•	•				•	•			•										•	•		•			•
Ammodytes spp		•	•		•					•		•		•	•										•					•	•
G. semisquamatus		•	•			•					•	•			•										•	•	•				•
C. rupestris			•			•					•	•			•										•	•	•				•
Indet. flatfish			•		•	•					•	•			•										•	•					•
T. esmarkii		•	•		•					•		•		•	•										•					•	
Sebastes spp		•	•					•				•			•										•			•			
T. trachurus			•			•	•				•	•			•																

Table 4.8: Ichthyoplankton species presence over time, ordered from most frequently observed (top) to most rarely observed (bottom).

These periods were used to model interannual noise in dynamic linear models of each time series. Periodograms indicated dominant periodicity at a ~15 year interval (Figure 4.8; Table 4.9), though annual plots suggest this was most strongly discernible in the case of the 'Lesser sandeel' group, and to a lesser extent the 'Dab/Dragonet' group (Figure 4.9). This lead to model fits in the case of the 'Dab/Dragonet' and 'Lesser sandeel' groups that described quasi-periodic variability in abundance, though in the case of 'Sprat' and 'Lemon sole' groups, there was clearly shorter term interannual variability, described by the random walk component of the model which was a better descriptor of interannual variability than a long term oscillation (Figure 4.10). Validations on each time series with the final 5 years removed indicated the models approximately described the variability observed, though this was most convincing in the case of the 'Dab/Dragonet' group (Figure 4.11). Correlations indicated the validations approximated the observed data (Table 4.10) with moderately positive and significant correlations in each group.

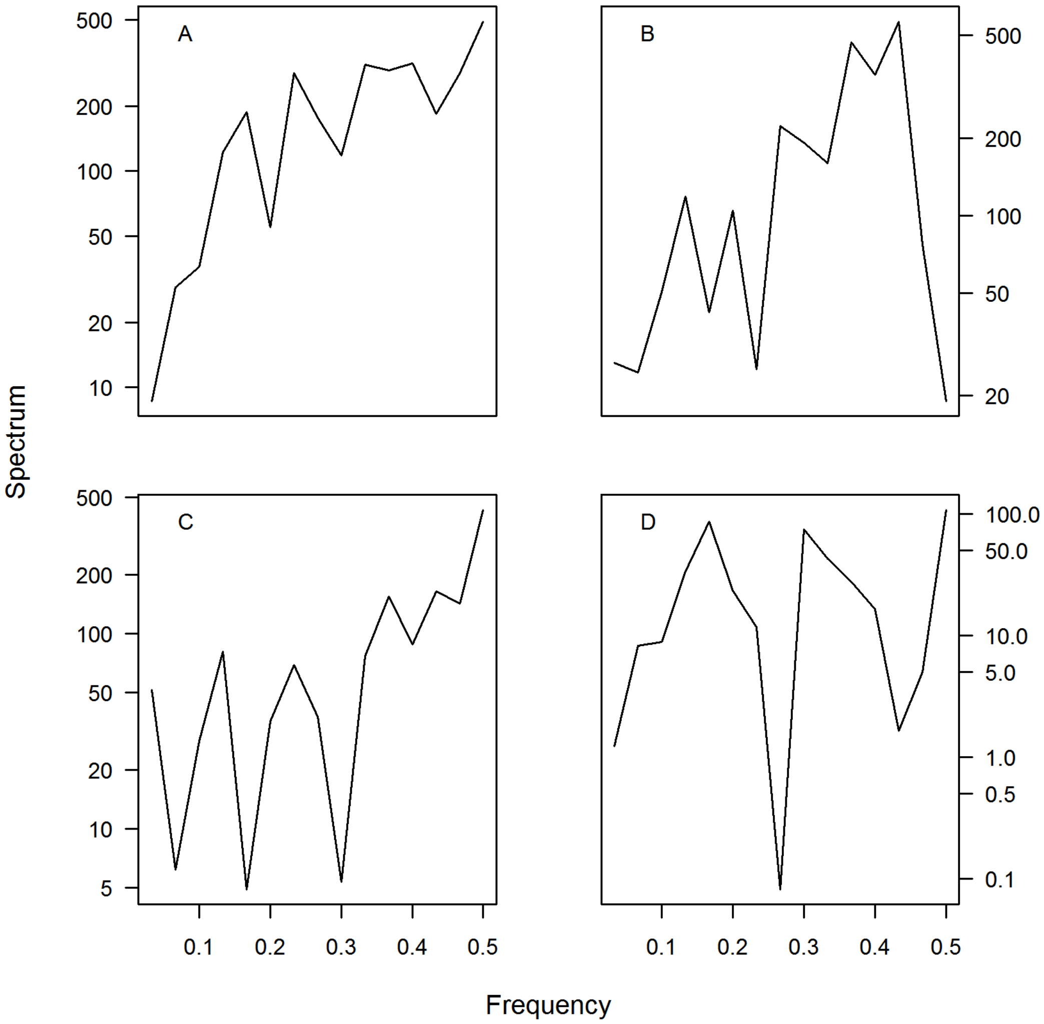


Figure 4.8: Periodograms of annual mean aggregate abundance of A: 'Sprat' group, B: 'Dab/Dragonet' group, C: 'Lesser sandeel' group, D: 'Lemon sole' group.

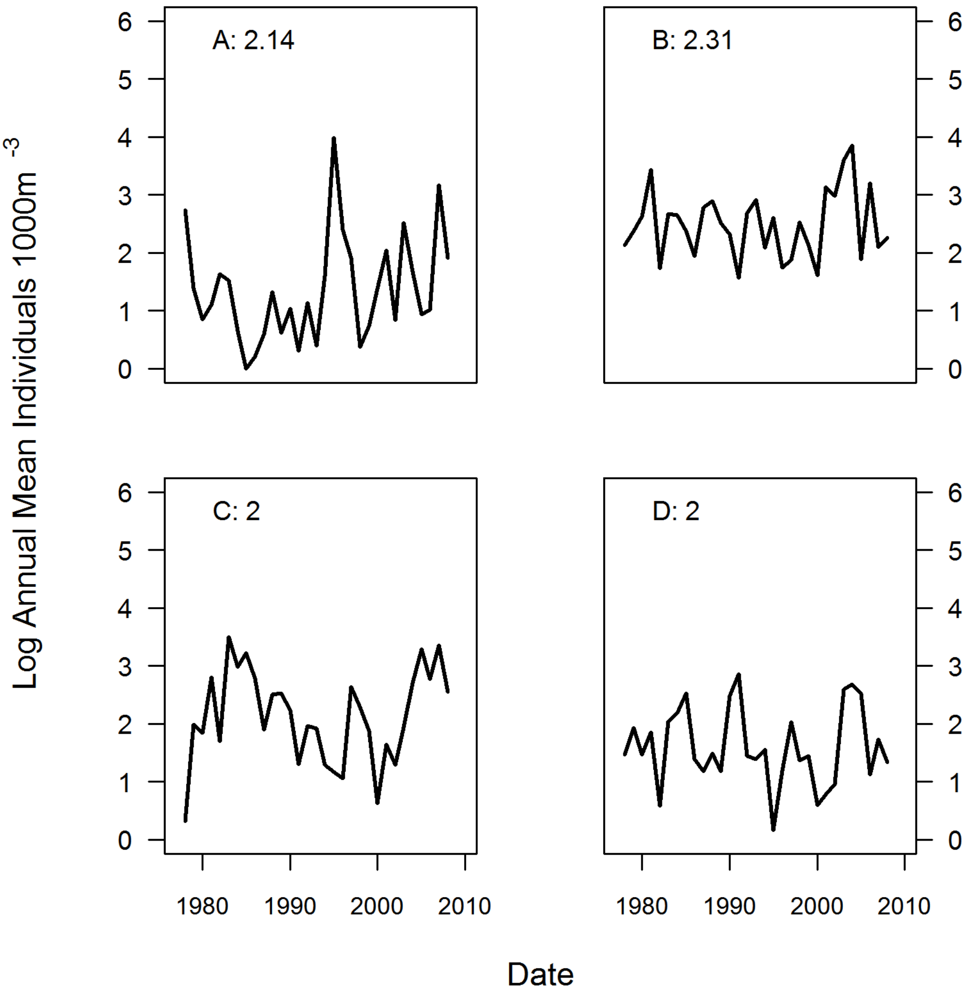


Figure 4.9: Annual mean abundance for A: 'Sprat' group, B: 'Dab/Dragonet' group, C: 'Lesser sandeel' group, D: 'Lemon sole' group. Values indicate the number of peaks of the dominant oscillation identified by periodograms.

Group	Peak Frequency	Number of periods	Wavelength (Years)
'Sprat'	0.466	2.14	14.48
'Dab/Dragonet'	0.433	2.31	13.41
'Lesser sandeel'	0.5	2	15.5
'Lemon sole'	0.5	2	15.5

Table 4.9: Spectral analysis of ichthyoplankton time series of species summed according to CCA axis scores. Wavelength determined as time series * peak frequency.

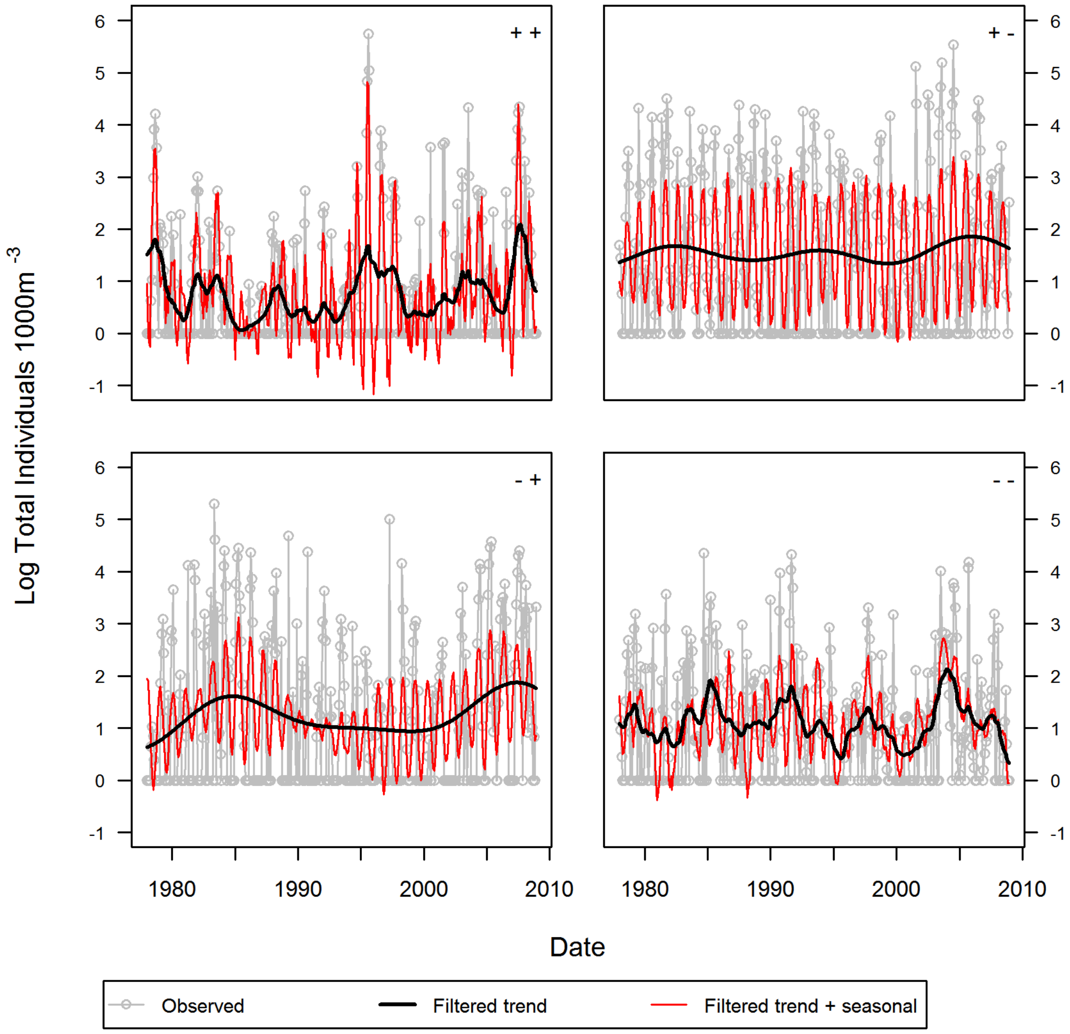


Figure 4.10: Dynamic linear models describing interannual (black) and seasonal (red) variability in: 'Sprat' (++) group, 'Dab/Dragonet' (+-) group, 'Lesser sandeel' (-+) group and 'Lemon sole' (--) group.

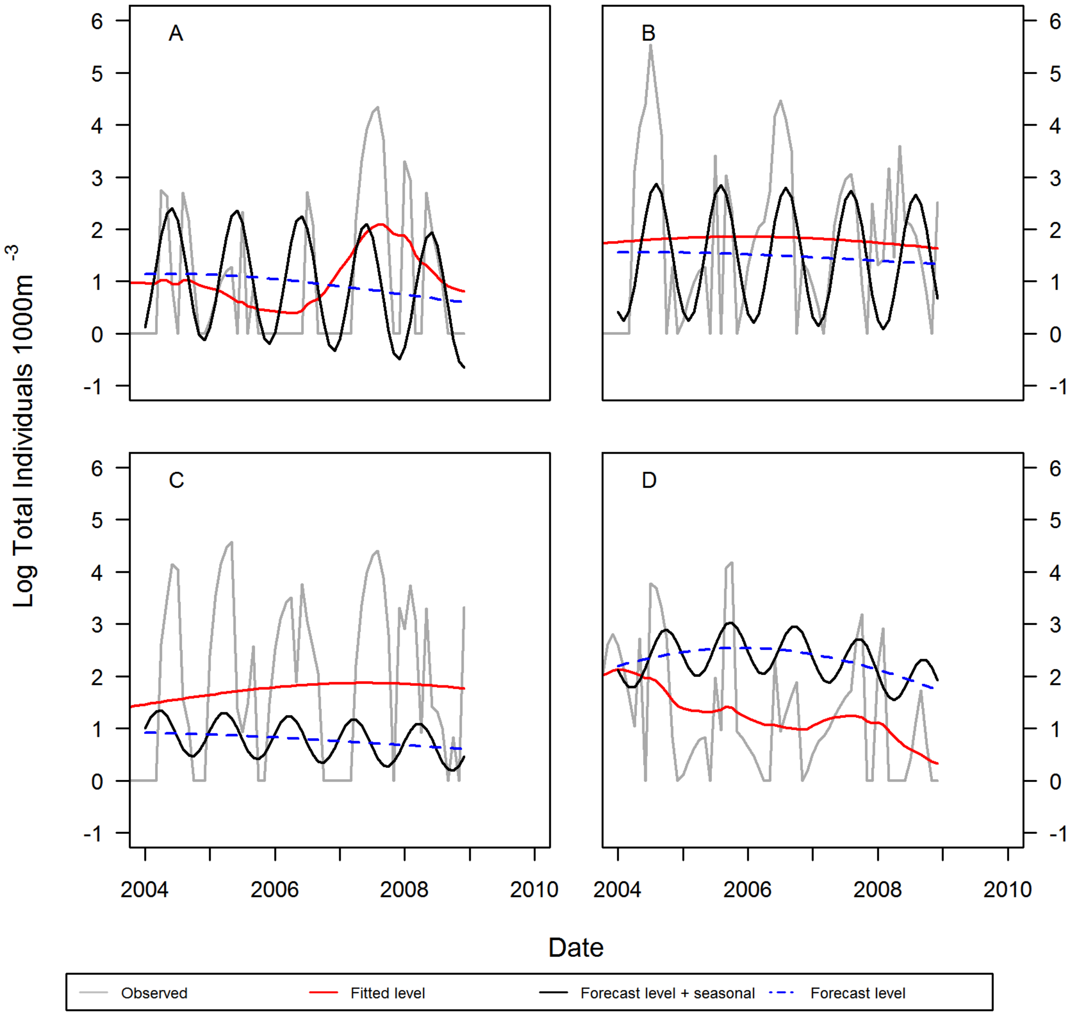


Figure 4.11: Validation forecasts against A: 'Sprat' (++) group, B: 'Dab/Dragonet' (+-) group, C: 'Lesser sandeel' (-+) group and D: 'Lemon sole' (--) group. Red line is post hoc model fit against full time series, blue dashed line is validation forecast against time series minus 5 years, and black line is forecast + seasonality.

Group	**Spearman ρ**	**p**
++	0.43	$<0.001^{***}$
+-	0.45	$<0.001^{***}$
-+	0.32	0.011^{**}
--	0.32	0.011^{**}

Table 4.10. Spearman correlation coefficients for ichthyoplankton validation forecasts and withheld part of the time series. All groups show moderate positive and significant correlations.

FFBS sensitivity analysis, 10 iterations of the model fit on 1 year fewer data per iteration indicated model fits to be conservative (Figure 4.12). This indicated some variability in the level of ichthyoplankton abundance, particularly in the case of the 'Sprat' and 'Lemon sole' groups (Figures 4.12A and D), and much less variability in the 'Dab/Dragonet' and 'Lesser sandeel' groups (Figures 4.12B and C).

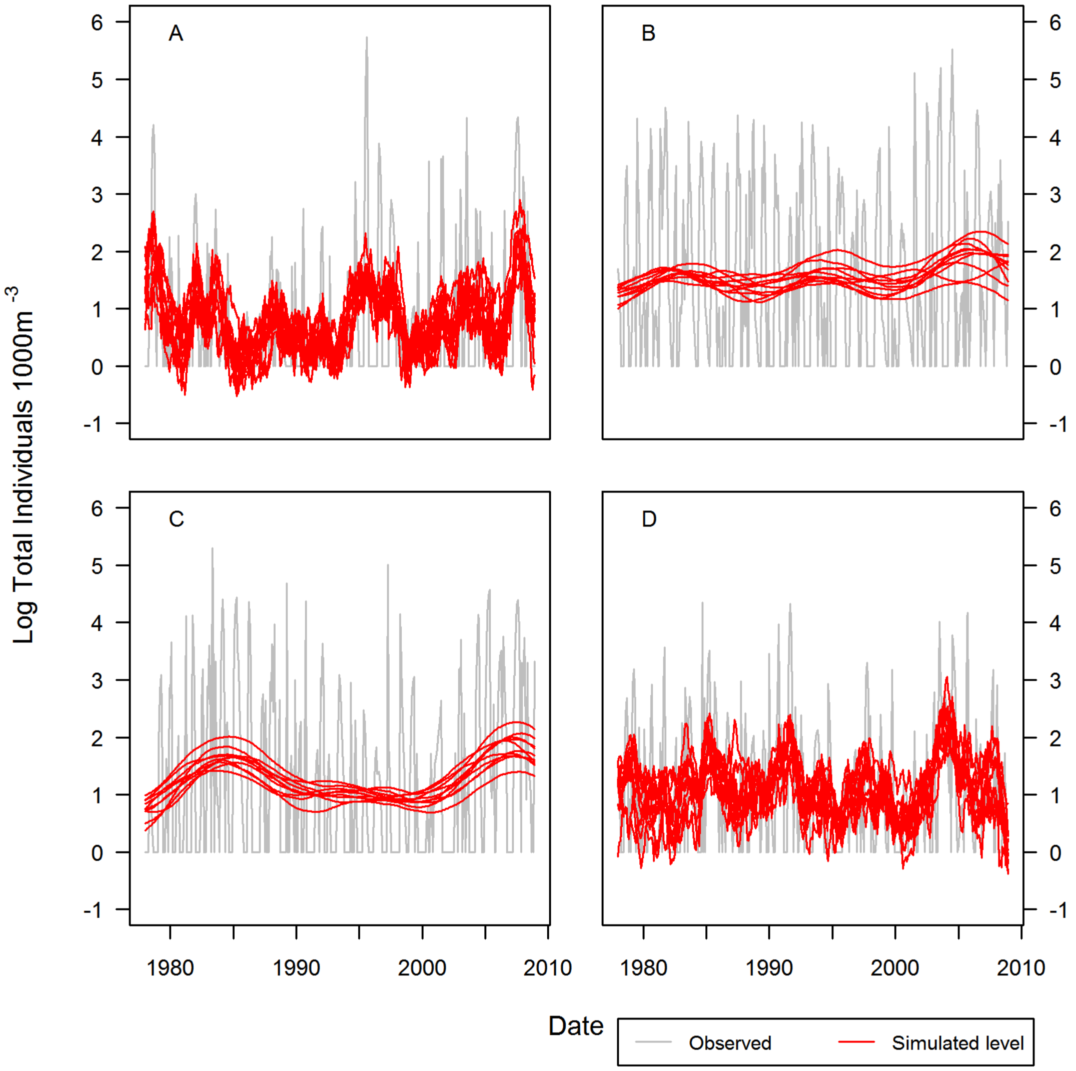


Figure 4.12: FFBS stress tests of ichthyoplankton model fits. Each line indicates a model run with year less data than the preceding run, up to 10 years of data removed. A: 'Sprat' group, B: 'Dab/Dragonet' group, C: 'Lesser sandeel' group, D: 'Lemon sole' group.

Group	78-08 Mean	09-13 Mean	% Difference	% of 78-08 Total	% of 08-13 Total	T	p
++	1.54	0.47	-69.48	14.88	7.23	-12.22	<0.001***
+-	3.75	3.12	-16.87	36.12	47.84	-10.55	<0.001***
-+	2.65	2.76	+4.16	25.53	42.37	1.02	0.309ns
--	2.43	0.17	-93.18	23.45	2.54	-33.69	<0.001***

Table 4.11: T-test results comparing forecast abundance (individuals 1000m^{-3}) of each ichthyoplankton group compared to the long term mean. Seasonal variation not included in these figures, due to underestimation of seasonality by the dynamic linear models.

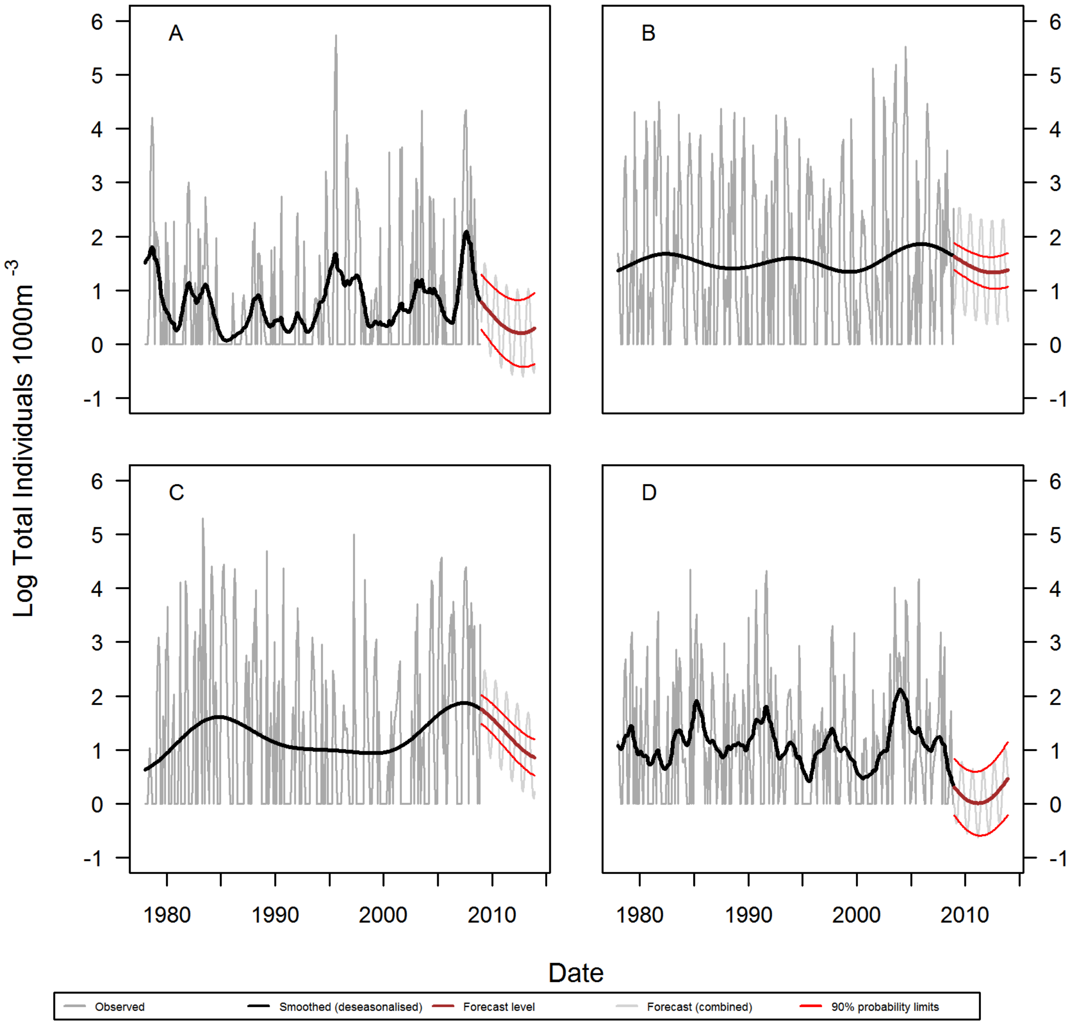


Figure 4.13: DLM forecasts of ichthyoplankton abundance. Black line: deseasonalised abundance. Dark grey: observed data. Light grey: forecast. Brown: deseasonalised forecast. Red: 95% confidence intervals. A: 'Sprat' group, B: 'Dab/Dragonet' group, C: 'Lesser sandeel' group, D: 'Lemon sole' group.

