The Plankton Ecology of SEA7

(Non-Technical Summary)

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The purpose of this report is to provide the DTI with an assessment of the plankton ecology for the Strategic Environment Assessment (SEA) of area 7. The boundaries of SEA 7 extend between approximately 54ºN - 60ºN and 5ºW - 24ºW and represents the single largest region of all the SEA areas. Owing to the size of the area being assessed this report divides the region into two sections (Figure 1). The basis of this division follows the 200m depth contour generally accepted as being the boundary between the shelf edge and oceanic realms. The first section being waters found on the continental shelf and are therefore more prone to freshwater runoff from land and anthropogenic inputs. The second section represents waters off the shelf edge, these waters are of a more oceanic origin and are less impacted by inputs from land-based sources.
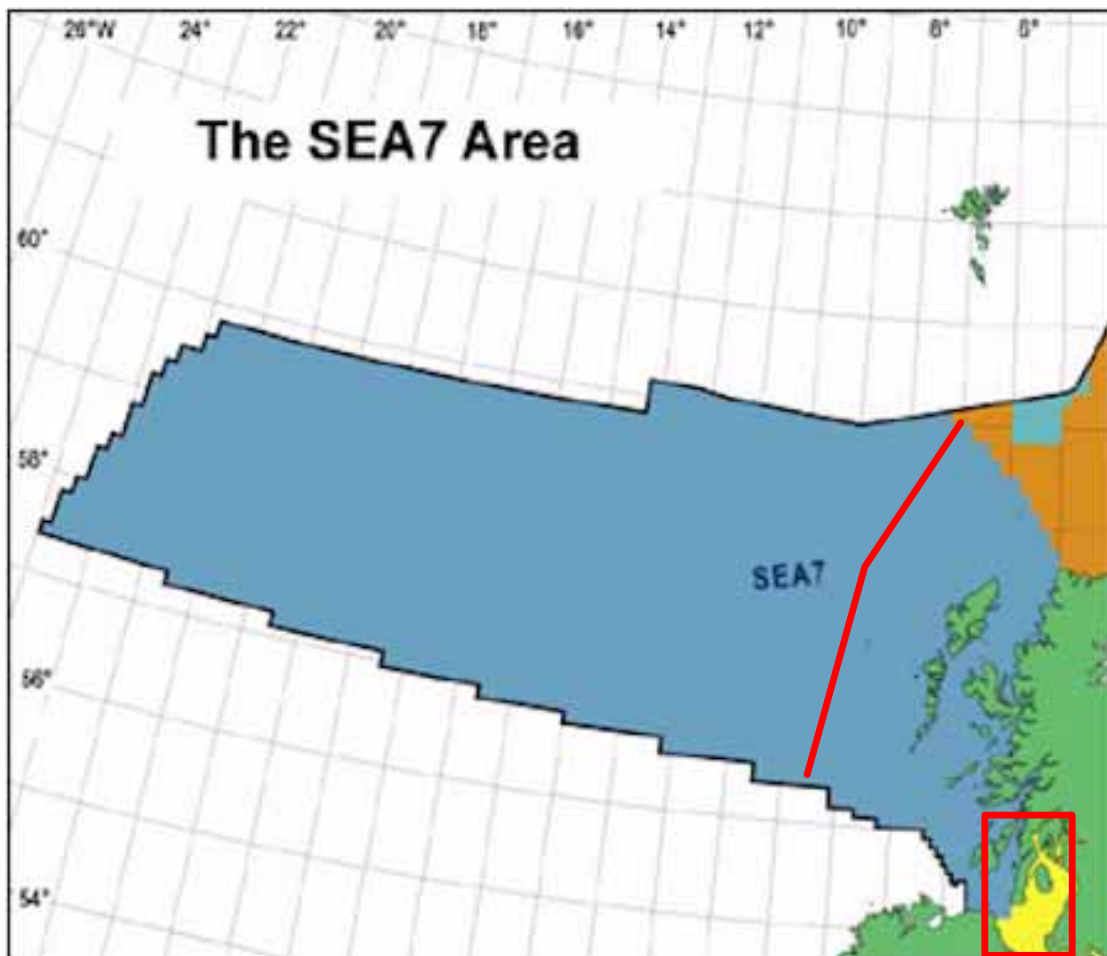

Figure 1. The SEA 7 area showing division used in this report (red-line) to represent waters on the shelf edge and those of more oceanic origins. The red-box represents the Clyde Sea area used in the nutrient-salt analysis.