Forecasts therefore indicated a possible change from an assemblage dominated by 'Dab/Dragonet' and 'Lesser sandeel' groups at the expense of 'Sprat' and 'Lemon sole' groups (Table 4.11). This is likely an artefact of the model inasmuch as the irregular interannual variability modelled by a random walk model in the case of Figure 4.13A and 4.13D cannot replicate this time series characteristic in a forecast, reverting to the less important long term periodic term which FFBS plots indicated was not an important component of the time series model for these groups. In this regard only the forecasts in Figure 4.13B and C were likely to be supported by additional observations in future as a consequence of having interannual variation that was more approximate to the quasi-periodic model terms.

4.3.3 *Change in phenology of abundance peaks*

Abundance peaks were variable, as would be expected given these are exclusively meroplanktonic larvae that are present in the DTS as a result of the spawning of their parents (Figure 4.14). The 'Sprat' and 'Dab/Dragonet' groups peaked earlier over time, from September to December in the 1980s to May to July in the 2000s. The 'sandeel' group peaked in spring between April and May, appearing to move later to the mid 1990s and then stabilising around May after this point. There was no obvious trend in peak abundance of the 'Lemon sole' group.

Figure 4.14: Phenology of peaks of each ichthyoplankton group. A: 'Sprat' group, B: 'Dab/Dragonet' group, C: 'Lesser sandeel' group, D: 'Lemon sole' group.

Spatial plots indicated that certain groups had quite strongly seasonally ordered abundance peaks in keeping with the average annual plots. The 'Dab/Dragonet' group is a resilient assemblage that has maintained high abundance relative to other groups throughout the course of the time series. Abundance (Figure 4.16) was always greatest towards the end of summer. Other groups were more heterogeneously present in abundance. The sprat dominated group was much more variably abundant but again was mostly found in summer. 1995 appeared to be an important year for this group, which flourished after this point, compared to the preceding 17 years (Figure 4.15). Lesser sandeel and their associated species showed some change in timing from an early spring peak in the 1980s to a mid spring peak in the 2000s. There appeared to be switching between a double peak as observed in 1982 and 1990, and singly peaks as observed in 1986 and 1998 (Figure 4.17). Similarly the lemon sole dominated group peaked occasionally twice in a year, as in 1978 and 1985, but otherwise was a single peaking group in autumn (Figure 4.18).

'Sprat' group abundance peaked at the same time as phytoplankton abundance had undergone a step change upwards. This is not to suggests sprat and associated larvae feed upon phytoplankton, rather that the warming and wind regime effects upon phytoplankton abundance also offered some benefit to this group reflected in its abundance. Whether this was a result of enhanced survival of the group, or enhanced spawning of adults near to the DTS cannot be determined, though fish larvae die rapidly in suboptimal conditions.

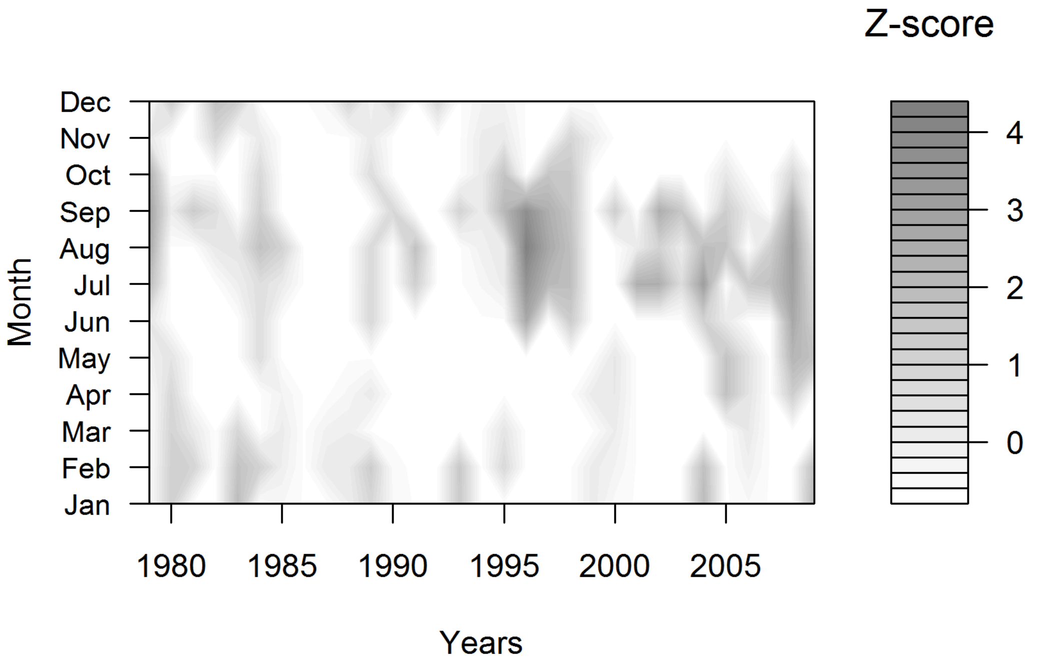


Figure 4.15: Spatial plot of 'Sprat' group normalised abundance.

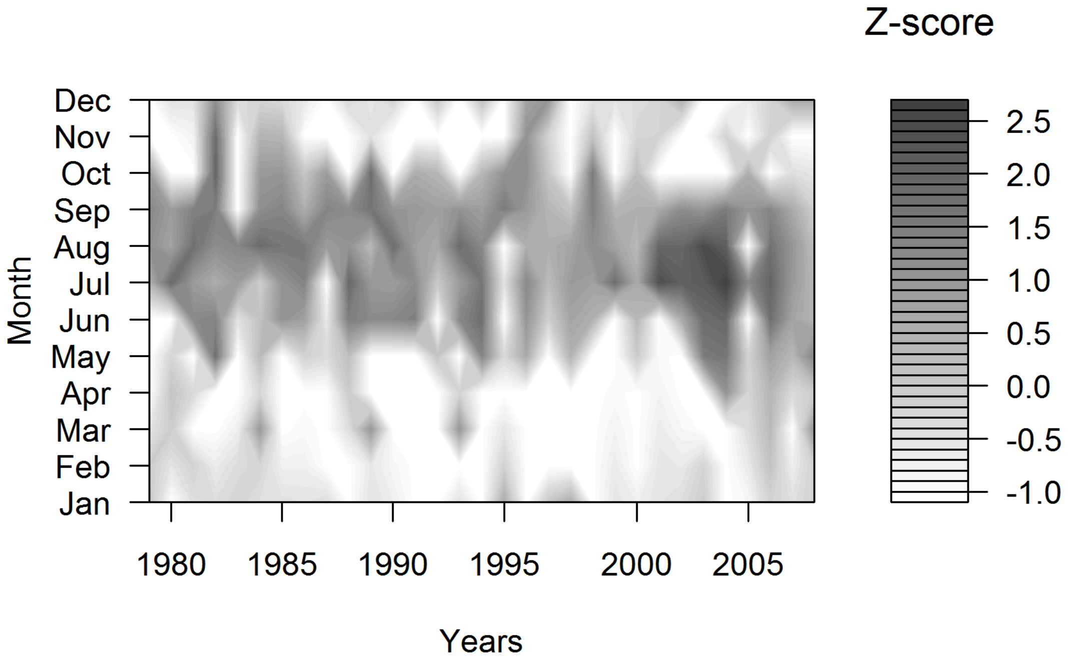


Figure 4.16: Spatial plot of 'Dab/Dragonet' group normalised abundance.

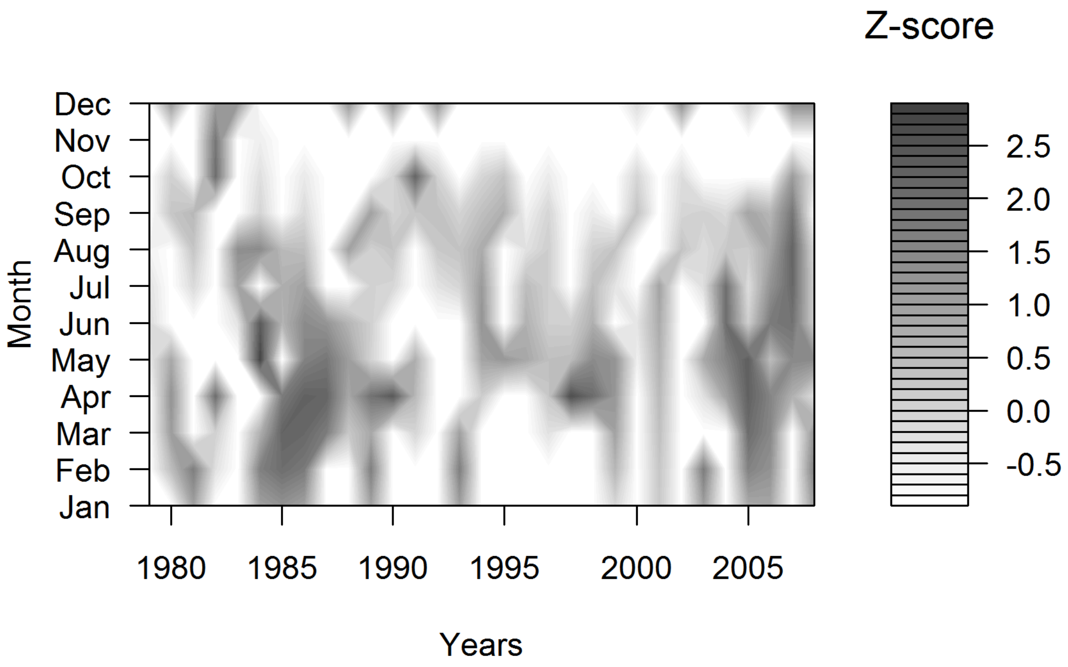


Figure 4.17: Spatial plot of 'Lesser sandeel' group normalised abundance.

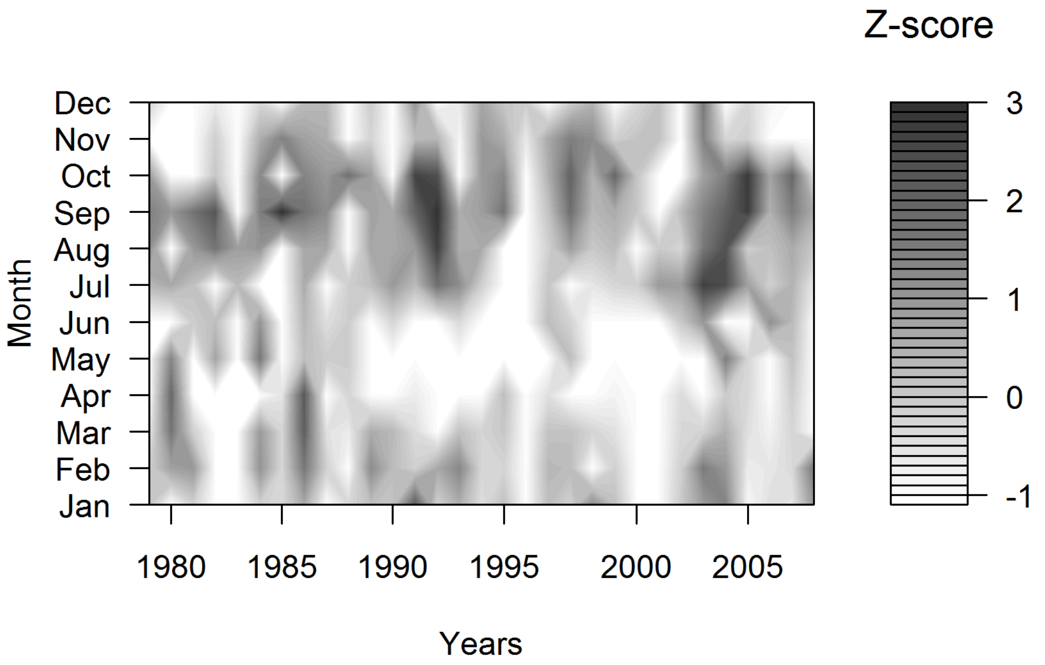


Figure 4.18: Spatial plot of 'Lemon sole' group normalised abundance.

There was only weak evidence of a role for either CCA1 or CCA2 linear constraint time series in determining timing of seasonal peaks in abundance of each group. The key coefficients of GLM models are summarised in Table 4.12. CCA2 was non-significant in all cases and removed from the models, meaning CCA1 was the single predictive term investigated. The 'Sprat' and 'Dab/Dragonet' groups exhibited borderline significance against CCA1 which suggested a possible negative effect of increasing CCA1 on the timing of peak abundance of these groups. Larvae of early spawning fish dominated by lesser sandeels showed no relationship between peak abundance and CCA1, nor was there a relationship in the case of the late spawning group dominated by lemon sole.

Group	Slope	Intercept	T	P
'Sprat'	-0.21	8.95	-1.88	0.068·
'Dab/Dragonet'	-0.09	7.87	-1.93	0.067·
'Lesser sandeel'	0.05	4.77	1.26	0.221
'Lemon sole'	0.06	9.58	0.77	0.480

Table 4.12: GLM output of time of peak abundance versus CCA1, which is strongly and positively correlated with SST, and moderately and negative correlated with cloud cover and wind speed.

The relationship was non-existent in the case 'sandeel' and 'Lemon sole' groups, and weak over time in the two borderline significant cases, as shown in Figure 4.19, and in both cases a truncated LC range in the case of the 'Sprat' group and a handful of outlying results in the more recent samples of the 'Dab/Dragonet' group may have been a factor in these slopes. The summer groups appeared to peak earlier as CCA1 became more positive and therefore calm, warm conditions became more prevalent. In this regard the DTS is superficially similar to the English Channel study of Genner *et al* (2010), but the winter effects observed in that study and that of Malzahn and Boersma (2007) were not observed in this study. The evidence is not strong enough to consider this a persistent effect of change in sea conditions to which fish larvae have exhibited sensitivity.

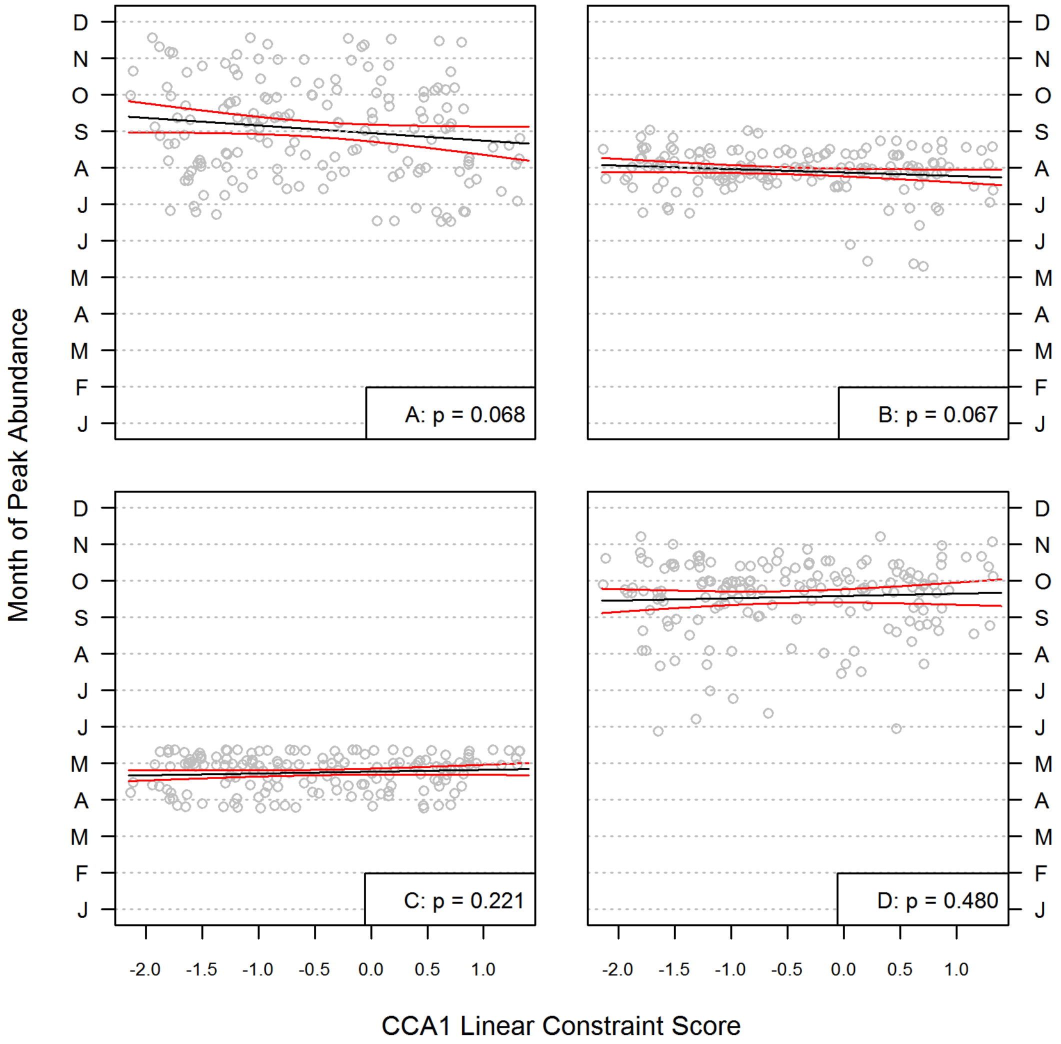


Figure 4.19: Regression lines between CCA1 linear constraint score and the month of peak abundance of each of the four groups. A: 'Sprat' group, B: 'Dab/Dragonet' group, C: 'Lesser sandeel' group, D: 'Lemon sole' group. No model was significant at α = 0.05, though the 'Sprat' and 'Dab/Dragonet' groups were borderline significant.

4.4 Discussion

Ichthyoplankton showed no obviously strong trend in abundance over time. There was a breakpoint identified between 1998 and 2007, which was so wide a range as to indicate there was no breakpoint. The technique simply tries to minimise RSS and BIC and the break does not immediately mean there is a step change in abundance. As Spencer *et al* (2011) pointed out, looking for abrupt shifts in time series that have trends risks misidentifying a trend as a step-change event. Trends of course continue before and beyond any purported step. Likewise in a relatively stable time series, variations in seasonal variability may favour the breaking of a time series into a number of different abundance vs time regression lines in order to minimise RSS. This does not mean there is a genuine break, and visual inspection will show if there is a clear change in level of abundance. As in this case, there was only a small increase in abundance post breakpoint so it was considered a spurious identification and disregarded. While there have been major changes in abundance of phytoplankton, and the nature of peak zooplankton abundance post 1995, there was no such change in ichthyoplankton.

This is reflected in the factors that were important in determining the overall abundance of ichthyoplankton in the DTS. Namely prevalence of warm water and clear calm weather, as well as high abundance of phytoplankton. Warm water assists growth (Gallego *et al*, 1999), wind can either promote encounter rates with food when strong, or promote clearer water and greater visual acuity when weak (Doyle *et al*, 2009; Pepin *et al*, 1995; Sundby, 1997 Peterman and Bradford, 1987). Calmer and clearer weather probably assists fish larvae by aiding visual predation in surface waters (Brodeur and Rugen, 1994). That the overall abundance of ichthyoplankton was best described by a model with phytoplankton abundance as a term rather than zooplankton abundance may at first appear to be counter-intuitive Generally speaking, as food density increases, so does fish larva abundance (Pederson and Rice, 2002). As fish larvae do not generally bring about top down control of zooplankton (Pepin and Penney, 2000; Cushing, 1983), there is no particular reason for peak zooplankton abundance to be the time of peak fish abundance, provided density is sufficient for above-starvation encounter rates between larvae and prey. The earliest stages of many fish larvae eat phytoplankton (Hunter, 1980) but the majority of ichthyoplankton that survive the first few days of life graze upon zooplankton, as the energy gain from diatoms and dinoflagellates is rarely sufficient to fuel rapid growth of fish larvae from small planktonic organisms to nektonic juveniles (Rønnestad *et al*, 1999). The statistical best fit of a model with phytoplankton but not zooplankton was therefore statistically if not biologically sound. Ichthyoplankton abundance was seasonal, as the movements and reproduction of the adult fish is, and this seasonality in large part coincided with the summer-autumn peaks in phytoplankton. The periodicity in phytoplankton that was partly explained by variability in the AMO wasn't present in the ichthyoplankton, with the possible exception of the spring spawning group dominated by *Ammodytes marinus* abundance, indicating it was not long term change in phytoplankton that was important, but the seasonal timing of lower trophic levels, particularly the second bloom of phytoplankton. Furthermore change in timing of peak fish larvae abundance had no strong relation to CCA1 (representing largely SST, unlike the conclusions of Genner *et al*, 2010 and Greve *et al* 2005), indicating the seasonality of phytoplankton was the more likely determinant of abundance of larvae. *Ammodytes marinus* is a special case, as adults overwinter after ceasing feeding the previous year in a minimally active state in burrows before breeding in late winter to early spring. Most adult fish must feed through the summer before breeding, so it is no surprise that most larvae appeared at this time and were not related directly to zooplankton abundance.

Community composition was best described by a CCA model with exclusively hydro-meteorological terms. Lower trophic level plankton, the NAO index, and the AMO anomaly were not important factors in determining community composition. Whereas AMO and NAO were important CCA model terms describing composition of phytoplankton and zooplankton, that has not been observed for the ichthyoplankton. This suggests there is no equivalent long period cycle of habitat switching by adults leading to changed composition of the ichthyoplankton assemblage operating in the DTS, compared to the English Channel (Edwards *et al*, 2013), and that the conditions in this region compared to the English Channel are less susceptible to change in the Atlantic, which makes sense considering the weaker Atlantic influence near the DTS (Pingree and Le Cann, 1989). The ichthyoplankton at the DTS site are there as a result of the spawning of parent species which for the most part do not as adults depend directly upon plankton for their food (clupeids and ammodytids being notable exceptions). This in itself is not interesting, as it is the case for nearly all fish that the adults have a different diet compared to their larvae. What it does signify is that the decadal scale variability of NAO or AMO does not have a consistent effect upon the spawning of fish species in the DTS which are subsequently represented in the ichthyoplankton. Wind and cloud featured strongly in CCA composite predictors of ichthyoplankton assemblage composition and in particular, the north-south v-component of wind speed had a strong correlation with CCA2. The residual current in the region is along a southeast-northwest axis, parallel with the coastline, and this is strongly wind driven (Gmitrowicz and Brown, 1993). The v-component of wind has become more positive, or more southerly, over the last 40 years. Wind from a southerly direction would lead to more surface water being blown to the north, and Ekman processes leading to the movement of subsurface water to the east. As the frontal zone in the area forms as a result of tidal energy dissipating in deeper water and allowing stratification to occur, additional north and eastward transportation of water by wind would represent additional energy from the shoreward side meeting the front, expanding the size of the shoreward zone. Wind can influence coastal current plume width and front definition (Lentz and Largier, 2006; Raine and McMahon, 1998). Unfortunately it is possible only to track change in frontal zone position in the absence of CTD profiles at the site.

There was mixed evidence of the importance of long term variation in abundance, which as with phytoplankton and zooplankton appeared to operate at scales of approximately 14-15 years. In half of cases it was clear that this variation was not clearly visible against shorter term interannual variability, indicating the strong link between hydro-meteorological change and lower trophic levels of plankton wasn't as apparent in the ichthyoplankton. The strongest case for a long term periodic signal in abundance was present for the spring sandeel dominated group which had interannual peaks in the 1980s and again in the 2000s, though this appeared to be closer to a ~20 year period than a ~14 year period. Ichthyoplankton is meroplankton, present only when their parents spawn nearby, so there is no reason to expect this weather signal to propagate as powerfully to ichthyoplankton, unless it is something that affects the adults too, in which case it is necessary to occur over a wide area (Woodhead, 1964). The quasi-periodic variability used in the cases of phytoplankton and zooplankton did not result in particularly convincing dynamic linear models. Forecasts were wholly negative, which does not agree with the positive relationship between fish larva abundance and warm clear weather, which over the period studied increased in frequency. The lack of an overall negative trend in observed abundance would suggest there was not a sufficient justification for including interannual trend components with fixed structure like this, as there was no underlying predictive effect of the AMO on abundance or community composition at the site.