Information on the nutrient biogeochemistry (nitrate, phosphate and silicate) are presented for three geographical provinces, the oceanic and shelf edge realms outlined above and also for the Clyde Sea area this being a region noted as having elevated nutrient loadings from anthropogenic sources. The major sources of information on the nutrients of the SEA7 region come from the ICES and BODC data sets as well as from data presented in the scientific literature.

Information on the phytoplankton (the plant members of the plankton) comes from several sources including ICES, SAMS and the NIO at Southampton. This data is augmented by specific case-studies of the SEA7 region taken from the scientific press. Zooplankton (the animal component of the plankton) data is also presented as geographic plots from the Continuous Plankton Recorder (SAHFOS) data-set held by the Sir Alistair Hardy Foundation for Ocean Sciences.

The results presented describe the regional differences in the above variables within the SEA 7 region. It is noted that highest contributions of nutrient salts in coastal waters originate from the Clyde Sea/Irish Sea regions and that these concentrations decrease northwards reflecting the reduced agricultural and anthropogenic loadings to these more northern coastal areas. Offshore nutrient concentrations are also relatively high in this region as a result of deep-water winter mixing processes operating in the north east Atlantic.

Phytoplankton biomass generally follows the same pattern of distribution as the nutrient salts. Highest coastal chlorophyll concentrations are found in the Clyde Sea region and decrease northwards. Offshore chlorophyll concentrations reflect the movements of different water-masses with highest concentrations located around oceanic fronts.

The zooplankton data-set describes the major constituents of the zooplankton community in coastal and offshore regions as given by the CPR data. Variations in the zooplankton community composition for these regions is noted, as is the differences in seasonality of the different taxa described.

The impacts of mechanisms such as ballast water transport and climate change upon the biogeochemistry and plankton ecology for the SEA 7 region is also alluded to.

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1   INTRODUCTION TO THE STUDY AREA

The purpose of this report is to provide the DTI with an assessment of the plankton ecology for the Strategic Environment Assessment (SEA) of area 7. The boundaries of SEA 7 extend between approximately 54ºN - 60ºN and 5ºW - 24ºW and represents the single largest region of all the SEA areas. Owing to the size of the area being assessed this report divides the region into two sections (Figure 1). The basis of this division follows the 200m depth contour generally accepted as being the boundary between the shelf edge and oceanic realms. The first section being waters found on the continental shelf and are therefore more prone to freshwater runoff from land and anthropogenic inputs. The second section represents waters off the shelf edge, these waters are of a more oceanic origin and are less impacted by inputs from land-based sources.
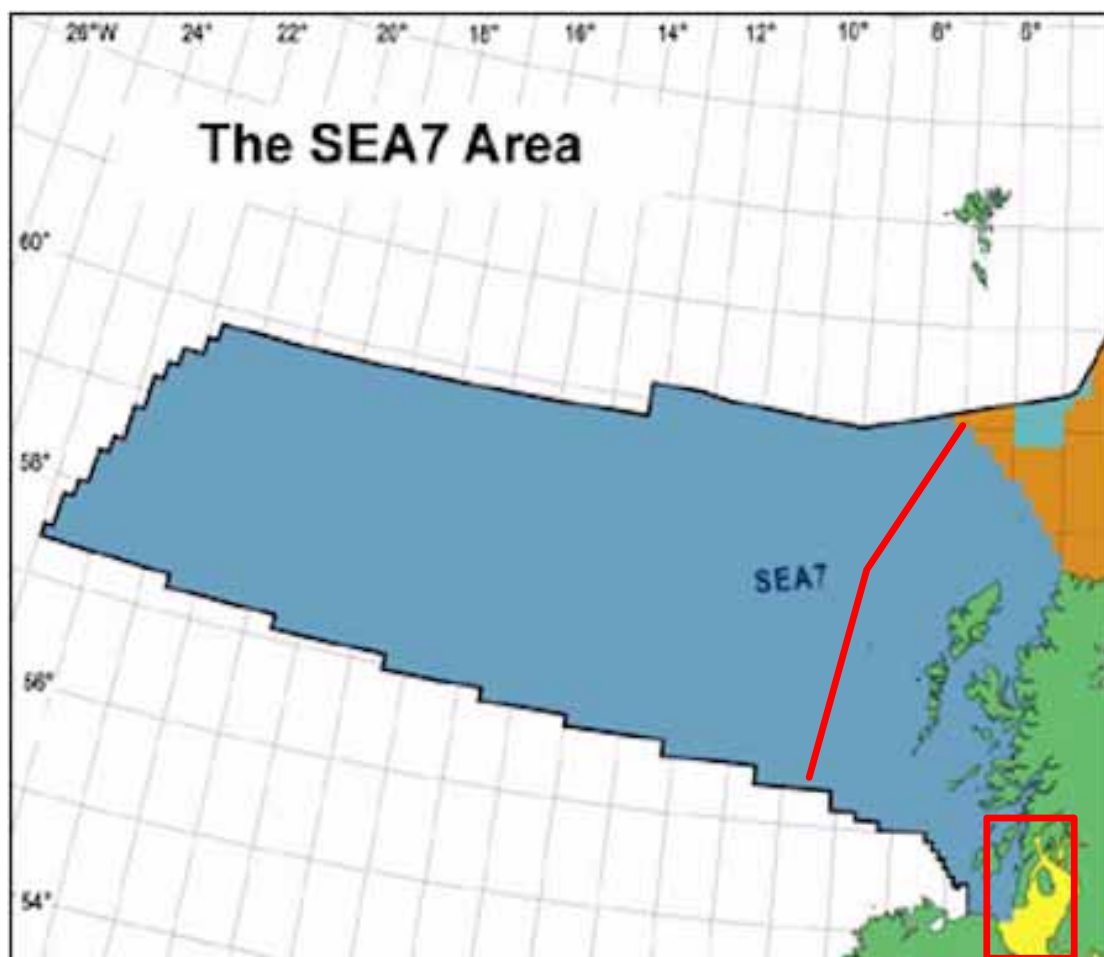

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1.1 Biological Background

The term plankton is taken from the Greek verb meaning "to wander" and refers to organisms whose powers of movement are insufficient to prevent them from being moved by water currents.

The plankton can be simply divided into two major components; the plant plankton and the animal plankton, referred to as the phytoplankton and zooplankton respectively.

The phytoplankton is of great importance as these are the primary producers of the oceans and thus provide the principal source of primary nutrition for organisms such as the zooplankton. As primary producers the phytoplankton require light to perform photosynthesis. However, due to an exponential reduction in light intensity with depth in seawater, phytoplankton abundance is greatest in the upper waters, a region referred to as the photic zone.

The phytoplankton itself can be further divided with three orders of algae predominating; the diatoms, the dinoflagellates and the smaller flagellates such as the coccolithophorids.

The diatoms are autotrophic (produce energy from photosynthesis) and generally range in size from 15 to 400μm. Diatoms are characterised by their siliceous cell or frustule. The diatom frustule is composed of two overlapping valves that fit together much like a pill-box or petri-dish.

The dinoflagellates are generally heterotrophic, so rely on preformed organic matter, though some are also capable of photosynthesis. They are of a similar size to the diatoms but have a larger portion of smaller forms. The dinoflagellates can be further sub-divided into naked and armoured forms. Both forms are capable of locomotion by means of two whip-like appendages called the flagella.

Smaller flagellates make up part of the nanoplankton (organisms 2-20μm in diameter) and picoplankton (organisms 0.2-2μm in diameter), along with bacteria, fungi and a number of the smallest diatoms and dinoflagellates. Although they are small is size they are thought to make a considerable contribution to primary production, and act as an important food source for many larvae (Tait, 1992; Mandali de Figueiredo, 2003).

The zooplankton is the "animal" constituent of the plankton and contains a wide variety of organisms. These organisms can be divided into holoplankton and the meroplankton. The holoplankton consists of permanent members of the plankton where all developmental stages are retained in the plankton. The meroplankton are temporary members of the plankton where only some developmental stages are within the plankton, such as the eggs or larvae of an organism.