This is likely to be the case for two reasons. Firstly, the DTS is close to the shore and probably close to the along shore front that will develop in spring as warmed sea stratifies offshore and remains mixed inshore. Fish larvae are known to be concentrated in these frontal zones (Dickey-Collas *et al*, 1997), and it is suspected that wind has interacted with the stratified and mixed water bodies with the effect of modifying the location offshore that the frontal zone develops. Diversity varies according to the food available to the stock, which can lead to hydrographically isolated assemblages of different diversity (Gissel and Munk, 1998), so while there was little evidence for 1992-2001 being particularly different for phytoplankton and zooplankton, there may be an oceanographic reason for this change. Wind processes to the north of the DTS near to the Firth of Forth in a region of strong freshwater influence are as important as tidal processes in facilitating or interrupting stratification (Sharples *et al*, 2006). Larvae can disperse rapidly when unimpeded (e.g. Heath and McLachlan, 1987) so it is likely that the presence of a front would act to separate species spawned on either side, leading to differential assemblage diversity.

The second likely factor that would override the propagation of long term climate signals to fish larvae is of course the distribution and spawning behaviour of the adult fish. Temperature change can have effects on adult spawning (Sims *et al*, 2004; Edwards *et al*, 2013), and there have been NAO linked changes in fisheries associated with wind and temperature (Alheit and Hagen, 1997). The effects of changing conditions can have direct metabolic or indirect food effects on adults (Ottersen *et al*, 2001), and it is apparent that across the North Sea, there have been changes in distribution of fish larvae, which indicates through either, or a combination of, change spawning patterns of adults and changed conditions for larvae at spawning sites (Edwards *et al*, 2011). In the DTS, the combinations of variables from CCA that best described community composition did not have decadal periodic variation, so there was no corresponding periodic variation in most fish larvae.

There were some intriguing observations in the DTS however, consistent in part with the general trend for more northward progression in the ranges of southern species (Beare *et al*, 2004; Iversen *et al*, 2002; Neumann *et al*, 2012). *Buglossidium luteum* was absent during 1992-2001. *Trachurus trachurus* was absent after 1992. *Sprattus sprattus* abundance in this period when *Clupea harengus* abundance was low. This might suggest the warming over the course of the time series favoured sprats over herring, and certainly sprat recruitment increases at higher temperature in the Baltic Sea (MacKenzie and Koster, 2004), however the overfishing of herring before control measures in 1996 would be a more parsimonious explanation (European Commission, 2012). The period after 1992-2001 was when the some new warm water favouring groups appeared: *Entelurus aequoreus* after 2003 (Harris *et al*, 2007; Kloppmann and Ulleweit, 2007), *Echiichthys vipera* in 2008 (Beare *et al*, 2004), *B. luteum* returned. This suggested perhaps a wider effect on fish habitat use. 1992-2001 was not synchronous with any obvious change in character of any other trophic level of environmental predictor near to the DTS, leading to the question – were the fish larvae present in the DTS representative of a phenomenon occurring in the wider area?

As the WP3 net samples at approximately 25m depth, the gear probably does not always optimally sample fish larvae, which migrate vertically to avoid drift out of nursery areas (Fortier and Leggett, 1983). Changing wind may have an effect on stratification which could influence abundance estimates through a deeper or more shallow mixed layer depth. This further underlines the importance of CTD profiles, lacking for the majority of the time series. Furthermore sampling gear can be visually avoided (Brander and Thompson, 1989), which would mean as sampling has always been carried out during the day, that the net must additionally under-sample larger larvae. This is speculation, it was not possible to determine thermocline depth to weight abundances accordingly.

4.4.1 *Conclusions*

Fish larvae in the DTS are diverse with the offspring of sublittoral, pelagic and demersal fish being present. The main factors in determining community composition were SST, salinity, wind speed, cloud cover and the northerly component of wind speed. Zooplankton were not an important predictor if only because adults in the region do not spawn when zooplankton is at its most abundant, being mostly late summer spawners, except a group dominate by abundance of lesser sandeels as a result of the particular overwintering strategy of this species. There have been no obvious trends in overall abundance of fish larvae abundance, though the constituent parts of overall abundance have been variable over the course of the time series.

There is some quasi-periodic variability in fish larvae, notably the lesser sandeel group, which probably follows change in onset of production in spring, but most of the group of species observed has not exhibited this feature, which suggests the variability in lower trophic at the DTS does not manifest itself in synchronous change in fish larvae. The period 1992-2001 represents low diversity, though no variable tested here could explain this change. It is not known if the DTS region represents a system that is generally descriptive of conditions for fish larvae in the western central north sea, or if unresolved oceanographic features particular to the coastal location such as stratification boundaries affect the patterns here observed.

Chapter 5. A Maximum Entropy Model of Probable Distribution of Herring *Clupea Harengus* Larvae in the Western North Sea, with Comparison to the International Herring Larvae Survey

5.1. Introduction

There was some evidence that fish larvae in the DTS had undergone a sustained shift that did not appear to be related to any predictor available for the study, or the other trophic levels. In other words a change that was manifest in the DTS fish larvae but acting on the adults outside the area of the DTS. A sustained period of low diversity between 1992 and 2001 occurred against a relatively stable overall abundance time series. There was no apparent divide among migratory or non-migratory offspring in either low or high diversity assemblages. It was therefore of interest to know the extent to which the conditions with respect to fish larvae were descriptive of variability local to the DTS, or more widespread. To do this with the available hydrometeorological and biological predictors required a different model that could link relationships determined through study of longitudinal time series and spatial variability – determination of zones of particularly suitable niche for fish larvae.

Niche based models attempt to describe the niche occupied by a species as described by the conditions in the environment that are positive factors in its survival. The fundamental niche of a species would be any area with the conditions needed for its survival and reproduction. Many features would prevent a species occupying all of this area, such as physical barriers, competition, predation, disease, deleterious human interaction. The realised niche of a species is the subset of the fundamental niche that the species actually occupies. Ecospace (Pauly *et al*, 2000), is an approach to extrapolating a time-varying Ecosim simulation into a space-and-time varying simulation. Ecopath, ecosim and ecospace have been widely applied to pelagic systems (e.g. Pitcher and Cochrane, 2002; Araujo *et al*, 2006; Daskalov, 2002; Harvey *et al*, 2003) however their inputs require detailed estimates of many parameters and the model should consider a closed system.

Phillips *et al* (2006) posit that, from a niche based modelling perspective, presence of a species in a sample is indicative of this sample representing the realised niche. This makes the assumption that the species are present due to the suitable local habitat rather than immigration into an unsuitable area. Fish larvae mortality from starvation is concentrated in the earliest period after hatching (May, 1974), and thermal tolerance is narrowest as larvae (Rijnsdorp *et al*, 2009) so it is reasonable to assume fish larvae captured in the DTS samples are there as a result of finding suitable food and environment conditions. Niche modelling takes the conditions where a species was recorded as present, and projects the resulting relationships between those conditions and presence onto a new dataset of those conditions that were measured alongside species presence. If an area, or time, has conditions similar to those measured when species presence was determined, this represents fundamental niche and therefore potential distribution. The model purpose is therefore explicitly to describe fundamental niche; it cannot determine realised niche by extrapolation to a wider area. Phillips *et al* (2006) note that this weakness can artificially expand or decrease the fundamental niche of a species if the samples were taken from a narrow geographic range, relative to the size of the aimed for projection.

Maximum entropy (MaxEnt) modelling is the solution to selecting a probability distribution within which we expect a variable x to exist. In this context, entropy is a measure of uncertainty. Jaynes (1957) reasoned that the only non-arbitrary probability distribution to use was the one with the maximum entropy subject to what is already known, in conditions where we wish to make an inference based on partial information. In ecology this is always the case. Therefore for any possible probability of distribution of x, the distribution closest to uniform should be selected, subject to constraints imposed by our knowledge of how x is affected by other parts of the system.

The MaxEnt approach performed better than the Genetic Algorithm for Rule-Set Prediction (GARP: Stockwell and Peters, 1999) which was another presence-only method tested by Phillips *et al* (2006) when modelling terrestrial vertebrate distributions in South America. The use of the model approach in the challengingly homogeneous environment of the sea is less common. Brierley *et al* (2003) accurately reconstructed krill distribution from acoustic surveys using a MaxEnt approach. It has been used in marine management in the Baltic to identify suitable spawning grounds of *Clupea harengus* (Šaškov *et al,* 2011). It was used here to study herring larvae probability of presence in the North Sea, using DTS data. Herring were chosen as the International

Herring Larvae Survey (IHLS – www.ices.dk) was available to be used as a comparative dataset to examine MaxEnt projections.

Fish larvae disperse from spawning grounds and drift with currents, being retained in one area or another by hydrodynamic processes that lead to fronts (Grioche and Koubbi, 1996; Lee *et al*, 2005; Munk *et al*, 1999). Presence of larvae is strongly related to the spawning of adults, which over time discover and take advantage of suitable grounds (or 'forget' and cease to use them: McQuinn, 1997), which may be shallower areas that concentrate zooplankton (Doyle and Ryan, 1989; Dickey-Collas *et al*, 2010), or are sheltered areas (Boehlert and Mundy, 1998; Smith and Morse, 1985). If the oceanography of a region alters over time, this could affect the recruitment success of larvae, and the spawning decisions of adults. Larvae can be transported long distances in short times (Heath and MacLachlan, 1987; Munk *et al*, 1986), so for example change in oceanography that retards transport could harm survival by failing to connect larvae with nursery grounds (Norcross and Shaw, 1984), or it could open up new good habitat not normally utilised (Polacheck *et al*, 1992). Changing conditions as result of wider climate moderation can impact upon growth and community composition in nursery areas (Attrill and Power, 2002). Perturbations in adults can have a major effect on the presence of larvae in otherwise suitable conditions. The cold 1995/6 winter altered migration routes of sole (Horwood and Millner, 1998). In the southern North Sea, fish such as *Buglossidum luteum* and *Callionymis lyra* increased in abundance in the 2000s as a result of changing benthos, meaning there would have been a consequential change in larval assemblage. Overfishing of herring combined with high larval mortality collapsed the historic Dogger Bank ground, which is still not used by herring to spawn (Schmidt *et al*, 2009). This is because juveniles must join adult shoals to learn migration routes and spawning grounds (Petitgas and Alheit, 2010).

MaxEnt is a way of projecting some of these insights onto a map, although it is not without weakness. If the training data were taken from a limited geographic range (as here), or tested without a key variable, the model risks producing nonsensical distributions and the key is to interpret the output that makes sense, and understand the reason for the output where it does not. That said, a result that does not appear to make sense may still point to genuinely suitable habitat. The previously cited example of historic use by herring of the Dogger Bank indicates it is suitable habitat for larvae, but they remain absent.

The strength of MaxEnt over, for example, hydrography related dispersion models is the flexibility in what the analyst wishes to model. Existing ichthyoplankton modelling requires hindcasts or forecasts from ocean circulation datasets, knowledge of fish larval growth and mortality and knowledge of vertical distribution (Lett *et al*, 2008). This produces excellent short term forecasts (within a season) but is computationally intensive and requires modelling expertise to calibrate and validate circulation models before using their output. Spatial extent graphs from real sampling may be informative in much the same way as MaxEnt projects (e.g. Laprise and Pepin, 1995), however these kind of studies are inevitably short term due to the expense of regular sampling over a wide area. For example, the IHLS suffers from funding difficulties (Heath, 1993), and since 1990 an average of 60% of the survey as designed has actually been carried out in any one year (Payne, 2010). MaxEnt is by comparison easy to understand, easy to use, is well within the capability of a desktop PC and can produce results with minimal input information. In this study, the software was used to take all available herring larvae records from the equivalent period to the IHLS and apply their corresponding physicochemical and biological relationships to a wider dataset.

The long dataset at the DTS was used to explore the areas of suitable habitat for herring larvae to ask if the DTS ichthyoplankton represent more conditions external to the DTS or not. The late 1980s warming event was not universally observed in all examined trophic levels, which suggested localised conditions in the DTS area distinct from neighbouring seas, possibly as a result of the presence of a thermal front influencing the community composition, or transport of plankton along the coastal current without input from oceanic advection. This study can be seen as a first attempt to generalise the DTS presence to the wider sea around it. As said, MaxEnt output can be generated using as little as one environmental variable (Phillips and Dudík, 2008). The addition of further uncorrelated variables in future should they become available will result in further constraints to the maximum entropy distribution, greater distinction between suitable and unsuitable habitat and therefore more accurate projections. MaxEnt describes probable distribution and should not be taken to be a reconstruction of the realised distribution of herring larvae.

Herring larvae are spawned at a number of sites along the western edge of the North Sea (Figure 5.1). Over time the adult stock collapsed from south to north (Dickey-Collas *et al*, 2010) in the 1970s, recovered somewhat in the 1980s and was further overfished to collapse in the 1990s before management measures from a new fishery model was implemented (Schmidt *et al*, 2009), leading to some recovery in the 2000s. The presence of spawning grounds near to and distant from the DTS meant the IHLS was a suitable resource against which to evaluate the plausiblity of MaxEnt forecasts.

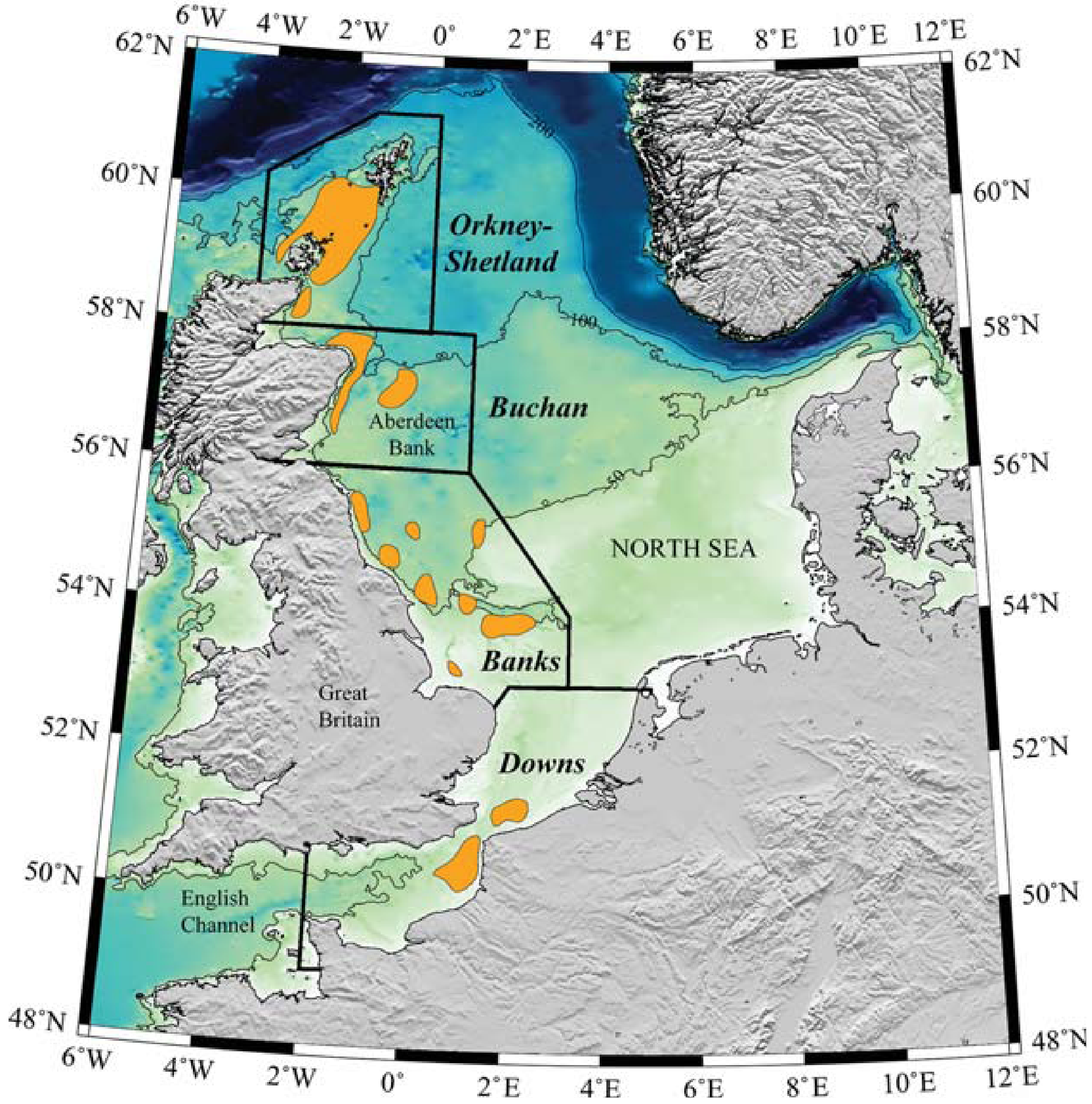


Figure 5.1 Herring larval abundance centres 1972-2008 – from Payne, 2010. Depth contours S to N are 50, 100 and 200 metres.

5.1.1 *Study Aims*

There were a number of questions raised by chapter 4 that merited investigation in a different way. Firstly, were the herring larvae at the DTS site representative of a community to the shoreward or seaward side of a frontal zone? To answer this question, the following hypothesis was tested:

- There will be no difference in probability of presence of herring larvae across the study area.

Secondly, did the period of low fish larva diversity in the 1990s indicate a change to more restricted suitable habitat for fish larvae across the western North Sea? Was it symptomatic of an effect of the changing relationship between NAO and plankton discussed in the literature? To answer this question, the following hypothesis was tested.

- There will be no difference in probability of presence of herring larvae between two periods, 1969-1989 and 1990-2008.

Finally and most importantly, does MaxEnt accurately project probability of presence of herring larvae with restricted information from which to learn? This was tested with the following hypothesis:

- There will be no difference in the location of areas predicted to have high probability of presence compared to IHLS data from equivalent periods.

5.2 Methods

5.2.1 *An explanation of maximum entropy modelling*

MaxEnt (http://www.cs.princeton.edu/~schapire/maxent/; Elith *et al*, 2011) modelling uses presence-only data to identify suitable habitat from a restricted set of records applied to a wider dataset of environmental variables. Presence-only data avoid the problem of questionable reliability of absence records, inasmuch as in the case of the DTS ichthyoplankton, absence of evidence of ichthyoplankton from a coarse temporal resolution time series at a limited range of depths is almost certainly not evidence of absolute absence. The quantity of interest that can be approximated using MaxEnt is the probability of presence of a species, dependent on the environmental conditions. Using the notation of Elith *et al* (2011), let $y=1$ denote presence of a species, $y=0$ denotes absence, z denotes a vector of environmental predictors and the background, or area of interest, to be all locations with L. If $f(z)$ is the probability density of environmental predictors across the area of interest L, this can be subsetted into $f_1(z)$, the probability density of environmental predictors across L where $y=1$ and $f_0(z)$, the probability density of envrionmental predictors across L where $y=0$. As MaxEnt uses presence-only records as input, $f_0(z)$ cannot be modelled. However probability of presence of a species conditional on the environmental predictors, $Pr(y = 1|z)$, can be estimated as:

$$Pr(y = 1|z) = f_1(z)Pr(y = 1)/f(z) \tag{5.1}$$

Therefore, with knowledge of $f_1(z)$ and $f(z)$, the unconditional probability of presence of a species, $Pr(y = 1)$ is the only unknown. MaxEnt first estimates the ratio of $f_1(z)/f(z)$ which identifies which, if any, variables denoted by z are distinct between presence sites and background sites. It does so by determining many iterations of the probability densities $f_1(z)$ and $f(z)$ from random subsets of z, and calculates $f_1(z)/f(z)$ based on the iterations of $f_1(z)$ and $f(z)$ that differ the least. The distance of $f_1(z)$ from $f(z)$ is the relative entropy of $f_1(z)$ with respect to $f(z)$. The model is fitted not on these probability distributions, but on transformations of the distributions from predictors to, as MaxEnt terms them, "features". $h(z)$ denotes a vector of features and a weighting coefficient, β. Minimising relative entropy is equivalent to maximising the entropy of $Pr(x|y=1)$, that is the probability of species y being present in site x (Phillips *et al*, 2006). The MaxEnt probability distribution is equal to the Gibbs probability distribution (Phillips *et al*, 2006) which as an exponential distribution maximises likelihood of sample points:

$$f_1(z) = f(z)e^{\eta(z)} \tag{5.2}$$

where $\eta(z) = \alpha + \beta.h(z)$; α is a normalising constant to ensure $f_1(z)$ integrates to 1. Therefore, calculating $e^{\eta(z)}$ gives an estimate of $f_1(z)/f(z)$, determined from transformed predictors. Each feature has error bounds calculated to avoid over-fitting. By placing a maximum allowable deviation from sample feature means, features with ranges that differ between sample and background beyond these bounds do not result in undue influence of extreme values and correspondingly poor generalisation potential. The error bound λ_j for feature h_j is calculated as:

$$\lambda_j = \lambda \sqrt{\frac{s^2[h_j]}{m}} \tag{5.3}$$

where the variance of feature h_j is $s^2[h_j]$ over m presence sites. The parameter λ is a regularisation constant that determines the extent of the error bound, conceptually equivalent to 1.96 for 95% confidence intervals calculated on normally distributed data. This value is determined from a meta analysis performed by Phillips and Dudík (2008). In this study, the values determined by Phillips and Dudík (2008) were used. Going back to estimation of $Pr(z=1)$, which is not identifiable from presence-only, MaxEnt avoids the issue by transforming the exponential model, $f_1(z) = f(z)e^{\eta(z)}$ to a logistic model:

$$Pr(y = 1|z) = \tau e^{\eta(z)-r}/(1-\tau + \tau e^{\eta(z)-r}) \tag{5.4}$$

where r is the relative entropy of $f_1(z)$ from $f(z)$ and τ is the probability of presence of a species at sites with typical conditions. The former is determined from many subset iterations as described earlier, while the latter is set at 0.5 but could be modified based on more information about a species. Increasing τ would widen the range of suitable conditions in *L*, while decreasing it would narrow the range. Therefore the probability of presence of a species conditional on environmental predictors can be estimated without reference to the unconditional probability of presence of a species by insertion of the parameter τ.

Model performance versus a random projection was assessed using receiver operating characteristic (ROC) curves that plotted sensitivity, that is the true positive rate (sensitivity) versus false positive rate (1-specificity). The model specified by MaxEnt for a species was applied to 10 bootstrapped sets of the presence records and the area under the curve (AUC) was visually inspected to confirm a better than random probable distribution. The important issue was the difference between the MaxEnt ROC and a random prediction. Contribution of features was assessed by jackknife resampling of training gain from models excluding each feature, and models with only one feature. Training gain was the penalised average log likelihood of a species being present conditional on environment features.

5.2.2 *Data acquisition and preparation*

The DTS is a single point time series that does not have a spatial component; however the trends in species revealed in Chapters 2-4 indicate the wider North Sea trends summarised in Chapter 1 were not altogether clearly observed in the DTS, which would suggest the conditions at the sampling site have not always been representative of the wider North Sea area, probably due to different stratification effects. The data used for determining trends in each trophic level of the DTS that were sampled were taken from a range of sources (summarised in Chapter 2). Of those data, the spatial extent of equivalent datasets was investigated and from this a list of datasets that could be used to conduct MaxEnt analysis was assembled (Table 5.1).

Parameter	**Source**	**Units**
SST	ICES	°C
Salinity	ICES	none
Wind Speed	NOAA (ICOADS 1°x1°)	M s^{-1}
U-wind (East-West)	NOAA (ICOADS 1°x1°)	M s^{-1}
V-wind (North-South)	NOAA (ICOADS 1°x1°)	M s^{-1}
Cloud Cover	NOAA (ICOADS 1°x1°)	Okta
Zooplankton Abundance*	SAHFOS	Individuals m^{-3} (normalised)

Table 5.1: Datasets acquired for MaxEnt analysis. *Zooplankton from SAHFOS WinCPR v1.1 only extends to 2001. Data sources as chapter 2, except SAHFOS: Sir Alister Hardy Foundation for Ocean Science.

Each dataset was clipped to represent an area with a buffer of 1-2 degrees around the intended study area (see Figure 5.2) and imported into DIVA GIS (http://www.diva-gis.org/) and converted to a 0.05° by 0.05° grid. A detailed vector of the UK coastline was downloaded from the United States Geological Survey Coastline Extractor (Figure 1; http://www.ngdc.noaa.gov/mgg/coast/) and from this, a simplified polygon was created with its left edge tracing around the UK coast (islands and small estuaries not included) and extending outwards to the 2°E meridian line. The Irish Sea, Severn Estuary and small part of Northern France were removed. The ICES datasets had the widest spatial coverage in the box as these were data from CTD casts over many years as well as the finest temporal resolution as the original dates of samples were preserved. The ICOADS and SAHFOS datasets were of comparable original spread but had been aggregated into boxes covering 1°x1° at a regularised monthly temporal resolution. To convert the datasets into the heterogeneous and noisy character of the ICES dataset, Latitude and Longitude of the centre of each box was determined and a random value between -1 and 1 was added to these coordinates for each month, this spread values out in space but retained them within their local 1°x1° box. These datasets were then imported into SAGA GIS (http://www.saga-gis.org/). Inverse distance weighted spatial interpolation (furthest neighbour distance: 50 grid spaces, maximum neighbours used for interpolation: 250) was used on a grid of dimensions set in DIVA GIS to fill all grid boxes, with the greatest interpolation influence given to the nearest neighbour data. The simplified UK coastline polygon created above was then used to clip the larger grid to show only data for the North Sea in the box in Figure 5.1. This process was repeated for each predictor and was performed on two subsets of the data. 1969 to 1989, and 1990 to

2008. As the late 1980s had been the point at which CPR PCI changed in intensity, and was likely the result of a loss of effect of NAO across the North Sea, this was the point at which the subsets were split. Herring larva data used was from August to November, as this date range covers the majority of IHLS sampling in the area in question (Fässler *et al*, 2011). The majority of herring in the DTS (89.56%) were sampled during this period. Each grid therefore averaged the value of the environmental variable for 21 or 19 years for a third of the year. Zooplankton were different; SAHFOS WinCPR data only exists to 2001 in its public domain form, and the taxonomic resolution of the CPR record is not identical to the DTS record. Also the abundance values in each case are very different due to the different sampling methods. Zooplankton taxa that were shared between DTS and CPR were identified, and summed. Though zooplankton had not been found to be an important CCA predictor, they were included due to their spatial hetergeneity and recognition that the PCA type fitting done internally by MaxEnt would not necessarily come to the same best fit. These values were then log transformed and normalised to mean 0 and standard deviation of 1 to make them as equivalent as possible.

These data were used as projection layers for MaxEnt. Training data for the DTS herring time series was slightly different; the physical parameters were taken from the same sources as the projection parameters, but were left in their original form (i.e. 1°x1° box). The inshore set of parameters was used in this model, as the two water parameters, salinity and SST, had been preferentially picked over offshore by CCA model term selection algorithms used in Chapter 4. There is the possibility of reduced detectability of species sensitivity to small spatial changes, given the quite wide geographical range of physical variables used to represent coincident environmental variables. Given the lack of genuinely coincident physical measurements made in the tenure of the DTS, this was unavoidable, and the values had been demonstrated to have important effects upon DTS plankton community composition in any case. DTS zooplankton were summed, transformed and normalised as for the CPR to make these data as equivalent as possible. CPR data was not used for training firstly because good quality concurrently sampled zooplankton data existed and secondly because to do so would mean discarding zooplankton and ichthyoplankton data from the training dataset from 2002 to 2008. All environmental backgrounds are illustrated in the appendix (see Table 5.1).

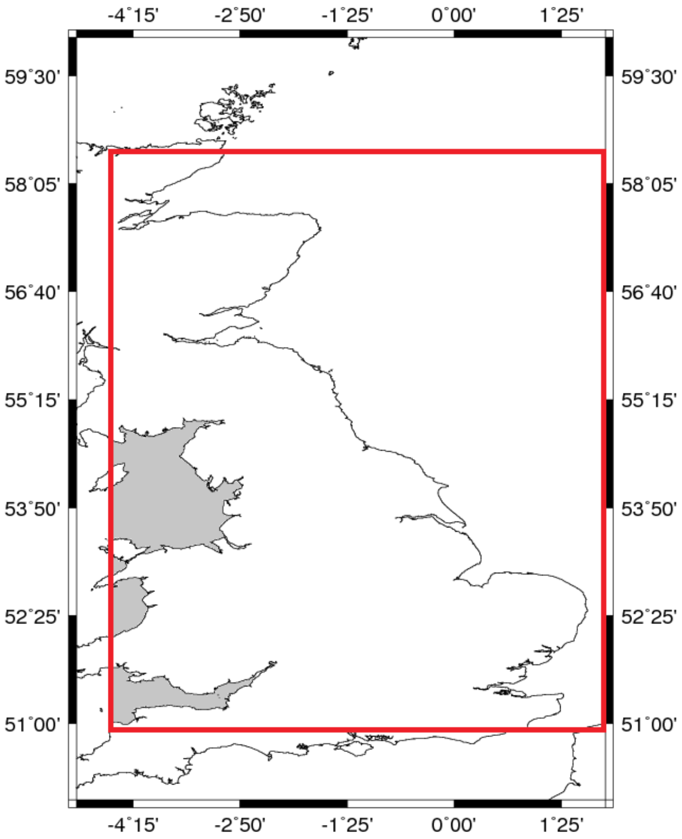


Figure 5.2: UK Coastline with the MaxEnt projection bounding box in red. Shaded seas were not included. The small part of the French coastline in the bottom right of the red box was also removed from analysis and the inverse distance weighted spatial interpolation used to create the spatial datasets was applied over this small area.

Comparisons were made with data from the International Herring Larvae Survey (IHLS – www.ices.dk). As with the projection plots, abundance data from IHLS was aggregated over two roughly approximate periods – 1972-1989 (1969-71 not available in the public domain, as the method is considered not to be consistent prior to 1972 – Heath, 1990), and 1990-2008. The data were then smoothed using the same inverse distance weighting method as previously mentioned.

5.3 Results

5.3.1 *The physicochemical and zooplankton characteristics of each period*

5.3.1.1 *1969-1989*

SST in the period August-November ranged between 8.96 and 14.63ºC in the 1969-1989 period. The southern North Sea was warmer than the northern North Sea. Salinity ranged from 23.36 at some inshore sampling points to 35.29 offshore. There was a strong north-south division, with the north being more saline. Wind speeds in the 1969-1989 period ranged from 5.87 to 10.71m s^{-1}, with a strong inshore-offshore gradient, stronger winds being found offshore. U-wind was positive in the 1969-1989 period (0.41 to 4.67m s^{-1}), indicating predominantly southerly contribution of U-wind to wind direction. V-wind was spatially variable (-1.22 to 3.27m s^{-1}), with no clear pattern over the area. Cloud cover was greater to the North, with a range of 4.42 to 6.49 okta across the whole area. Normalised CPR abundance had a central patch of higher abundance offshore, and ranged from -0.3 to 1.08 standard deviations of the long term mean (Table 5.2)

5.3.1.2 *1990-2008*

SST ranged between 5.43 and 13.15ºC in the 1990-2008 period, with a more heterogeneous distribution. Offshore southern North Sea water was warmer than inshore or northern North Sea water. Alongside this warmer souther North Sea was a much more saline map ranging from 31.50 to 35.21, compared to the 1969-1989 map. Wind speed ranged from 5.14 to 10.98m s^{-1}, with a similar inshore-offshore gradient in strength. U-wind ranged from -0.69 to 4.24m s^{-1} with a more patchy map apparent. V-wind was more positive in the 1990-2008 period (-1.33 to 4.10m s^{-1}) compared to the 1969-1989 period. Cloud cover was similar, ranging from 3.55 to 6.81 okta, with some more patches of clearer weather, particularly around the Firth of Forth and the Wash. In the 1990-2008 period, normalised CPR abundance range was -0.5 to 0.97 standard deviations, appearing to be lower generally than in 1969-1989. There were patches of low abundance in the south (Table 5.2)

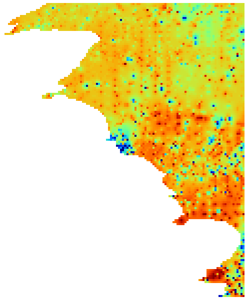
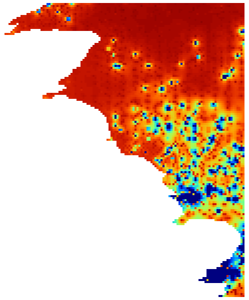
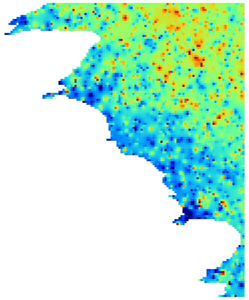
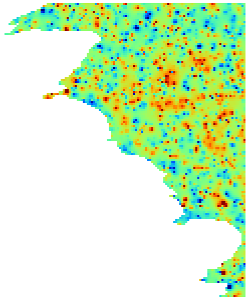
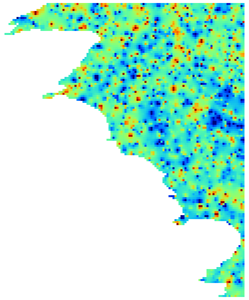
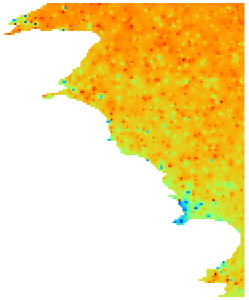
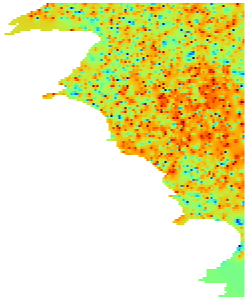
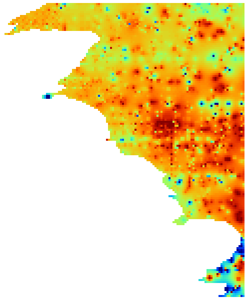
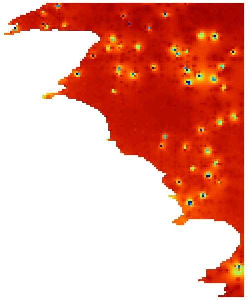
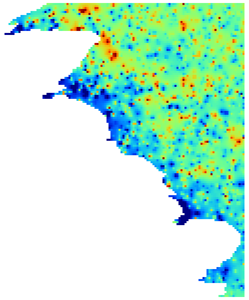
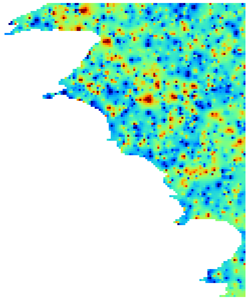
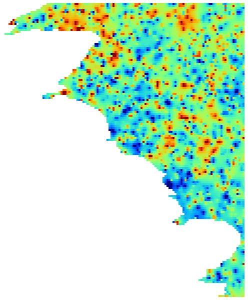
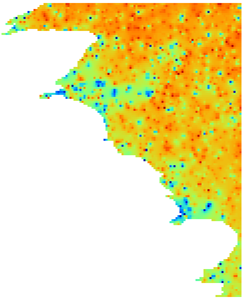
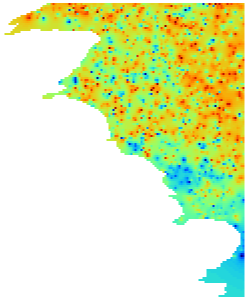
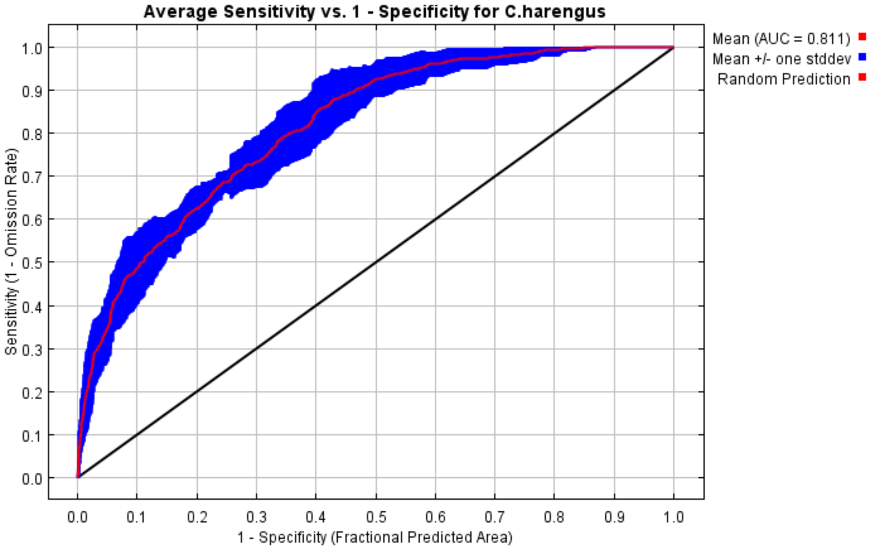
Period	SST	Salinity	Wind Speed	U-wind	V-wind	Cloud Cover	CPR abundance
1969-1989							
1990-2008							
Range	4-16	23-35.5	4.5-13	-1.6-6.1	-2.2-5.5	0-8	-1.5-1.5
Units	ºC	none	m s^{-1}	m s^{-1}	m s^{-1}	okta	none

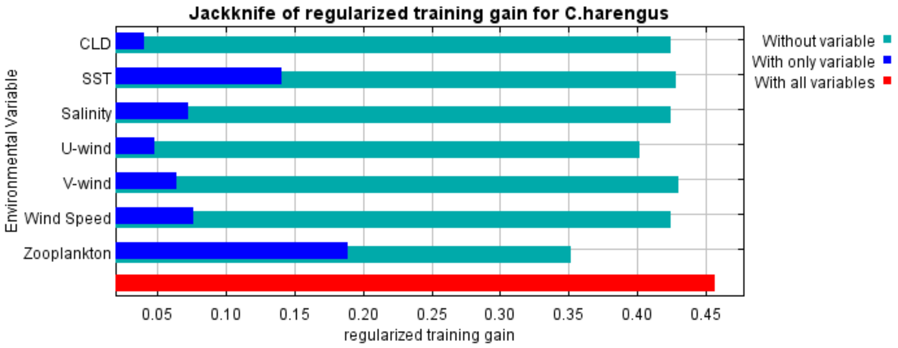
Table 5.2: Temporally and spatially aggregated hydrometeorogical and zooplankton values used for projection of MaxEnt model outputs of herring probability of presence. Colour ranges in each case are linear with 100 divisions from minimum to maximum of each range. Data are aggregated over August-November and are means of all recorded values for the year range, with inverse distance weighted interpolation between points (see methods).

5.3.2.1 *Clupea harengus probable distribution - 1969-1989*

The ROC plot for 1969-1989 were conspicuously different from a random distribution, meaning that the heterogeneity in conditions was sufficient to differentiate suitable habitat for herring larvae as determined from DTS presence/absence from unsuitable habitat (Figure 5.3). SST and Zooplankton were the most important individual variables. Zooplankton abundance was considered to be the most important by virtue of both being a reasonable single factor determinant of herring larva presence, but also because its omission had a greater negative effect on training gain than other variables (Figure 5.3).



1969-1989 ROC plot

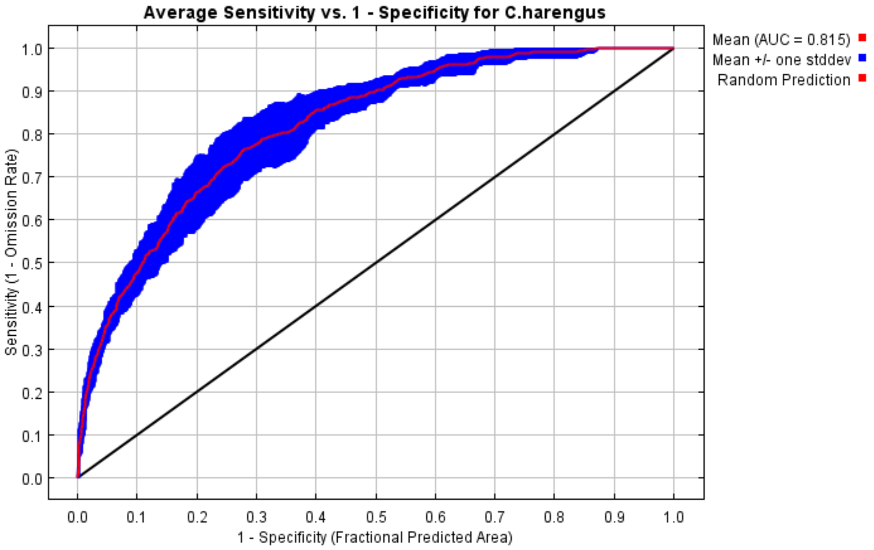


1969-1989 training gain jackknife plot

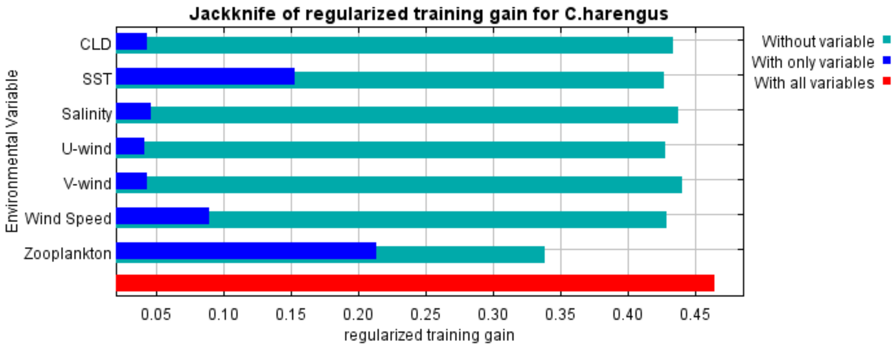
Figure 5.3: 1969-1989 Difference from random ROC plot and Jackknife Predictor Contribution to training gain.

5.3.2.2 *Clupea harengus probable distribution – 1990-2008*

The period 1990-2008 was largely similar to that of 1969-1989. The ROC curve was indicative of a MaxEnt model of comparable specificity as the 1969-1989 model (Figure 5.4). The jackknife profile of predictors was largely similar as well, with Zooplankton again standing out as the most important variable on its own, with SST being another important predictor (Figure 5.4).



1990-2008 ROC plot



1990-2008 training gain jackknife plot

Figure 5.4: 1990-2008 Difference from random ROC plot and Jackknife Predictor Contribution to training gain.

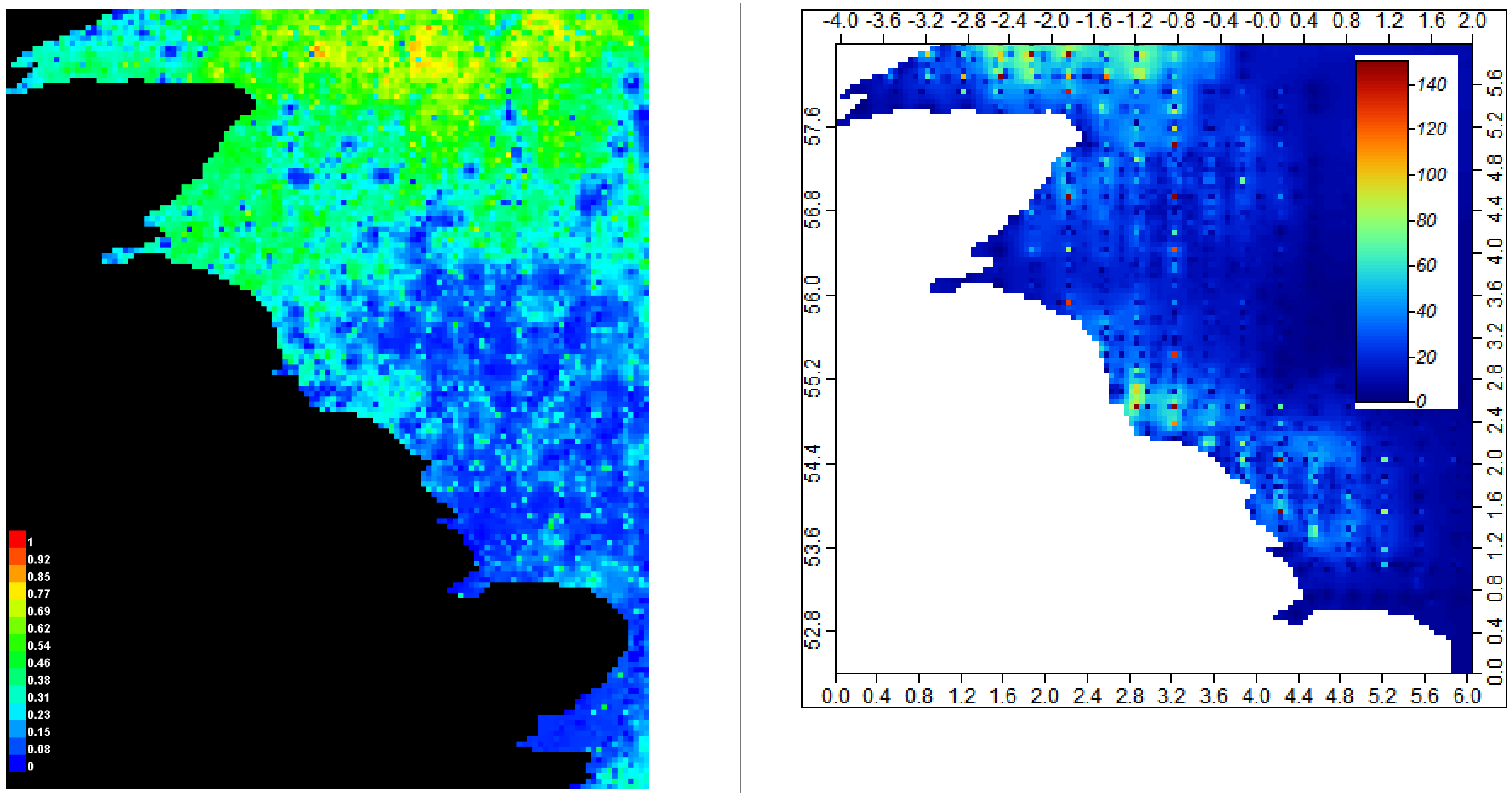
5.3.3.1 *MaxEnt projections - 1969-1989*

In 1969-1989 the probability of presence of herring larvae from the MaxEnt projection was below 0.5 in the southern North Sea, and above 0.5 in the northern North Sea, in the vicinity of the Buchan spawning ground. This output was similar to the data from IHLS over 1972-1989, which had more samples with herring larvae present in the northern samples than the southern ones (Figure 5.5). The MaxEnt projection actually placed the regions with highest probability of presence closer to the Buchan ground than was actually the case, with greater frequency of occurrence of herring larvae to the north of this region in the IHLS data. The second conspicuous feature projected by the MaxEnt model was a region of greater probability of presence on the Yorkshire coast, to the north of Flamborough head. This again was visible in the IHLS data.

The MaxEnt projection determined probable presence further offshore than the scope of the sampling done by the IHLS. These projections are therefore questionable and would appear to be distant from the spawning grounds mapped in Figure 5.1. MaxEnt models can 'clamp' distributions where a contributing environmental predictor is outside of the range of the training data, as was the case in 1969-1989 salinity. Therefore the lower probability of presence in this period, while similar to the IHLS data, is likely to be an artefact of this clamping effect.

5.3.3.2 *MaxEnt projections – 1990-2008*

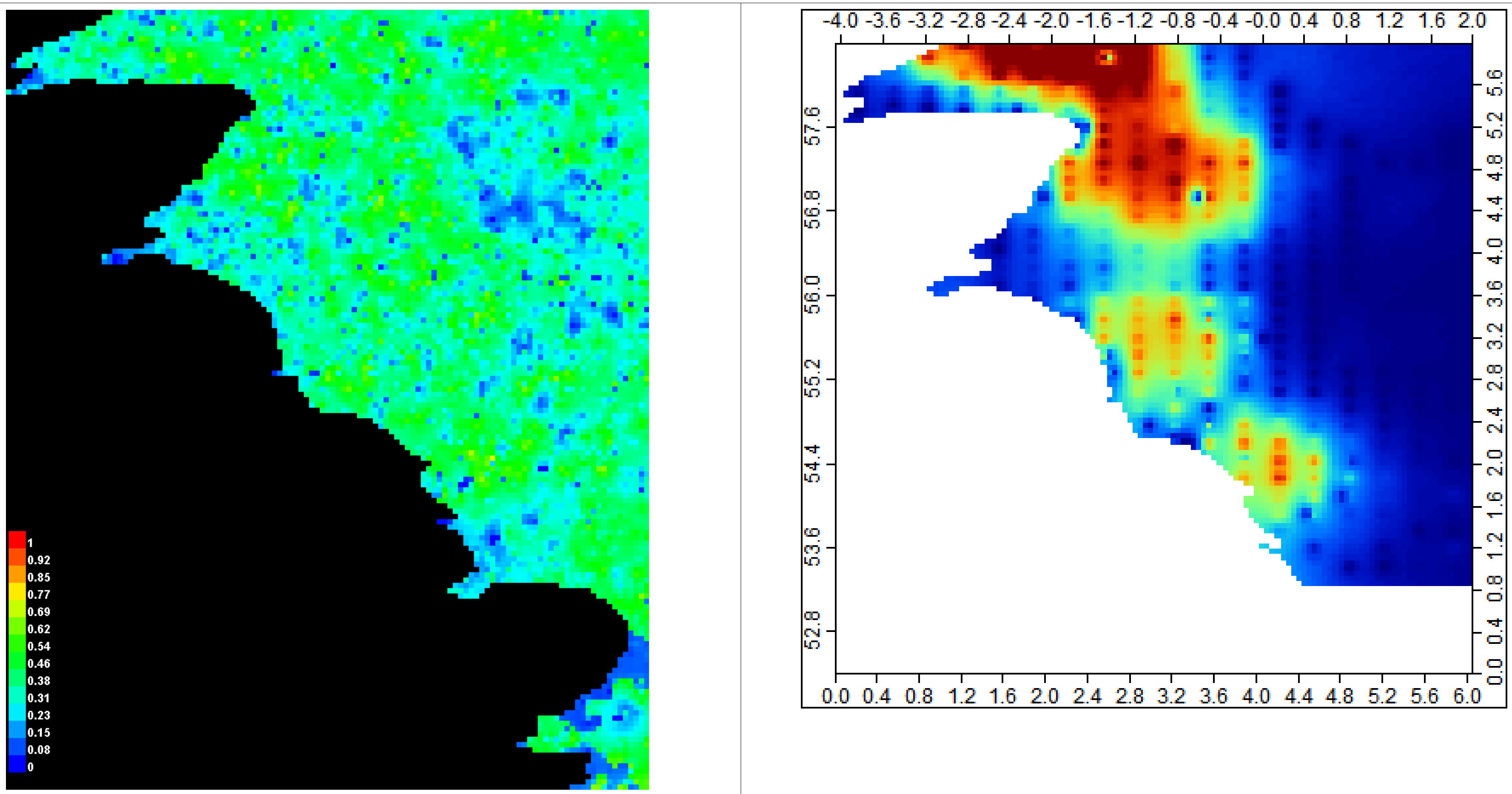
In the period 1990-2008, IHLS data indicated that the frequency with which herring larvae were observed in samples had increased substantially (Figure 5.6). At the same time, the MaxEnt projection indicated conditions across the North Sea were more amenable to herring presence. This however demonstrated a failing of the MaxEnt model, and its input data. No stratification data were available in the form of CTD profiles, so there was no data in the training process of the model that could differentiate mixed from stratified water. Furthermore by having data from just the DTS site, the inshore-offshore dynamics of herring larvae when drifting was not described by the model, resulting in an excessively homogeneous projection in the later period. There was little difference in the jackknife plots in either period, meaning the extension of the range of sea with probability of presence over 0.5 was as a result of the more homogeneous salinity data in 1990-2008, than a major change in those factors in the MaxEnt training data.



1969-1989 ASON probability of presence

1972-1989 September-October IHLS data

Figure 5.5: Comparison of 1969-1989 ASON probable distributions of *Clupea harengus*, and IHLS presence data for the equivalent 1972-1989 period. The colour scale in the MaxEnt projections indicate the probability of presence of the species (blue = 0 probability, red = probability of presence of 1). Colour ranges in the IHLS map range from blue (absent) to red (many observations).



1990-2008 ASON probability of presence

1990-2008 September-October IHLS data

Figure 5.6: Comparison of 1990-2008 ASON probable distributions of *Clupea harengus*, and IHLS presence data for the equivalent 1990-2008 period. The colour scale in the MaxEnt projections indicate the probability of presence of the species (blue = 0 probability, red = probability of presence of 1). Colour ranges in the IHLS map range from blue (absent) to red (many observations).

5.4 Discussion

As far as herring larvae were present when a certain combination of physical and biological factors were present, the MaxEnt model could characterise these conditions and project probable distribution onto the North Sea map. This was confirmed by the areas under the curves of the ROC plots for both 1969-1989 and 1990-2008 being much greater than 0.5 and therefore better than a random distribution. Where the MaxEnt approach failed was in matching probability of presence to real world data from the IHLS, as a result of factors not made explicit in the model. What MaxEnt did not do was identify regions with frequently observed herring larvae in the IHLS as being unsuitable, suggesting with further input data it could perform to a higher standard.

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North Sea spawning stock of herring is divided into four components, from north to south: Orkney and Shetland, near to the Buchan coast, on the Banks along the northeast English coast and the Downs component, in the English channel (Cushing, 1955; Heath *et al*, 1997). The extent of the MaxEnt projection was sufficient to cover the middle of these two, the Buchan and Banks components. The DTS herring would have come form the Banks component, as it is the closest, and each spawning ground has high population integrity (Iles and Sinclair, 1982). In 1969-1989 the projected distribution matched quite closely with the IHLS data, but by 1990-2008, the model had projected much more suitable habitat for fish larvae than the IHLS data indicated was actually inhabited.

This is not to say that the MaxEnt model had lost sensitivity, as the similar ROC plots between periods would testify. There are regions of the North Sea historically occupied by herring that are no longer (Schmidt *et al*, 2009), and regions that have historically had much higher adult migration than is the case now (Smout and Stewart, 2012), as a result of multidecadal cycles in herring larvae in association with long term change in suitable conditions (Alheit and Hagen, 1997). These regions may be suitable locations for fish larvae, but the coastal fidelity of spawning grounds of herring would suggest a strong coastal oceanography contribution to the dispersal of larvae. Drifting larvae in the north of Scotland spawned in inshore or offshore zones remain hydrodynamically separated and recruit to separate populations of herring (Heath, 1990), as they do at the Buchan ground, where the coastal front and thermocline both concentrate larvae in horizontal and vertical space (Munk *et al*, 1986). The IHLS does only sample in coastal zones, but the CPR clupeid maps covering 1948-1985 and 1986-2006 indicated very low abundance in the open north sea (Edwards *et al*, 2011), though these data are necessarily only the smallest larvae because of the CPR gear design (Lynam *et al*, 2013). It is the case that MaxEnt over-projects possible distribution, and this is likely to be as a result of shortcomings in the relevance of input data.

There are a number of steps which could be taken to enhance MaxEnt performance. The regularisation parameters developed by Phillips and Dudík (2008) were determined from distribution data of Australian amphibians, reptiles, birds and plants (although optimised for application outside of this area), so it may be the case that a further refinement alongside more complete relevant environmental data would be to calibrate these parameters for the fish larvae in the DTS samples. Additionally, sufficient information about predator distribution was not found, which is probably as important in determining mortality as food availability and environmental variation (Batty, 1989). Chaetognath, interspecific competition and jellyfish data were not available in sufficient species resolution (or at all) in public domain CPR datasets to incorporate the effect of predators, despite these groups clearly affecting growth of populations of fish larvae (Fortier and Harris, 1989). The importance of coastal fronts and stratification in determining fish larvae dispersal, suggests that getting this information into a MaxEnt model would be necessary to generate probable distributions that more closely matched reality. The sea floor substrate is important in determining where herring lay their demersal eggs (NOAA, 2006; Šaškov *et al*, 2011). Anomalously dense phytoplankton blooms that sink to the substrate before being grazed have killed herring eggs through dissolved oxygen depletion (Morrison, 1991), which obviously can have an influence on distribution if it was to occur repeatedly when herring spawn. Substrate data are available (jncc.defra.gov.uk) though obviously this was not a useful dataset for this study with its single sampling point. Dissolved oxygen and other physicochemical data would need to be taken as CTD or bottle profiles.

Maximum entropy as a concept is not new (e.g. Jaynes, 1957), yet only recently has it become a more widely used tool in data-poor niche modelling. It has been applied to successfully model distributions in the pelagos (Brierley *et al* 2003), and has been demonstrated to be a useful approach in predicting distribution of commercially important fish (Vignaux *et al*, 1998) and octopus (Hermosilla *et al*, 2011), as well as accurately predicting spread of invasive marine species (Poulos *et al*, 2012). Its use in the marine environment appears to outperform alternative approaches (Pittmann and Brown, 2011; Stockwell and Peters, 1999). If MaxEnt was to be extended to other species, information like substrate would be important as it is necessary for recruitment of some species found in the DTS, such as *Pomatoschistus minutus* (Wilkins and Myers, 1992), *Phrynorhombus norvegicus* (Chanet *et al*, 2003) and *Symphodus melops* (Beldade *et al*, 2006). Frontal zone dynamics are generally important for the distribution of fish larvae, a number of other species besides herring (e.g. Munk and Nielsen, 1994; Lee *et al*, 2006). Prey selectivity would suggest further refinement of the important zooplankton effect on probability of presence would be valuable. *Clupea harengus* and other larvae are ontogenetically selective, more so than perhaps a crude summing of all 'suitable' prey species would illustrate (Checkley, 1982, Batty *et al*, 1990).

5.4.1 *Conclusions*

Three hypotheses were tested:

There will be no difference in probability of presence of herring larvae across the study area. Was rejected, as there was variability in the probability of presence, mostly as a result of spatial variability in SST and zooplankton abundance.

There will be no difference in probability of presence of herring larvae between two periods, 1969-1989 and 1990-2008. The large barren region in the southern North Sea in 1969-1989 was probably a model artefact of downgrading sites with out-of-range values, as was the case for salinity. This made it impossible to assess if the projections were substantially different or not.

There will be no difference in the location of areas predicted to have high

probability of presence compared to IHLS data from equivalent periods. Taking 1990-2008 as the most 'projectable' map as a result of in-range salinity, there appeared to be little connection between the MaxEnt projection and the IHLS data. Though offshore regions weren't sampled by the IHLS, the strong north to south distribution of herring larvae wasn't recreated by MaxEnt. There was insufficient difference in conditions offshore to differentiate habitat. This is as a result of having no stratification information.

This means that unfortunately the ultimate question, regarding the representativeness or otherwise of the DTS with respect to the sea around it remains unanswered. MaxEnt could be re-run with further information but without stratification information in particular it is unlikely to provide a satisfactory answer to this question.

Chapter 6: General Discussion

6.1 No consistently observed change in all divisions of plankton investigated at the Dove Time Series

There was insufficient evidence to suggest that the widespread reorganisation of the plankton community as observed in the CPR was also observed in the DTS. Change in plankton alone is not sufficient to be descriptive of regime shift, this requires sustained change in other trophic levels to be observed. There has been ongoing change in SST, salinity, wind speed, cloud cover and NAO and AMO indices which has variously affected each trophic level of the plankton investigated in the DTS. In particular, a shift upwards in the abundance of phytoplankton, and in the peak to trough ratio of zooplankton had occurred after 1995, some 10 years after the proposed regime shift in the CPR, which appears to have been as a result of earlier stratification. Diatoms grow in place of dinoflagellates in spring as their high surface area to volume ratio and high growth rate compensates for the initially lower light conditions (Margalef, 1978). This would appear to be a similar basis to the NAO and westerly weather linked change in phytoplankton observed by Aebischer *et al* (1990) and Henson *et al* (2009). The fish larvae at the DTS didn't exhibit a follow-on response, suggesting habitat switching may have occurred among adult fish, rather than a sea-wide regime shift that would of course preclude this. Investigations of fish larvae were not conclusive in the extent to which the DTS was representative of the western central North Sea more generally.

Because the changes observed did not reflect in their timing, those changes observed in the CPR more generally across the central North Sea, it is likely that the particular hydrography of the DTS has played a role in influencing plankton abundance, diversity and the timing of peak abundance. It would be beneficial to sample at more than one location along a transect with contemporaneously measured oceanographic data to characterise the eco-hydrodynamic nature of the area close to and further from the coast. It follows that the profound reorganisation of the plankton community in the CPR in the mid 1980s as described by Edwards *et al* (2002) would appear from the evidence of the DTS not to be replicated. The CPR differs perhaps because it is representative of ecological patterns averaged across inshore and offshore waters. Because the DTS is a single point time series, it has revealed alternative points of change, particularly in phytoplankton and zooplankton, which are not in synchrony with those observed for the central North Sea in the CPR, this is likely due to the coastal location of the DTS. The NAO has driven changes in oceanography that have been linked to change in plankton (Alheit *et al*, 2005), but this requires careful consideration of what mechanism actually brings about observed changes. For example it is long term decline in deep water advection of overwintering copepodites of *Calanus finmarchicus* from the Norwegian Sea to the North Sea that led to an increase in the relative abundance of *Calanus helgolandicus* compared to *Calanus finmarchicus* (Heath *et al*, 1999). The NAO influences westerly winds and overturning circulation thus affecting *Calanus* only indirectly, which is why after some time the correlation between NAO and *Calanus* was lost (Beaugrand, 2012), and why there was always a differential correlation between the NAO and *Calanus finmarchicus* and *Calanus helgolandicus* (Fromentin and Planque, 1996). This highlights that what can be an important signifier of ecological change in at one time, may not be important at all at another time, particularly if the means by which it drives change is not understood.

There was some evidence of biological change in tandem with oceanographic change at the DTS published previously, such as succession of species with anomalously high abundance at the time of the transit of the GSA, and the late 1980s warm water event observed in the CPR (Bonnet and Frid, 2004; though they did not have supporting oceanographic data), however if these species represented a major oceanographic event, they necessarily signified another one in the late 2000s (Figure 6.1). It might be the case that high abundances of particular species relative to the long term mean are indicative of an advective process being affected upstream, along the coastal current described by Gmitrowicz and Brown (1993) however the coastal current around the UK is relatively weak, apart from off western Scotland (Hill and Simpson, 1988) and wind-driven currents are weak in the vicinity of the DTS (Pingree and Le Cann, 1989). Further study of the role of currents in transporting plankton southwards, with particular reference to the location of the DTS versus the offshore front in the sea off Northumberland may serve to explain the mechanism by which these occasional spikes in abundance come to be observed.

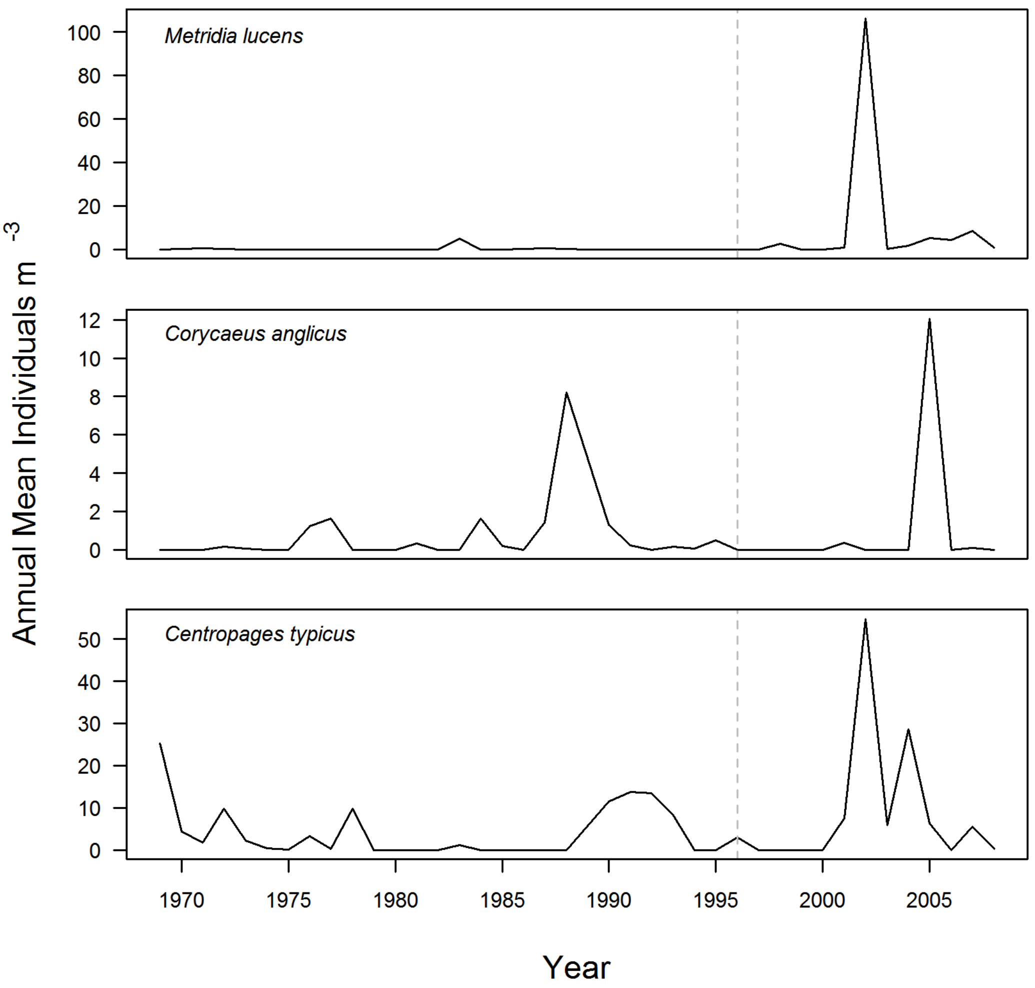


Figure 6.1: Three species sampled by WP2 net that were identified by Bonnet and Frid (2004) as indicators of transit of different water masses past the DTS. Grey dashed line separates data available to the authors, and new data from this thesis.

6.2 Mechanisms of Change in the Dove Time Series Plankton Community

At the DTS, in the case of phytoplankton there was strong evidence that the conditions driven by the sign of the AMO anomaly was the reason for sustained change in abundance and community composition, after 1995. Greater phytoplankton abundance class occurred and was sustained as a result of the sign of the 2nd constrained correspondence axis, the variability of which was composed mainly of variability in the AMO anomaly. This indicates the conditions associated with positive AMO anomaly (earlier stratification) favoured greater abundance of phytoplankton. The AMO varies at a number of periods, two in covariance with long and short term solar variability (Gleissberg and Sunspot cycles), and one which is approximately 14 years, and correlates with the Fram Strait Sea Ice Export time series (Miclaus and Dima, 2011; Schmith and Hansen, 2003). 1995 was a low point of this cycle, which coincided with a very cold winter in 1995/6 in the North Sea (Armonies *et al*, 2001; Gunther and Niesel, 1999), Arctic (Hansen and Hoppe, 1999) and on land in the UK (Met Office, 2011). The winter NAO index in 1995/6 was sharply negative (Halpert and Bell, 1997). This was accompanied by abnormally weak circulation in the North Sea, coupled with northerly winds deflecting Atlantic water that would ordinarily circulate to the south into the North Sea in winter to the east (Pingree, 2005). Unusually cold water was entrained at depth in the North Sea at this time (Brown *et al*, 1999). As the AMO has moved into the positive anomaly after this point, the conceptual effect over the North Atlantic has been for decadal scale cycles in the Atlantic Meridional Overturning Circulation affecting atmospheric heat transport (NAO), promoting stronger westerlies which lead to nutrient transport into the open North Sea through wind driven circulation, and more thorough wind mixing (Stepanov and Haines, 2013; Figure 6.2). At the DTS site, lower cloud cover in spring has likely resulted in stronger irradiance leading to earlier stratification and more PAR availability. Spring phytoplankton in the DTS has increased over time and peaked earlier, which is likely to be as a result of these processes. Monthly sampling will of course obscure the influence of the lunar cycle on phytoplankton, and in coastal mixed zones it is the case that concentration of chlorophyll tends to peak when the tidal range is narrowest (Balch, 1981; Sharples *et al*, 2006), this would be a useful parameter to measure and if possible calculate for backlogged samples.

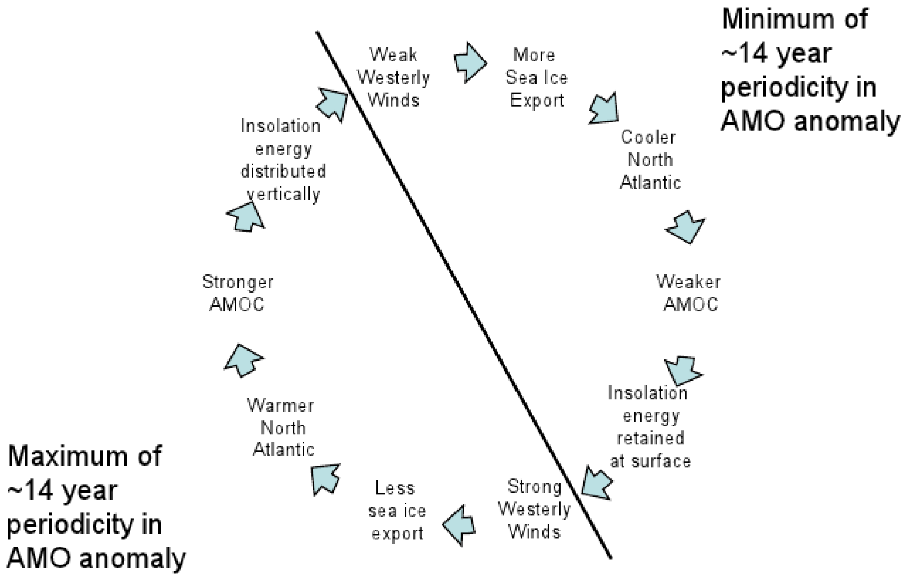


Figure 6.2: Conceptual diagram of interaction between sea ice export, SST and mixing in the North Atlantic.

AMO was a major component of the linear constraint predictor of zooplankton maximum to minimum ratio, which increased markedly at the same time as phytoplankton abundance. This move to a high peak zooplankton system occurred as a result of favourable spring conditions for phytoplankton. Small copepods in summer formed these spikes in abundance and indicated that changing timing in phytoplankton abundance lead, possibly through changed composition of prey after the spring bloom, to conditions favourable to much higher abundance than had been observed before.

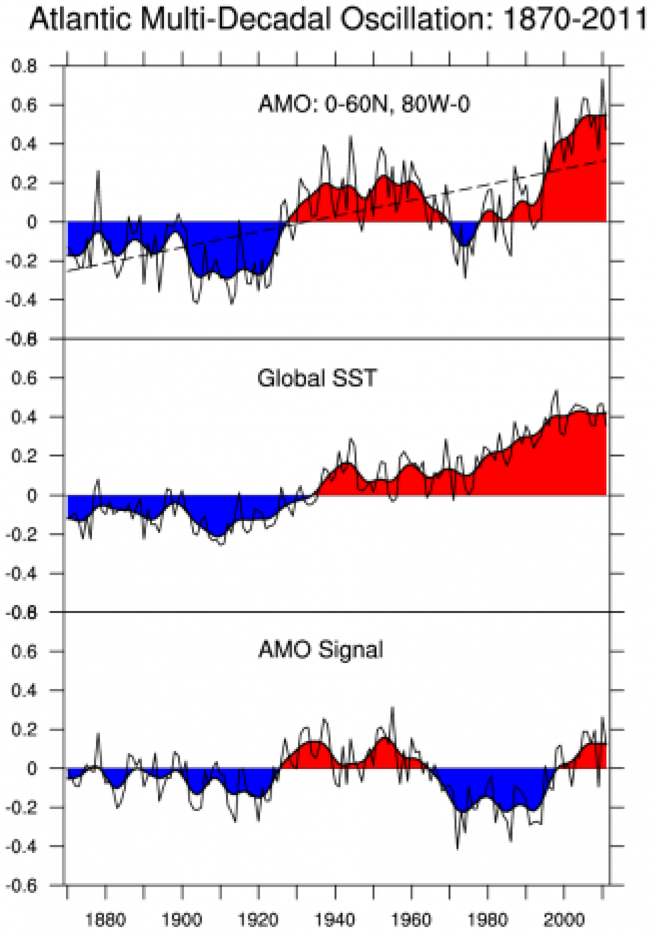


Figure 6.3: The AMO, global SST trend, and detrended AMO. From NCAR (2013).

Looking at Figure 6.3, the AMO contains substantial information about global SST trends, so the sustained higher abundance after 1995 actually occurred during negative phase of the AMO, once detrended. If the NAO lags the AMO by approximately 10 years, there is a possibility that what currently enables higher abundance of plankton (earlier stratification) as a result of a negative AMO in the 1990s, will lead to poorer conditions as a result of the positive AMO in the 2000s.

If the link between AMO and wind (and sea ice) is an accurate representation of the reasons for the differences in plankton pre and post 1995, the rapid melting of the Arctic ice cap in the 21st century (NSIDC, 2012) may have a role to play in this time series, distant from the ice itself but apparently responsive. Additionally, though this scenario is an attractive description of those events post 1995, it does not explain why if 1995 was one minimum in the FSSIE, and thus the GSA transit period near to the DTS in 1979 (Dickson *et al*, 1988) would be approximately contemporary with the preceding minimum, was there not a similar period of enhanced phytoplankton abundance, and high amplitude maximum:minimum zooplankton abundance ratio?

Perhaps the answer lies in the positive anomaly of AMO in the 1950s inducing a lagged negative NAO in the 1960s, and late 1970s. The complex teleconnections between these measures of atmospheric and oceanic heat fluxes require highly technical decomposition (Wyatt *et al*, 2012). What does this mean biologically? Like Beaugrand (2012), discussing the NAO and *Calanus,* in the DTS are there certain as yet unknown ranges of positive or negative values of the AMO at which it can exert a strong positive effect on plankton, and other ranges where it does not have an effect? This depends on the affinity plankton have for different conditions, and their tolerances to change in conditions as found in the seas around the UK. The linearity or otherwise of response of all the plankton at the DTS to change in AMO relative to its periodicity is a question for the future, and one for which a long dataset like the DTS provides an excellent validation opportunity.

Fish larvae appear to be separated from this hydro-meteorological process, probably because the adult fish migrate and over time their spawning centres move depending on the differential recruitment success of larvae released in the centre and periphery of these zones (e.g. Edwards *et al*, 2013). Spawning locations are where larvae can survive, feed and recruit at a favourable rate to maintain the population (Qasim, 1956). Changing hydrometeorology can influence important determinants of successful recruitment, such as turbulence (Borja, *et al*, 2002). There have been discrete periods of high and low diversity among fish larvae at the DTS, the most notable being a long period between 1992 and 2001 when diversity was notably lower than the preceding periods. This long term discrepancy in larval supply to the DTS site could be due to migration of spawning adults, a change in frontal zone dynamics or a change in stratification depth relative to sampling depth, or a combination of all of these factors.

It is notable that the NAO index was not a predictor of community composition of phytoplankton or ichthyoplankton, and was a subordinate predictor of zooplankton community composition compared to the AMO. The NAO has been implicated as the most significant correlate with environmental and biological change in the plankton. There is clearly something about the DTS that does not correspond to the changes observed by for example Edwards *et al* (2002). Fromentin and Planque (1996) highlighted that the collapse in *Calanus finmarchicus* in the North Sea occurred as NAO index moved to positive phase, the conclusion of which was the positive relationship between NAO and SST in the North Sea rendered the sea inhospitable to the species.

Beare *et al* (2002) further suggested that reduced inflow from the Norwegian trench, the source of overwintering CV copepodites, decreased in the 1990s. While there is input from the Atlantic, the Norwegian stock of *Calanus finmarchicus* copepods transports 25 times as many copepodites to the North Sea (Heath *et al*, 1999). So copepodites were being transported in lower numbers and when they did arrive, the temperature was too high for the physiology of the species, harming survival and promoting occupation of the zone by Calanus helgolandicus which is adapted for warm-temperate conditions. The much stronger contribution to DTS abundance from coastal zooplankton types such as *Acartia, Centropages hamatus, Temora longicornis* compared to *Calanus* means such a marked effect would not necessarily be observed in the DTS. This likely to be why observations in the DTS do not mirror those observed offshore in the CPR. The WP3 dataset has historically been used for determining the species makeup of C5 and older *Calanus*, but given the fixed depth versus the different temperature mediated vertical response of both species, where warmer water makes *Calanus finmarchicus* migrate to deeper water than *Calanus helgolandicus* (Jónasdóttir and Koski, 2011), this seemed unlikely to be informative. It would be a valuable exercise to revisit the time series and process the WP2 dataset in full for Calanus species composition to determine if it reflects the findings of the CPR or not. Presumably because of its location, Atlantic, rather than Norwegian stocks of *Calanus finmarchicus* CV copepodites are found at the DTS. Beaugrand (2012) showed that the relationship between *Calanus finmarchicus* and both NAO and AMO indices was not consistent over time and space. Beaugrand's thesis was that the NAO as the primary correlate with SST in the North Sea exerts influence over SST within a range that correlated strongly with *Calanus finmarchicus* abundance prior to the 1980s regime shift event determined from CPR data. After this point, abundance of *Calanus finmarchicus* in the North Sea was unrelated to the variation in the NAO, as it was no longer varying within a range descriptive of suitable conditions for survival.

Change in NAO therefore appears to no longer be a particularly powerful predictive variable with respect to the abundance and composition of plankton in the North Sea generally, leading to revision of the concept of the mechanism of NAO effects (Beaugrand, 2012) and more generally an appeal to identify mechanisms first to test against biological time series, rather than fitting the data to the mechanism (Lees *et al*, 2006; Heath *et al*, 1999). This study could fairly be accused of the latter. The CPR represents data spatially aggregated across inshore and offshore waters, meaning the biological response such as it was has been derived from samples mostly offshore, and thus subject to unimpeded circulatory influence from the North Atlantic. The DTS probably is strongly influenced by coastal mixing processes and frontal dynamics that might explain the incongruent time series compared to the CPR. Whether the NAO is unimportant because of the coastal element, or the global climate change influence on its relationship with plankton and stratification as a whole remains to be determined.

The DTS phytoplankton is poorly sampled. As removing small species likely to be undersampled enough to change their abundance class revealed only autumn blooming species would be retained, this is evident (Chapter 2, Figure 2.1). This begs the question, does the relationship between phytoplankton and SST, wind, AMO, zooplankton and cloud cover determined in Chapter 2 give the investigator useful information, or misleading information? It is undoubtedly the case that spring phytoplankton by virtue of their small size, an evolutionary response to nutrients being available in a turbulent environment requiring rapid growth (Reynolds, 1996; Margalef, 1978), are not well sampled by a 63µm net. Fortunately, the combinations of these variables represented conditions that were largely seasonally divided. While absolute abundances couldn't be determined and even the semi-quantitative abundance classes were not adequately calibrated with regard to the sampling inefficiency, even poorly sampled species were found at greater abundance at certain times of year, meaning the relationships determined with CCA analysis were likely to be sound. Net clogging, at times of high abundance of small species, could interfere with estimates of abundance, which was one reason abundances of groups relative to each other were not compared statistically.

Consequently, the decline in overall phytoplankton abundance in the mid 1990s was not an artefact of poor sampling efficiency. The time series and its covariance with the heavily AMO loaded CCA2 linear constraint time series were indicative of a real long term change. What is important to consider when looking at the phytoplankton time series in this study, is that the constituents with the most conspicuous change in abundance immediately after 1995 were those phytoplankton abundant in summer and autumn. This is important when asking why zooplankton did not follow the same long term trend. The phytoplankton which declined from a level of high abundance in the 1970s to much lower abundance by 1995 were summer and autumn species. Spring phytoplankton had low abundance (because of inappropriate sampling gear) which exhibited a much shallower decline from the 1970s to 1995. The summer and autumn species were of minor importance in determining zooplankton abundance and so their more pronounced declines did not translate into a decline in zooplankton. The increase in spring phytoplankton occurred as the likely result of stronger seasonal stratification, which suggests an ultimately temperature-related reason for these spikes in abundance of small copepods. Bearing in mind these copepods reached peak abundance some 2-3 months after peak spring phytoplankton abundance there must have been a change in conditions more generally applicable to the plankton as a whole which lead to this change in the magnitude of peak abundance.

The formation of along shore fronts is a function of the dissipation of tidal energy into sufficiently deep water that a pycnocline can develop and persist over the course of a season (Hill, 2005). Phytoplankton that can remain in the upper mixed layer of stratified water will grow more effectively than those that are in mixed water that will not retain them in the euphotic zone. It so happens that the depth at which tidal amplitude ceases to affect stratification is approximately 50m, and the distance offshore in the western central North Sea that this becomes a consistent feature is approximately 10km (Hill *et al*, 1993). This means the DTS is located at precisely the point along the shore where this seasonal front can develop (Pingree and Griffiths, 1978). Tides ebb and flood, meaning there is not a fixed line along which a zone forms. It will move with the tide, and the spring/neap cycle will further affect the location of the front (Hill, 2005), and the direction of residual currents along the boundary (Hill, 1994). The passage of atmospheric depressions strongly influence the direction of residual currents (Hill and Simpson, 1988). Additionally the eddy features which form as a result of shearing between zones can straddle the front by 10-25 kilometres (Simpson, 2005; Brown *et al*, 1999). The advective transport of plankton by along coast currents, diffusion by eddies and entrainment by baroclines are important factors in quantifying the convergence or divergence driven transport of plankton relative to a given site (Hill, 1990; Hill, 1991; Pingree and Griffiths, 1978).

The result of these features of frontal zones, combined with lacking any flow meter data or CTD profiles to go along with plankton samples at the DTS (until very recently – B. Wigham pers. comm. 2012), means it is not possible to ascertain what frontal dynamics were in effect near to the DTS in any given sample. Frontal zones can now be determined remotely using satellites (Smyth *et al*, 2001), such as the Advanced Very High Resolution Radiometer (NOAASIS, 2012), and these information sources should be used in future study of the DTS. The role of the front in determining plankton dynamics, particularly in spring and summer, is likely to be more important than any factor employed in chapters 2-5. The use of geographically separated datasets from ICES and NOAA was an attempt to determine if there was a consistent affinity among phytoplankton in the DTS for variability in either the inshore or offshore datasets. This was a compromise particularly for salinity which was only patchily available from ICES over the times and locations of interest. For some datasets (salinity, cloud cover) there was a clear distinction between the two regions, for others (SST, wind speed), there was much less difference. This suggests the combination of all factors was unlikely to offer a satisfactory divide between better inshore and offshore goodness of fit in models. And so it was, in most cases there was a mix of either inshore or offshore types, and for the most part those datasets that were quite different between regions were of subordinate importance to the more conserved datasets such as SST and wind speed.

The analyses of chapters 2-5 can go some way to describe the changes observed in the DTS. Ocean-atmosphere cycling in the North Atlantic is expressed by SST variation that is mostly caused by solar output variation, though there is medium term cyclical variation in association with sea ice transport from the Arctic. The NAO is the lagged atmospheric response to this variability which means positive phase NAO correlates with negative AMO anomaly at ~6-10 year lags (Stepanov and Haines, 2013; Wyatt *et al*, 2012). Sea ice export plays a role in SST and mixing regulation by affecting buoyancy, with a wind and insolation feedback system regulating sea ice export, at 14 year periods (Miclaus and Dima, 2011). Over this quasi-decadal time scale, westerly winds cycle from strong, leading to warm-temperate oceanography in the North Sea and the blocking of Arctic low pressure systems, to weak, with colder boreal oceanography and more frequent intrusion of low pressure systems into the North Sea. Strong westerlies lead to greater vertical mixing, which leads to greater nutrient availability in spring. Warmer air temperatures lead to earlier stratification, so spring phytoplankton blooms have been more dense, and have begun earlier. Warmer temperature appears to have led to more dense zooplankton swarms, particularly of small copepods *Acartia* and *Oithona*. Since 1995 at the DTS this appears to have lead to a change to a sustained higher abundance plankton community, compared to the previous period.

Previously, Clark *et al* (2003) suggested *Sagitta* (*Parasagitta*) abundance was critical to the overall zooplankton abundance at the DTS by regulating *Pseudocalanus* (then the most abundant copepod in the DTS) abundance, and this occurred as a result of phytoplankton phenology changing depending on wind conditions, leading to suitable prey for *Sagitta*, leading to two cohorts in good years. Clark *et al* (2003) considered all *Sagitta* to be *Sagitta elegans*. Better taxonomists than this author have divided *Sagitta* near to the DTS into *Sagitta setosa* and *Sagitta elegans* (Meek, 1928); as they have to the North of the DTS (Fraser, 1937). Differentiation is generally possible only when seminal vesicles are developed, which they were not in most cases. Here is proposed an alternative hypothesis, that would merit further investigation. *Sagitta elegans* feeds on *Calanus* spp., while *Sagitta setosa* feeds on small copepods and *Oikopleura* (Tönnesson and Tiselius, 2005). *Sagitta setosa* can have up to 6 cohorts in 1 year (Øreslund, 1986), compared to 4-5 in *Sagitta elegans* (English Channel: Russell, 1932), so more cohorts might suggest unidentified *Sagitta* are more likely to be *Sagitta setosa* rather than *Sagitta elegans*. It is suspected that conditions post 1995 would favour *Sagitta setosa* population growth, and the alteration in abundance of small calanoid juveniles (including *Pseudocalanus*) after 1989 presented by Clark *et al* (2003) and observed in this study (Chapter 3, Figure 3.9) was not a step-change event associated with GSNW, but a temporary dip in abundance of this group as the abundance of the constituent *Pseudocalanus* was diminished by warmer conditions (Isla *et al*, 2008) which meant in the early 1990s it could not match the abundances of *Acartia* and *Oithona* which after 1995 held record abundance previously held by small calanoids. In this regard, and with the benefit of an additional 13 years of data, *Sagitta* appears to vary in much the same way as other small copepods, and the increased abundance of Sagitta has not brought about a reduction in the abundance of DTS copepods it preys upon (Figure 6.4). It is likely the increase is mostly due to *Sagitta setosa*, reacting to an abundance of their favoured prey (Krause *et al*, 1995), rather than *Sagitta elegans*. Verifying this would be a fascinating project.

This demonstrates the importance of long term monitoring in understanding the trends observed. The conditions as described above appear to be an explanation of the state of the plankton with respect to changing wind, mixing and stratification, but only after 1995. If this cycle is consistently effective, then there should have been further boosts to abundance of phytoplankton and zooplankton after the GSA passage in the late 1970s, and lower abundance prior to this. There wasn't, which means the NAO, AMO and the general state of the wind regime across the North Atlantic since 1995 have converged to favour development of a higher abundance system at the DTS, but have not replicated precisely this condition set prior to 1995, in the DTS record. There are longer term cycles that affect marine species (Cushing, 1976), and it may not always be apparent that multiple periods of variability are affecting a system. There is every reason to continue monitoring the DTS and reviewing the mechanisms of longer term variability should they manifest themselves 50 years from now.

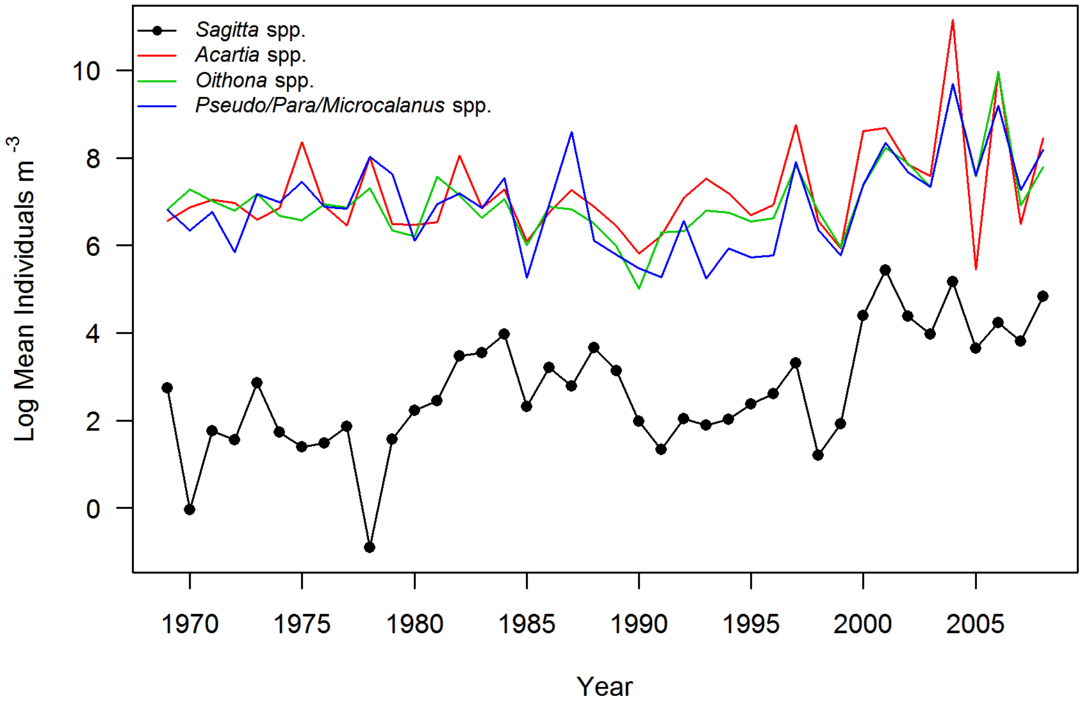


Figure 6.4: Time series of small copepods and *Sagitta* spp. over time at the DTS.

6.3 Improvements to the Dove Time Series monitoring programme

The phytoplankton analysed in chapter 2 were opportunistically examined as they were the unintended by-product of small mesh zooplankton sampling. When faced with a time series like this the options available to maximise information while minimising errors present a challenge. The choice of a semi-quantitative scale of abundance was one with a backing in literature (Škaloud *et al*, 2006; Legendre and Legendre, 1998), though difficulties remained in analysing these data. These difficulties stem mainly from the sampling gear, and also the age of some of the samples and the degradation of cells within. Seawater acts as a natural buffer but its effects do not last over time, meaning there will inevitably have been some shrinking and wastage of non-siliceous phytoplankton (Smithsonian Institute, 2012).

Gear efficiency varied seasonally. The spring period was consistently of lower abundance class than the autumn period. The continued greater abundance class in the later part of the year seemed to be related to cell size. The spring community is dominated usually by long chains of small individual cell size diatoms. This is overtaken by large dinoflagellates and diatoms in the summer and autumn periods. It seemed that the 63µm mesh size was more inefficient in the spring than in the summer. Bearing in mind this was a zooplankton targeted sampling gear, the mesh size was too coarse for reliable sampling of small phytoplankton. Therefore the species cell dimensions were examined from literature sources and a correction factor applied to their abundance class in order to counteract the effects of the mesh size. As can be seen from the comparison graphs in chapter 2, this worked only to an extent and the sampling imbalance remained. Therefore the continued sampling of phytoplankton in this manner will continue to be semi-quantitative at best. A more appropriate approach would be one that samples water without filtration, such as a Niskin bottle or integrative hose sampler.

Zooplankton analysis requires some clear guidance to be developed. In the past, WP2 and WP3 hauls have been analysed alongside each other as if comparable when this is not the case (Evans and Edwards, 1993; Bonnet and Frid, 2004). There is no way to compare a discrete depth value in individuals m^{-3} with an integrated depth value in individuals m^{-3} . WP3 is specifically a midwater trawl, aimed at zooplankton retained by a 1mm mesh, that is with a minimum linear dimension greater than 1.42mm. The future results of the sampling plan should be quantitative and conservative. Therefore the WP3 net should analyse only species that satisfy the criterion of being larger across their minimum linear dimension than the mesh itself is on its hypotenuse. As a personal observation, the use of a filtering cod end could be revised to be a non-filtering container for ease in dealing with jellyfish in summer months. The mesh becomes totally clogged with nematocysts which are difficult to clean, and probably dramatically reduce the filtration efficiency of the net leading to bow wave formation, making quantitative comparison between samples uncertain (UNESCO, 1968). The WP2 net remains the most useful zooplankton tool in the DTS. 200µm may be inadequate for abundance estimation of juvenile stages and smaller taxa, though trends may be preserved (Calbet *et al*, 2001). Small mesh nets with smaller mouths may underestimate large species abundance, through easier avoidance as is the case for Calanus finmarchicus (Anderson and Warren, 1991). This means the gear used to sample will diminish in efficiency with increasing escape potential (McGowan and Fraundorf, 1966; Richardson *et al*, 2004). Also at this size, nets can clog rapidly with suspended particulate matter, as is prevalent at the site (M. Baptie, pers. obs.). The zooplankton from the 63µm time series were not included due to the decision by Pitois *et al* (2009) to publish an analysis. There is potential to exploit the 63µm time series for its microzooplankton such as tintinnids, rotifers and large unicellular organisms such as euglenoids and *Tiarina fusus*. The fact *Acartia* and *Oithona* have been so abundant in the 2000s, and are both prey-switchers that can graze upon microzooplankton means it would be interesting to study the dynamics of microzooplankton. The important element to be included in a formal analytical procedure is to compare like with like in terms of sampling method. The existence at Newcastle of a FlowCAM system is an ideal opportunity to re-analyse the DTS and identify which taxa should have abundance estimated from which sampling method, since the software can make multiple measurements to establish size. The DTS can be improved without affecting the comparability of old and new techniques. Table 6.1 summarises the problems with the DTS based on the experiences the author had with the times series analysis.

Tool	Problem	Solution
P200 net + 63µm cod end	Net and cod end too coarse for phytoplankton	Only enumerate zooplankton species with minimum linear dimension greater than 89µm Only record presence/absence of phytoplankton species. Commence phytoplankton sampling using discrete water samples
WP2 net + 200µm cod end	Net and cod end too coarse for small zooplankton	Only enumerate zooplankton species with minimum linear dimension greater than 283µm
WP3 net + 200µm cod end	Net too coarse for mesozooplankton	Only enumerate zooplankton species with minimum linear dimension greater than 1430µm

Table 6.1: Summary of issues with the DTS

Several improvements could be made using existing equipment, or inexpensive additions (with the exception of extra boat surveys). There is only so far one can take statistical analysis of the time series as it stands. This study has demonstrated that dynamic linear modelling of time series can create excellent fits of existing data, but forecasts are much less convincing (because there is no consistent interannual signal derived from an abiotic factor). Some changes are necessary to address issues, others are recommended to add value to the time series. As Boyce *et al* (2010) remark, time series need to be run for more than 40 years to distinguish long term change from background variability, and this should be the aim of the DTS in all its sampling. These proposed changes are summarised in Table 6.2:

Tool	Purpose	Benefit
Standard Operating Procedures	Standardise sampling, analysis and data formatting	Continuity of data in time.
Niskin bottle	Discrete depth water sample	Quantitative phytoplankton, full size range, biomass and contemporaneous physicochemical parameters to validate CTD, gross/net primary production estimation
Weighted hose	Integrated surface to depth sample; alternative to discrete depth sampling	Faster sample analysis at cost of lost vertical resolution
Additional WP3, shallower depth	Sampling above thermocline if present	Horizontal sample of plankton concentrations
Adjust WP3 to vertical or oblique tows	Thermocline issue avoided by sampling whole water column	Reduce abundance distortions caused by water column stratification.
Seasonal inshore-offshore transect	Find coastal front position.	Possible explanation of trends in DTS of certain species
CTD profiles, flow meters	Contemporaneous physicochemical profiles	No longer reliant on 3rd party data, characterise stratification and circulation at the site
Stable isotope food-web analysis	Explicit knowledge food web pathways, input to wider Ecopath type models of North Sea.	Divides genuine trophic relationships from covariance in response to another factor
Genetic analysis, fluorescence microscopy	Bacterial production, microflagellate abundance and type	Begin a microbial loop time series
Partnership with EA	Collaborative use of boat time in exchange for data to expedite some of the above	Foster links, provide data for WFD/MSFD programmes, less expense for Newcastle University if EA can do some of this work
Satellite information	Free data to look at oceanographic dynamics of DTS region	Remotely sensed chlorophyll, yellow substance, SPM, SST fronts

Table 6.2: Proposed improvements to DTS

It is hoped that this thesis has revealed the degree of variability in the DTS plankton community. It is also hoped that this thesis has revealed that as much as the available environmental datasets can explain some of this variability, there are major shifts that are not explainable by these data alone, and there are shortcomings in the sampling methods which restrict the utility of these data in describing the effects of environmental change on plankton at the site. The suggested improvements to the DTS range from the simple (taking a hose to get an integrated water sample, possibly even an effective zooplankton sampling tool: De Vries and Stein, 1991) to the elaborate (modifications to the survey schedule, adding a genetics component). It is recommended that the simple steps are taken now, and the elaborate ones in future.

Unfiltered water samples are crucial for quantitative phytoplankton data;

filtration based phytoplankton sampling always loses the smallest organisms, and filtration efficiency varies between organisms based on size, shape, delicacy. Samples from the same water could then be analysed for nutrients, salinity, suspended particulate matter, chlorophyll, phaeophytin, primary production. These variables were unavailable for analysis of the DTS phytoplankton as contemporaneous data, which is a great loss. It can be changed for the future.

The deployment of a CTD probe, with in-situ fluorometric determination of approximate chlorophyll as well as temperature, salinity, turbidity, pH, PAR, allows generation of profiles to go alongside the DTS samples. Stratification depth and extent are both important variables that could not be included as explanatory variables despite their importance in determining the onset of the productive period in the North Sea, the location of concentrations of plankton within the water column, and the movement of frontal zones over time. It also stops dependence on other organisations for data, and may reverse the situation and allow Newcastle University to contribute to these datasets. The WP3 net at present is towed on 100m of cable, this tows at approximately 25m depth, which may be below the thermocline if it is there, which means this net is likely to underestimate zooplankton abundance for that part of the year. Monitoring programmes at fixed depth risk underestimating abundance extrapolations (Ohman and Smith, 1995). Ichthyoplankton is often concentrated in upper layers or close to the thermocline, which would suggest the ichthyoplankton abundance sampled by the DTS is possibly an underestimation. Including a genetic component is perhaps beyond immediate implementation but would allow quantification of bacterial abundance and perhaps identification too. This part of the plankton foodweb where bacteria recycle organic matter locked in for example dead plankton, chitin moults, zooplankton faecal pellets, supporting a grazing community of eukaryotic flagellates was nearly totally unsampled by the existing methodology. It is not the area of expertise of the author and there will undoubtedly be stumbling blocks to creating a representative description of this community but would certainly provide a more complete picture of the DTS community dynamics. Satellite data are free in the public domain and would assist in future as the time series grow to useful lengths. Consideration of approaching the Environment Agency offering a monitoring platform (Water Framework Directive, Marine Strategy Framework Directive, OSPAR) for in return for data would be a straightforward and cost effective way of achieving some of the above objectives.

Reanalysis of the entire DTS using the recently acquired FlowCAM system is strongly recommended, provided care is taken on avoiding clogging of the system and samples too large for it are analysed as well. The subsample technique was not identical between nets (Evans and Edwards, 1993). A zooplankton sample analysed by hand can take anywhere from 10 minutes to several days depending on the diversity and abundance of the sample, as well as choices in subsampling. There are as has been mentioned previously several areas at which error can creep into the results of a sample analysis. When analysing difficult samples, tiredness can be expected to have an influence after an analyst has looked at 1000 specimens (Salas, 2010). Without wanting to cast unjustified doubt on all analysts who have worked on the time series, the temptation to subsample a borderline abundance sample at 6pm on a Friday is greater than in the middle of the week. This example is perhaps flippant but the point to appreciate is the level of concentration an analyst can apply to a sample can vary widely without any conscious decision on the part of the analyst. Using a system such as FlowCAM or ZooScan eliminates this source of error.

The retention of a permanent image archive of all specimens that pass through the system means these samples can be revisited and errors corrected by future analysts. For example this author had profound difficulty with separating small calanoid copepods, and did not divide larvaceans into *Oikopleura* spp. and *Fritillaria borealis* as these were often quite shrivelled by preservative. Nauplii and other larval stages (e.g. Euphausiid calyptopi) were another group with potential to be further resolved taxonomically. The smaller calanoids such as *Acartia, Microcalanus* and *Centropages* spp. hatch as much smaller nauplii than do *Calanus* or *Temora* spp. There is therefore an opportunity to use the 63µm time series to investigate the history of copepod larval dynamics. These image archives remain available for another analyst to improve upon the work in this thesis.

6.4 Statistical Analysis of Time Series and Perspectives on Future Modelling Work in the Dove Time Series

Dividing the analysis into an explicitly predictor-linked (CCA, GLM) and an explicitly time series structure linked (DLM) stage was a technique that established groups sensitive to sets of environmental and biological variables but examined their fluctuations in time without reference to those explanatory variables. The intention was to reveal the underlying cyclicity of oscillations in SST and SLP signified by the AMO and NAO, which was partly successful, but in many cases was matched by interannual variability without such structure of at least the same magnitude. This reflects the conclusion reached earlier that across the North Sea, there has not been consistent meteorological and oceanographic control of plankton communities (Beaugrand, 2012). In other words, one element of the conditions that favour high abundance in the plankton at the DTS might oscillated without a corresponding oscillation in the plankton that currently are at high abundance. This is because the interactions between atmosphere and sea are complex and lagged which will cause periods of synchronisation and desynchronisation of 'good' or 'bad' conditions that are not adequately explained by for example the phase of the winter NAO. Lees *et al* (2006) were right to criticise use of the term 'regime shift' without a full understanding of the mechanism by which such an event takes place.

Dynamic linear, or state space, models do a good job of tracking variability by decomposing time series into level and error terms for each part of a time series as parameterised by the modeller, and determines best fit through continual updating of estimates of each for each new datum in the time series. This means the trend and seasonal time series are sensitive to short term variation in each part. Seasonal variation can change quite dramatically, as observed in the case of zooplankton with high copepod abundance peaks after 1995, but this is taken into account by the model and means underlying trends cleansed of seasonal variation are likely to be accurate representations of the level of abundance of a group at that time. They are less successful when seasonality is less assured, as was the case with some fish larvae that were only intermittently present and not always at the same time of year. In this case, there is less useful information to be gained from attempting to smoothly model such data, as the use of Fourier series assumes a certain level of variability that can be fitted by one or more harmonics.

So it is with interannual variation as well. We may not yet have sufficient data to characterise all the complex oceanic cycles that affect the plankton, and the wider marine ecosystem. The trend versus step change problem described by Spencer *et al* (2011) when attempting to characterise the nature of long term change in the plankton can be avoided by suitable modelling of the interannual trend with seasonal variation excised (where appropriate). Doing this in the DTS illustrates that rapid lurches from one state to another as described in literature cited in earlier chapters does not appear to be a consistent feature across all of the groups studied in the DTS. The most conspicuous rapid change would be of phytoplankton abundance class, and zooplankton peak to trough ratio after 1995. These both occurred over 1-2 years, and have been sustained more or less since then, satisfying two criteria of DeYoung *et al* (2004). Part of the motivation to incorporate interannual periodicity was based on the suspicion that as there was no explicit description of the mechanism by which these changes had occurred and been sustained, there was no reason that what was observed in the phytoplankton colour index after 1985 for example cannot be reversed in time. Boyce *et al* (2010) alarmingly published models showing global decline of phytoplankton, which have been robustly challenged, but even this extensive study was based on data spread over little more than a century, and only for half this time at high sample density (Boyce *et al*, 2012). We understand how plankton grow, feed, reproduce and what they need to do this but we are still in our infancy when considering long term change, even if we do have many decades of samples and collectively deep experience of analysing the results of these samples. If the AMO periodicity operating at 60-100 year intervals is important enough to cause the virtual local extinction of some species for several decades, only for them to return again, can we call a change sustained for 10 or 20 years regime shift? Dramatic change of this sort may well be wholly natural, and resolving any anthropogenic caused deviation to any of these processes when the scientific community has only been looking closely for maybe one long AMO cycle is a profound challenge.

The DTS is minor in the scheme of things, certainly compared to the CPR. Where it can serve a useful purpose is in telling a different story, about coastal waters rather than the offshore waters of the open North Sea. There are two approaches that could broadly be applied and neither is particularly exclusive of the other. There are now at the time of writing long enough satellite derived chlorophyll time series to extract relevant pixel values from archived data to construct a useful spatially and temporally faithful time series for the DTS to incorporate into analysis in this way, which will have several uses. Firstly the semi-quantitative phytoplankton could be truthed with chlorophyll data to assess if the species with high abundance class were correlated with high chlorophyll and therefore speculatively hindcast the contribution of DTS phytoplankton abundance class to likely historic chlorophyll concentration. These and other variables (e.g. tidal cycle status, nutrient and suspended solids loads, light attenuation) could be used to better describe the mix of factors at work in determining phytoplankton abundance and diversity.

Refinement of the existing technique is one approach, the other would be to start to develop a more dynamic model of plankton with a linkage to the hydrodynamics relevant to the sampling site. An Ecosim (http://www.ecopath.org/) type description of the coastal ecosystem might be a possible avenue to explore, provided the connectedness or otherwise of the DTS to the open sea offshore of Northumberland can be established and taken into account. There is of course, as with all models of ecosystems, an imperative to have excellent quality data with which to calibrate and validate any output. The length of the time series does offer an opportunity to assess such a model, and should be encouraged as a future project, particularly if good quality and contemporaneously sampled oceanographic data become available. Dynamical models can help to explain what presently looks like unexplained variation in species abundances, as everything is connected, and a statistical response of a copepod to variation in a predictor heavily loaded with AMO variability tells only part of the reality of its variability.

It was hoped that MaxEnt, with its elegant statistical basis would provide a useful description of the similarity of the DTS to its surroundings, through the use of herring larvae as a proxy, validated against data from the IHLS. While not wishing to totally dismiss it as an approach, it offers little advantage over an Ecosim or ERSEM (e.g. Radach and Lenhart, 1995; Schismenou *et al*, 2013) model, in that it does not perform adequately without many more predictive variables, in which case one may as well take the time to parameterise a more detailed, and if coupled, fully hydrographic model. This would make an excellent further use of DTS data, and would make explicit the importance of local oceanography to the long term variability observed in all levels of the DTS.

6.5 The Possible Effects of Oceanographic Change on Plankton Community Structure

The seasonal cycle of each trophic group when considered as a whole follows what would be expected given what is known about the links between groups (Figure 6.6). Phytoplankton grow in spring, this is followed by growth in zooplankton grazing upon spring bloom phytoplankton, the nutrient recycling of which leads to further phytoplankton production, balanced against further zooplankton production. As the pycnocline deepens, an autumn bloom in phytoplankton takes place. Most annual abundance of fish larvae appeared in the plankton after the majority of zooplankton annual abundance, when temperatures are warmest and food availability balances predator abundance.

What has occurred in the DTS over time is a move broadly earlier in peak abundance of phytoplankton, zooplankton and ichthyoplankton. These peaks have not all changed by the same degree, with quite marked (though not linear in time generally) changes in elements of the fish larvae compared to more modest change in zooplankton, with phytoplankton somewhere between these two. Clearly fish larvae peak abundance hinges upon population growth rates exceeding mortality rates, and this depends upon suitable conditions being encountered, which in turn depends on the spawning choices of the adults. This unequal phenological change hasn't lead to particularly similar interannual trends in each group at the aggregate level, which leads to the conclusion that although phytoplankton have varied considerably, the higher trophic levels have been sufficiently redundant to absorb this change (Figure 6.5).

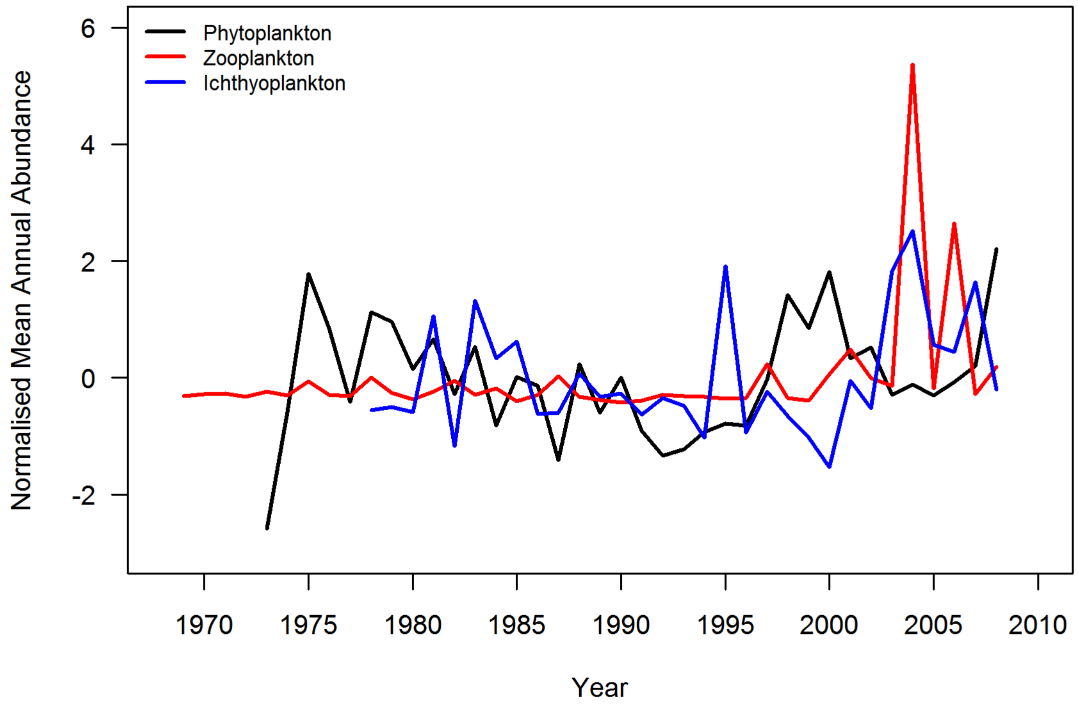


Figure 6.5: Each time series, normalised to mean 0, variance 1.

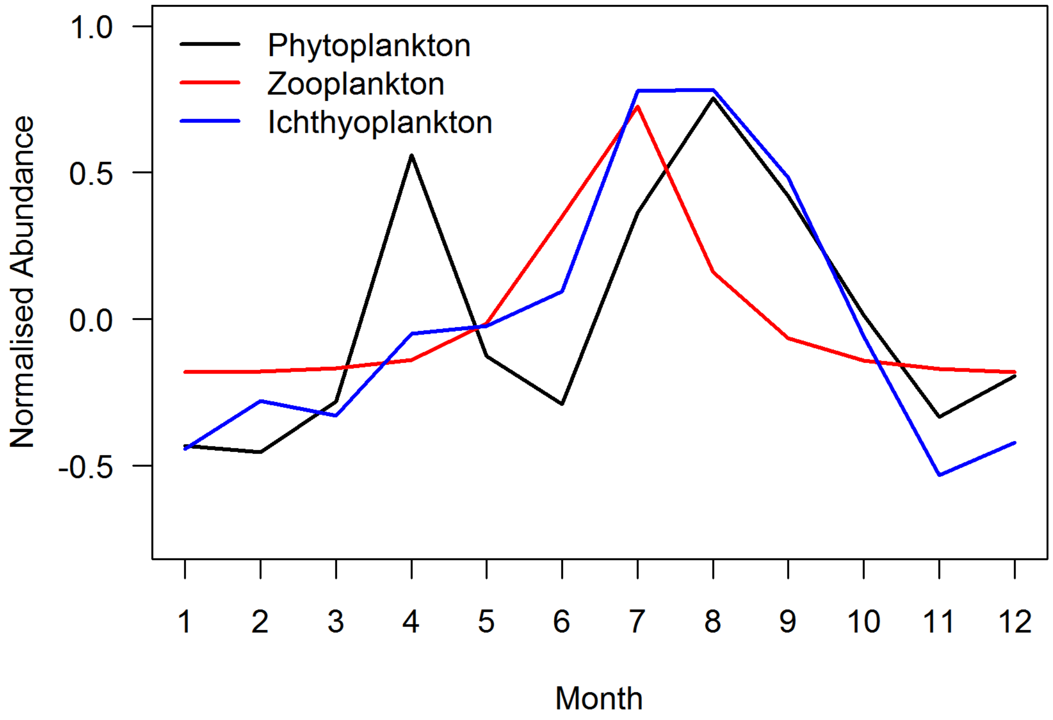


Figure 6.6: Long term month averaged normalised abundance of each trophic level studied in the DTS. Normalisations done within groups so are not indicative of relative abundance.

Both *et al* (2009) suggest that given the life history of members of a foodweb, it may actually be the case that a differential response by different trophic levels would signify a more stable ecosystem than would a foodweb with congruent responses to climate perturbation. This quality of an ecosystem was described as weak interactions by McCann (2000). Weak interactions limit energy flow and introduce negative covariance which is a feature of a resilient ecosystem (McCann, 2000). Fish predation on zooplankton even below a controlling level can stimulate phytoplankton growth under grazing pressure by increasing phosphorous recycling through consumption and excretion of zooplankton and by accelerating zooplankton metabolism by causing more escape behaviour (Vanni and Findlay, 1990). Hydrodynamic discontinuities can separate prey from predator or the opposite, resulting in effective top-down control being released or focused (Gissel and Munk, 1998). These are mechanisms by which the strength of interactions between lower trophic levels can weaken. The differential ability to adapt to a damaging change in conditions can have complex effects, such as proliferation due to release of a further negative pressure like grazing (Bothwell *et al*, 1994; Wiackowski *et al*, 1994). Global warming may favour larger phytoplankton and microzooplankton, and heavier microzooplankton grazing upon microflagellates and bacteria (Rae and Vincent, 1998) and therefore a changed prey community for zooplankton that would necessitate successful grazing on either larger forms or ciliated protists. This may favour altered copepod taxonomic composition. *Acartia clausi* and *Calanus helgolandicus* in the English channel graze up to 21% of ciliate standing stock daily (Fileman *et al*, 2010). *A. clausi* prey switches to ciliates facultatively during diatom blooms (Tiselius, 1989). As noted above, these forms are present in the DTS and could be examined in detail at the 63µm scale for long term change in microzooplankton abundance coincident with the anomalously high peaks in abundance of this copepod observed in recent years.

Zooplankton, as intermediate links in a food web can be co-limited by both food and predation (wasp-waist control – Fauchald *et al*, 2011) which becomes more likely as phytoplankton diversity increases, and the likelihood of top down grazing control decreases (Steiner, 2001). Changes in peak abundance of zooplankton can sustain top down control, or misalign prey and zooplankton peaks to allow bloom formation (Roelke, 2000). Decreased top down control by zooplankton on phytoplankton can also allow the diversification of species edible by zooplankton at the expense of large inedible species (McCauley and Briand, 1979). Top predators couple distinct energy channels by taking energy from lower trophic levels of a wide range of taxa (Rooney *et al*, 2006), so the more diverse a community becomes, the more able it is to support complexity. The DTS after 1995 had increased phytoplankton species richness, decreased zooplankton diversity, and increasing ichthyoplankton diversity (Figure 6.7). It might well be the case that the decreased diversity of zooplankton in the 2000s represents a weakened ability to support complexity, though this is contingent on the DTS being representative of the coastal region (Clark *et al*, 2001).

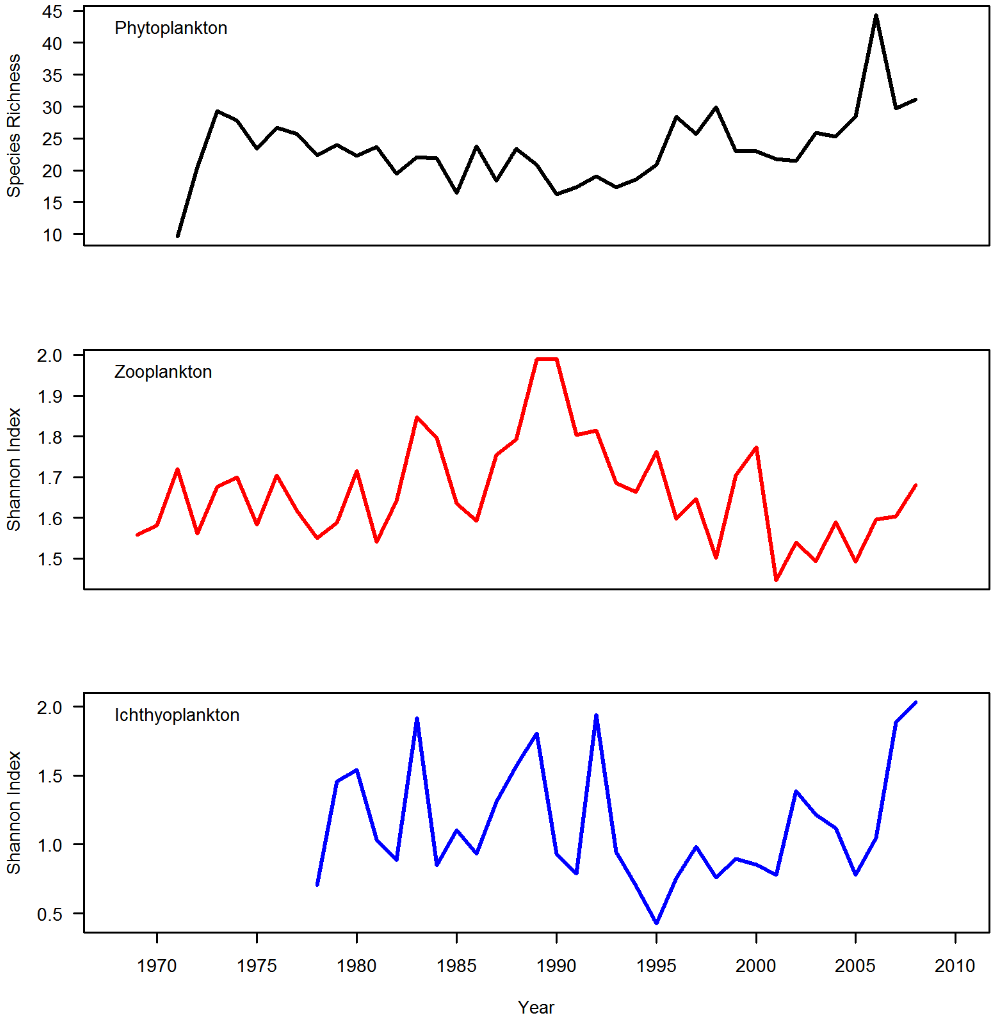


Figure 6.7: Species richness (phytoplankton) and Shannon index (zooplankton and ichthyoplankton).

6.6 Concluding remarks

Analysing three trophic levels of a 40 year time series has been a daunting, at times overwhelming. It has been the cause of much reflection and several painful overhauls of the analyses. This work has been produced with a constant reminder that the conclusions being drawn from the DTS and the chosen explanatory variables is a partial explanation of the variability and trends observed at all levels. Nonetheless: it is apparent that the phytoplankton and zooplankton at the DTS have responded to changed stratification, which has occurred as a result of long term variation in the Atlantic Multidecadal Oscillation. The modern period after 1995 sustained higher abundance of phytoplankton and zooplankton than was the case previously. The null hypothesis was rejected. The AMO cycles at a variety of periods, so there is no justification in considering this change as supportive of a wider north sea regime shift, as it is an inevitability that as the AMO cycle progresses, these conditions will diverge due to the complex manner in which NAO and AMO covary. The next step for the DTS is to begin hydrodynamic modelling of the plankton to describe the effects of local coastal oceanography than has been possible with the approach taken in this thesis. It is sincerely hoped that the efforts made in the preceding chapters go some way towards finding signals in the noise that will be a useful resource for other investigators.

7. Appendix

7.1 Phytoplankton Species List in Full and Monthly Observation Frequency

Taxon	**Month**											
Diatoms	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Class Mediophyceae												
Order Biddulphiales												
Genus Biddulphia												
Biddulphia alternans		░	░	░						░	░	
Genus Isthmia												
Isthmia spp.			░									
Genus Odontella												
Odontella aurita	░	░	░	▒						░	░	░
O. granulata		░	░									░
O. mobiliensis or *regia*	█	█	█	█	▒	▒	░	░	▒	█	█	█
O. sinensis	░	░	▒	▓					▒	▒	▓	▒
Order Chaetocerotales												
Genus Bacteriastrum												
Bacteriastrum delicatulum										░		░
B. hyalinum		░								░		
Genus Chaetoceros												
Chaetoceros spp.	░	░	░	▓	░	▒	▒	▒	▒	▒	░	░
C. aequatorialis				░								
C. affinis	░	░	▒	▓	░	░	▓	▓	▓	▓	░	▒
C. anastomosans	░		░	░		░		░		░		
C. compressus	░		░	░			░	░	░	░	░	
C. concavicorne	░	░	▒	▓	░	░	░	░	░	░	░	░
C. constrictus		░	░	▓	░	░	░	░	░	░	░	░
C. convolutus	░	░	░	▓	░	░	▒	░	▒	░	░	░
C. crucifer				░	░	░						
C. danicus	░	▒	░	▒				░	░	░	░	░
C. debilis	░	░	▒	▓	▒	░	░	░	░	░	░	░
C. decipiens	▓	▓	▒	▓	░	░	▒	▓	▒	▓	▒	▒
C. diadema		░	░	▒	░	░	░	░	░			░
C. didymus or	░	░	░	▓	░	░	▒	▒	░	▒	░	▒

protuberans	░	░	░	▓	░	░	▒	▒	░	▒	░	▒
C. eibenii			░	░			░	░	░	░	░	░
C. laciniosus	░	░		░	░	░	░	░	░	░		░
C. lorenzianus	░	░	░	▒	░	░	░	▒	▒	░	░	░
C. radicans			░	▒	░	░	░			░		░
C. similis	░	░	░	░	░			░				
C. subtilis				░		░		░				
C. tenuissimus			░	░		░	░	░			░	
C. teres		░	░	▒	░	░	░	░	░	░	░	░
Order Hemiaulales												
Genus Bellerochea												
Bellerochea horologicalis	░	░	░	░			░		░	░	▒	▒
Genus Cerataulina												
Cerataulina pelagica			░		░	░	░	▒	░	░		
Genus Eucampia												
Eucampia zodiacus				░	░	░	░	▒	▒	░	░	
Genus Hemiaulus												
Hemiaulas hauckii				░								
Order Triceratiales												
Genus Auliscus												
Auliscus sculptus			░									
Order Lithodesmiales												
Genus Ditylum												
Ditylum brightwellii	▒	▒	▓	▓	░	░	░	░	░	▒	▒	▒
Order Thalassiosirales												
Genus Detonula												
Detonula pumila										░		
Genus Lauderia												
Lauderia annulata						░			░			
Genus Planktoniella												
Planktoniella sol											░	
Genus Skeletonema												
Skeletonema spp.	░	▒	▓	▓	░	░	░	░	░	░	░	░
Genus Thalassiosira												
Thalassiosira spp.	▒	▒	▓	▓	▒	▒	▒	▓	▒	▒	░	░
T. aestivalis or *nordenskioeldii*		░	░	▒	░	░			░			

T. anguste-lineata				▒	░	░	░	░		░		
T. leptopus		░	░	░	░	░						░
T. punctigera		░	░	▒		░					░	░
T. rotula or *gravida*			░	▒	░	░	░					
Mediophyceae incertae sedis												
Mediopyxis helysia	▒	░	▒	▒	░	░	░			░	▒	░
Class Bacillariophyceae												
Order Fragilariales												
Genus Asterionellopsis												
Asterionellopsis glacialis	░	▒	░	▓	░			░	░	░	░	░
Genus Ceratoneis or Nitzschia												
Ceratoneis closterium or *Nitzschia longissima*	░	░	░	▒	░	░	░	░	░	░	░	░
Order Naviculales												
Genus Navicula												
Navicula spp.	░	░	▒	▓	░		░	░	░	▒	░	░
Genus Pleurosigma or Gyrosigma												
Pleuro/Gyrosigma spp.	▓	▓	█	█	▓	▓	▓	▓	▓	▓	█	█
Order Bacillariales												
Genus Bacillaria												
Bacillaria paxillifer	░	▒	▒	▒	░	░		░		░	░	░
Genus Fragilariopsis												
Fragilariopsis spp.	░	░	▒	▒	░			░	░	░	░	▒
Genus Nitzschia												
Nitzschia spp.	░		░	▒	░				░		░	░
Genus Pseudo-nitzschia												
Pseudo-nitzchia spp.	░	░	░	░	░		░			░	░	░
Pseudo-nitzschia “seriata” complex	░	▒	▒	█	▒	▓	▓	█	█	█	▓	▒
Pseudo-nitzschia “delicatissima” complex		░	░	▒	░	░		░	░	░	░	░
Order Rhaphoneidales												
Genus Rhaphoneis												
Rhaphoneis amphiceros										░		
Order Surirellales												
Genus Entomoneis												

Entomoneis alata		░	░	░			░			░		
Genus Surirella												
Surirella spp.		░								░	░	
Order Thalassionematales												
Genus Thalassiosira												
Thalassionema spp.	░				░				░			
T. nitzschioides	▒	▒	▒	▓	░	░	░	░	░	▒	░	░
Order Striatellales												
Genus Grammatophora												
Grammatophora spp.					░	░						
Class Coscinodiscophyceae												
Order Coscinodiscales												
Genus Azpeitia												
Azpeitia spp.			░									
Genus Actinoptychus												
Actinoptychus senarius	▓	▓	▓	▒	░	░	░	░	░	▒	▓	▓
Genus Coscinodiscus												
Coscinodiscus spp.	░	░	░	▒	░	░	░	░	░	░	░	░
C. concinnus	▓	▓	█	█	▓	▒	▒	▒	▒	▓	▓	▓
C. centralis	░	░	░	▒	░		░			░	░	░
C. curvatulus			░							░	░	░
Coscinodiscus cf *eccentricus*	▓	▓	▓	▓	░	░	░	░	░	▓	▓	▓
C. granii	░					░				░	░	░
C. marginatus	░							░				
C. radiatus	█	█	█	█	▓	▓	▓	▓	█	█	█	█
C. wailesii		░										
Order Corethrales												
Genus Corethron												
Corethron criophilum			░	░		░		░		░		░
Order Rhizosoleniales												
Genus Dactyliosolen												
Dactyliosolen fragilissimus				░	░		░	░			░	
D. blavyanus					░	░	░	░		░	░	░
Genus Guinardia												
Guinardia delicatula				░	░	░	░	░	░			
G. flaccida	░	░	░			░	░	▓	▓	▒	░	░

G. striata				░	░	░	░	▒	░	░		
Genus Rhizosolenia												
Rhizosolenia borealis	░	▒	▒	▓	░	░	░	░	▒	▓	▒	▒
R. hebetata f hebetata	░	░	░	░					░		░	░
R. imbricata	░	░	░	▒	░	░	▓	▓	▓	▒	░	░
R. setigera	░	░	▒	▒	░	░	░	▒	▒	▒	░	░
R. styliformis	▓	▒	▒	▓	▓	▓	▓	▓	▓	▒	▒	▒
Genus Proboscia												
Proboscia alata	▒	▒	▒	▓	▒	▒	▒	▓	▓	▒	░	▒
P. indica									▒			
Genus Neocalyptrella												
Neocalyptrella robusta		░					░			░		░
Order Leptocylindrales												
Genus Leptocylindrus												
Leptocylindrus danicus			░	░	░	░	░	▒	░			░
L. minimus		░	▒	▒	░			░	░			░
Order Melosirales												
Genus Melosira												
Podosira stelligera	▒	▒	▒	▒			░	░	░	░	▒	▒
Genus Stephanopyxis												
Stephanopyxis turris	░			░		░	▒	▒	▒	▒	░	░
Order Parariales												
Genus Paralia												
Paralia sulcata	▓	▓	█	▓	▒	▒	▒	▓	▓	█	█	█
Other Diatoms												
Indeterminate diatoms	▒	▒	▓	▓	▓	▒	▒	▓	▓	▓	▓	▒
Dinoflagellates												
Class Dinophyceae												
Order Gonyaulacales												
Genus Alexandrium												
Alexandrium spp.				░		░	░					
Genus Ceratium												
Ceratium spp.								░	░	░	░	
C. arietinum				░			░	░		░	░	
C. furca	▓	▓	▓	▓	▓	▓	▓	█	█	▓	▓	▓
C. fusus	▓	▒	▒	▒	▓	▓	▓	▓	▓	▓	▒	▒

C. horridum

C. lineatum

C. longipes (rough form)

C. longipes (smooth form)

C. macroceros

C. symmetricum

C. tripos

Genus Gonyaulax

Gonyaulax spinifera

G. verior

Order Actiniscales

Genus Actiniscus

Actiniscus pentasterias

Order Dinophysiales

Genus Dinophysis

Dinophyis acuminata

D. acuta

D. fortii

D. norvegica

D. odiosa or hastata

Genus Phalacroma

Phalacroma rotundata

Order Pyrocystales

Genus Pyrocystis

Pyrocystis or *Dissodinium* spp.

Order Noctilucales

Genus Kofoidinium

Kofoidinium velleloides

Order Gymnodiniales

Genus Polykrikos

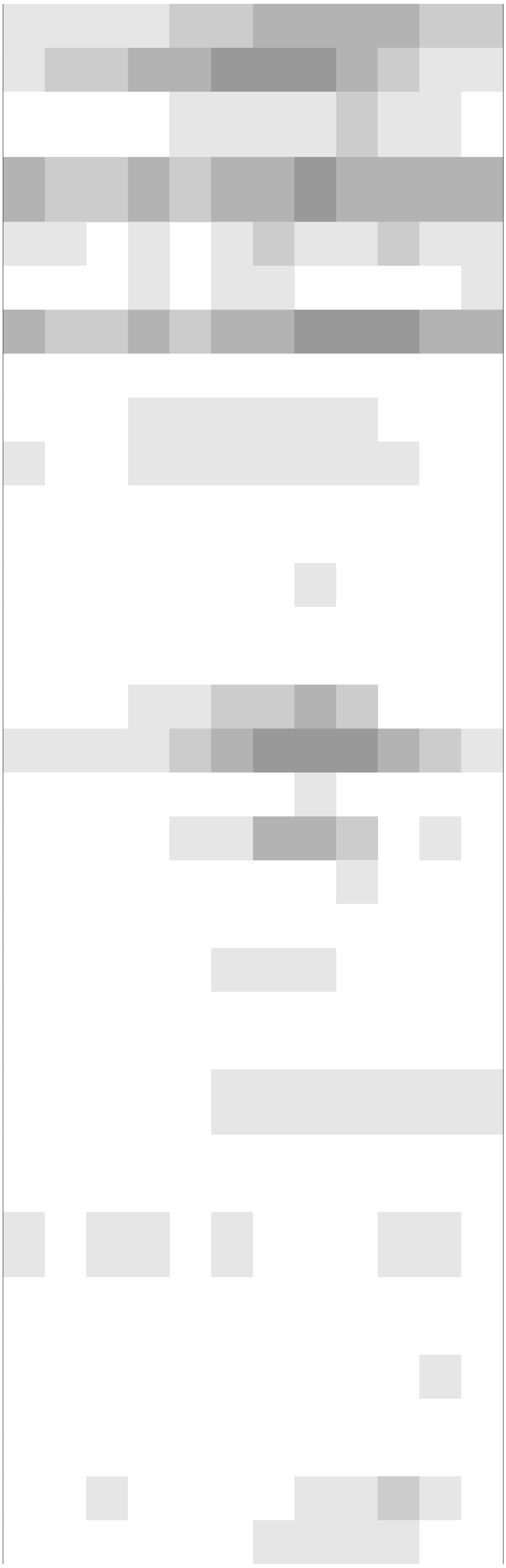
Polykrikos spp.

Order Prorocentrales

Genus Prorocentrum

Prorocentrum spp.

P. micans



Order Peridiniales												
Genus Protoperidinium												
Protoperidinium spp.	▓	▒	░	▓	█	█	▓	█	█	▓	▓	▓
P. brevipes	░			░		░	░					
P. conicum or *conicoides*	░	░	░	▓	▓	▒	▒	░	▒	░	░	░
P. curtipes or *crassipes*	░	░	░	▒	░	░	▒	▒	▒	▒	░	░
P. depressum	▓	▒	▒	▓	█	█	█	█	█	▓	█	▓
P. divergens	░			░	░	░	░	░	░	░		░
P. excentricum				░	░	░	░	░	░			
P. oblongum or *claudicans*		░	░	░	░	▒	░	░	░	░	░	
P. obtusum or *leonis*	░	░	░	░	░	▒	░	▒	▒	░	░	░
P. ovatum			░	▒	▓	▓	▒	░	░	░	░	░
P. pallidum or *pellucidum*	░		░	░	▓	▓	░	▓	▓	▒	░	░
P. pentagonum	░	░	░	▒	▒	▒	░	▒	▒	▒	░	░
P. steinii	░			░	░	░	░	░		░		
P. subinerme	░			░	░	░	░	░	░			
Other Dinoflagellates												
Dinoflagellate Cysts	■	█	█	■	▓	█	▓	▓	▓	█	■	■
Indeterminate dinoflagellates	░			░		░		░				
Other Groups												
Class Dictyophyceae												
Order Dictyochales												
Genus Dictyocha												
Dictyocha fibula	░	░	░	▒		░	░	▒	▒	▒	░	▒
D. speculum	▒	▒	▒	▓	░	░	▒	▒	▓	▒	░	░
Class Ebriophyceae												
Order Ebriales												
Genus Ebria												
Ebria tripartita								░				
Class Chlorophyceae												
Order Sphaeropleales												
Genus Pediastrum												
Pediastrum spp.			░								░	░
Phylum Cyanobacteria												
Spirulina spp.	░	░	░	░						░	░	
Phylum haptophycophyta												

Indeterminate Coccolithophores	░

Table A7.1: The diversity of the Dove Time Series phytoplankton sampled using the fine mesh net. Key: Light Grey: 0-5 observations, Mid Grey: 6-10 observations, Mid-Dark Grey:11-20 observations, Dark Grey: 21-30 observations, Very Dark Grey: >30 observations.

7.2 Time Series of Oceanographic and Meteorological Predictors Used in Analysis

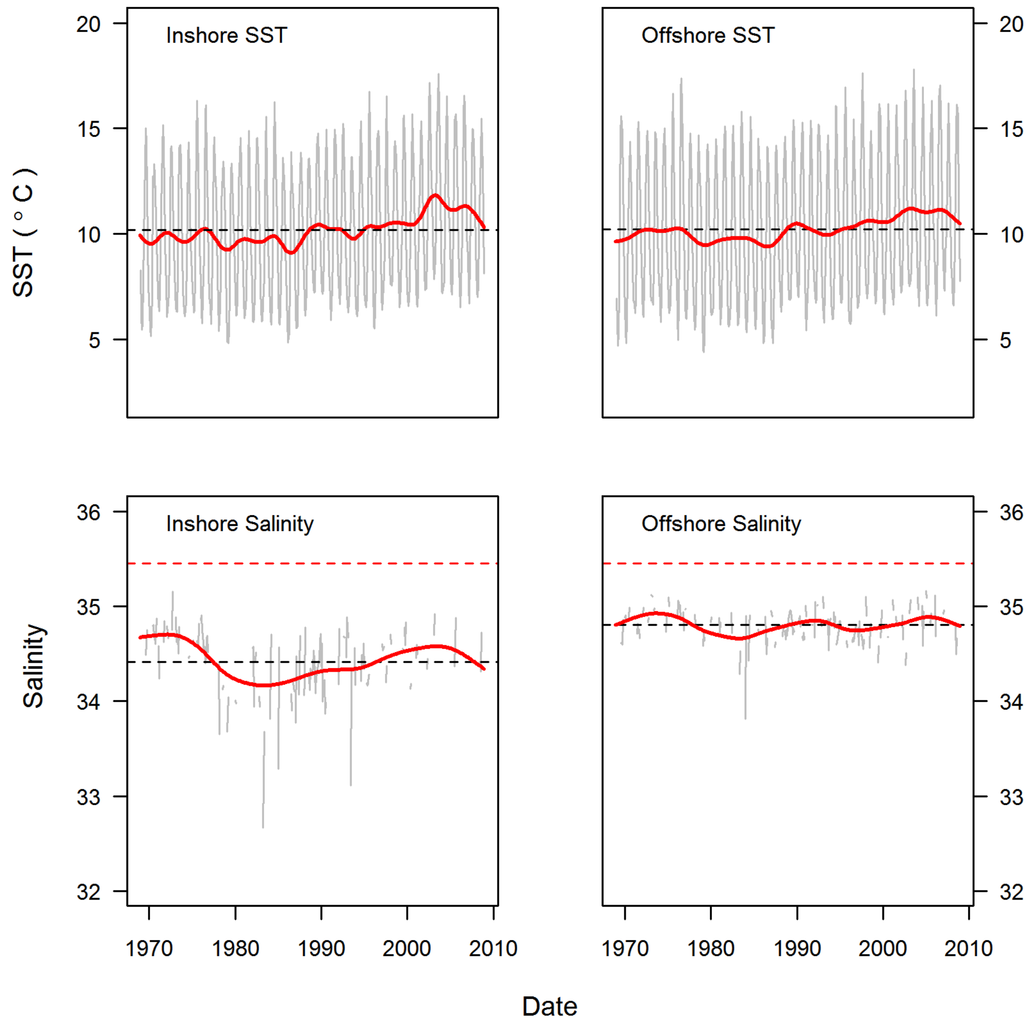


Figure A7.1: Time series of sea surface temperature (SST) and salinity, from inshore and offshore boxes. Inshore = 55 to 56N, -2 to -1E, Offshore = 55 to 56N, 0 to 1 E. Dashed black line is long term mean. Dashed red line in salinity plots is 35.45 salinity line. Thick red line is long term trend. Data from ICES.

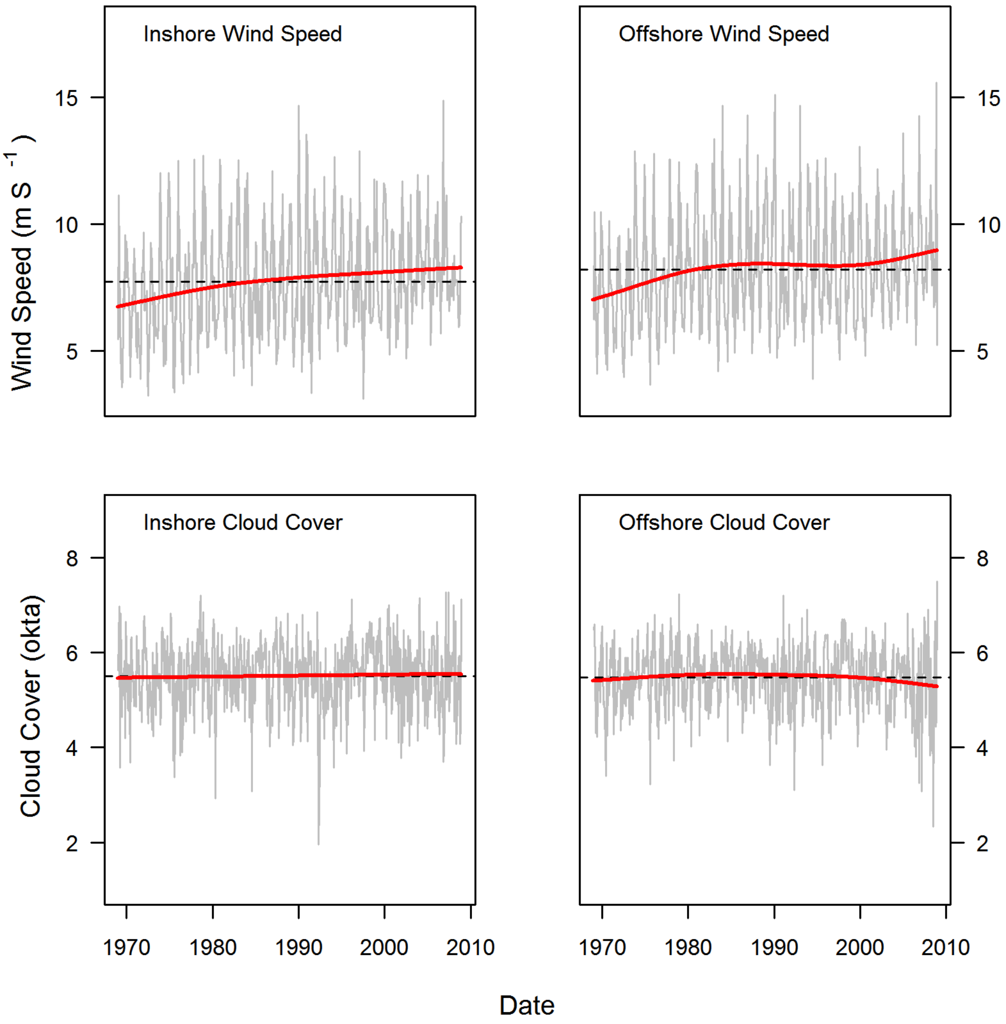


Figure A7.2: Time series of wind speed and cloud cover from inshore and offshore boxes. Inshore = 55 to 56N, -2 to -1E, Offshore = 55 to 56N, 0 to 1 E. Dashed black line is long term mean. Thick red line is long term trend. Data from NOAA.

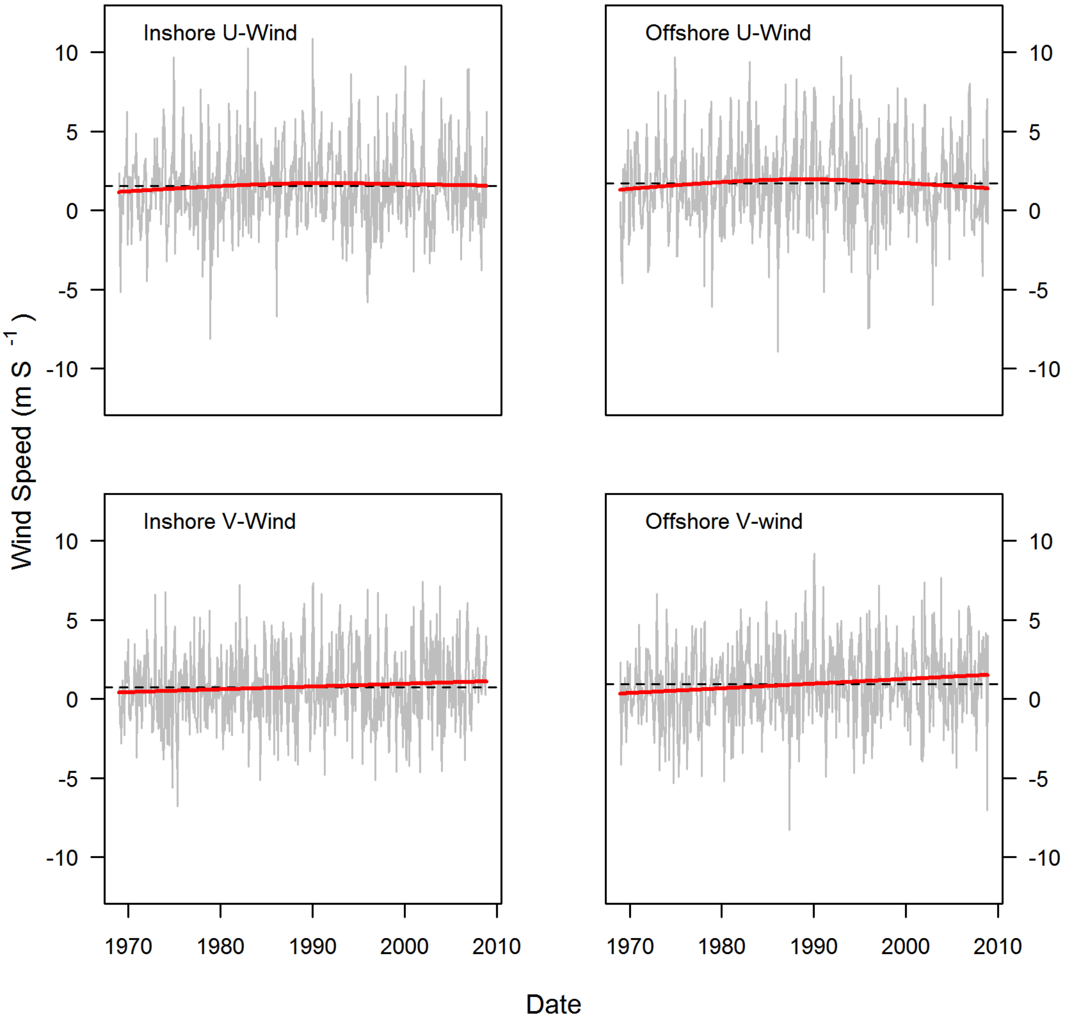


Figure A7.3: Time series of U (east-west) and V (north-south) components of wind speed from inshore and offshore boxes. Inshore = 55 to 56N, -2 to -1E, Offshore = 55 to 56N, 0 to 1 E. Dashed black line is long term mean. Thick red line is long term trend. Data from NOAA.

7.3 List of Acronyms

1. AIC – Akaike Information Criterion
2. AMO – Atlantic Multidecadal Oscillation
3. AMOC – Atlantic Meridional Overturning Circulation
4. ARIMA - Autoregressive Integrated Moving Average
5. AWI – Alfred Wegener Institute
6. BIC – Bayesian Information Criterion
7. CA – Correspondence Analysis
8. CCA – Constrained/Canonical Correspondence Analysis
9. CPR – Continuous Plankton Recorder
10. DLM – Dynamic Linear Model
11. DOM – Dissolved Organic Matter

12. DTS – Dove Time Series
13. EGC - East Greenland Current
14. EIC – East Iceland Current
15. ERSEM - European Regional Seas Ecosystem Model
16. FlowCAM – Flow Cytometer and Microscope
17. FFBS – Forwards Filtering Backwards Scattering
18. FSC – Faroe-Shetland Channel
19. FSSIE – Fram Strait Sea Ice Export
20. GAM – Generalised Additive Model
21. GLM – Generalised Linear Model
22. GSA – Great Salinity Anomaly
23. GSNW – Gulf Stream North Wall
24. ICES – International Council for the Exploration of the Seasonally
25. IHLS – International Herring Larvae Survey
26. NAC – North Atlantic Current
27. NAO – North Atlantic Oscillation
28. NOAA – National Oceanic and Atmospheric Administration
29. NSIDC – National Snow and Ice Data Centre
30. OSPAR – Oslo Paris Commission
31. PCA – Principal Component Analysis
32. PCI – Phytoplankton Colour Index
33. RSS – Residual Sum of Squares
34. SAHFOS – Sir Alister Hardy Foundation for Ocean Science
35. SPG – Sub-polar Gyre
36. SSM – State Space Model
37. SST – Sea Surface Temperature

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