By far the most abundant element of the zooplankton are the copepods, which are small holoplanktonic crustaceans ranging in size from 0.5mm to 6.0mm. These are generally herbivores feeding on phytoplankton and are themselves the main food

source for a great many organisms higher in the food chain such as larval and juvenile fish. The copepods can be divided into the calanoids, cyclopoids and harpacticoids by body shape, of which the calanoids are by far the most abundant.

Other crustaceans also form an important constituent of the zooplankton, the majority of which are the larval forms of large benthic crustaceans such as crabs, and are therefore in the meroplankton. Other such meroplanktonic animals include polychaete larvae and echinoderm larvae, as adult forms are also benthic. However, it is not only organisms that lead to a benthic lifestyle in the meroplankton, as fish eggs and larvae are also included (referred to as the ichthyoplankton), due to the fact that they are only part of the plankton during their pelagic egg and larval stages.

The gelatinous zooplankton, can also be important in the zooplankton and include, larvaceans, salps, doliolods, ctenophores and coelenterates. These organisms are generally carnivorous, feeding upon other zooplankton such as copepods and fish larvae. There importance is due to the fact that ctenophores and medusoid stages of cnidarians (coelenterates) can exhibit rapid growth to form large swarms which can lead to a significant predatory effect on copepods and fish larvae (Bunn *et al*., 2000).

All the plankton are linked together in a complex food web, a simplified version of which is shown in Figure 2. The importance of understanding this web is that any disruption to one element could have a causal effect, being detrimental to all other organisms.
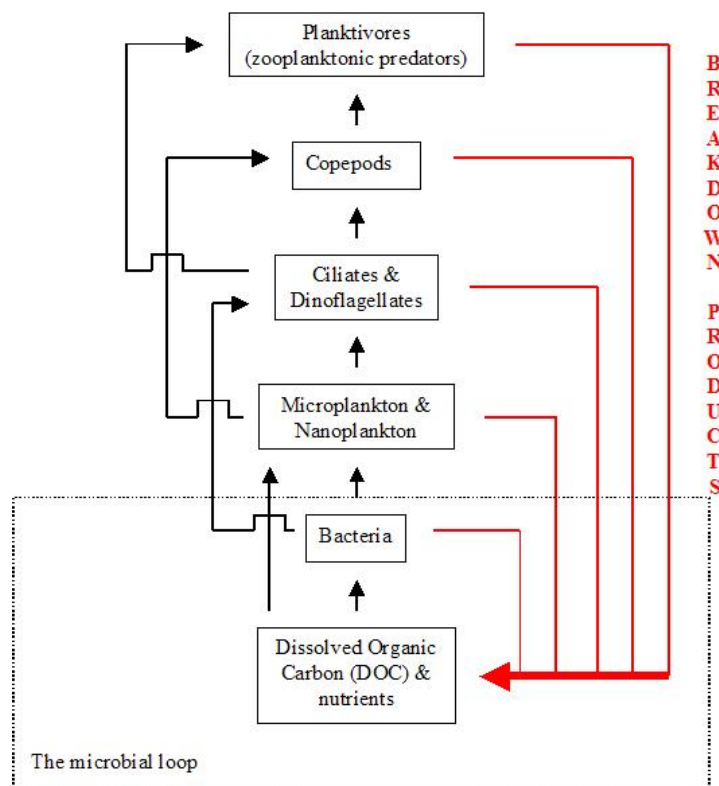

Figure 2. Simplified planktonic food web showing direction of consumption (black lines) and recycling of waste material (red lines), where breakdown products from phytoplanktonic groups also include the phytodetritus.

1.2 Physical processes affecting the plankton

The area covered by SEA7 extends from the highly indented west coast of Scotland with its many sea lochs and islands, over coastal and shelf seas, past the continental shelf break into the northern Rockall Trough, and as far west as the middle of the Iceland Basin (see Figure 3). The area therefore covers many oceanographic provinces with coastal waters receiving a moderate input of freshwater from land. The coastal region is also subject to strong seasonal forcing, by surface heating and cooling and by strong westerly winds, which prevail for much of the year. Freshwater buoyancy input has a modest influence, and its effects are limited to the sea lochs and waters influenced by the Scottish coastal current.
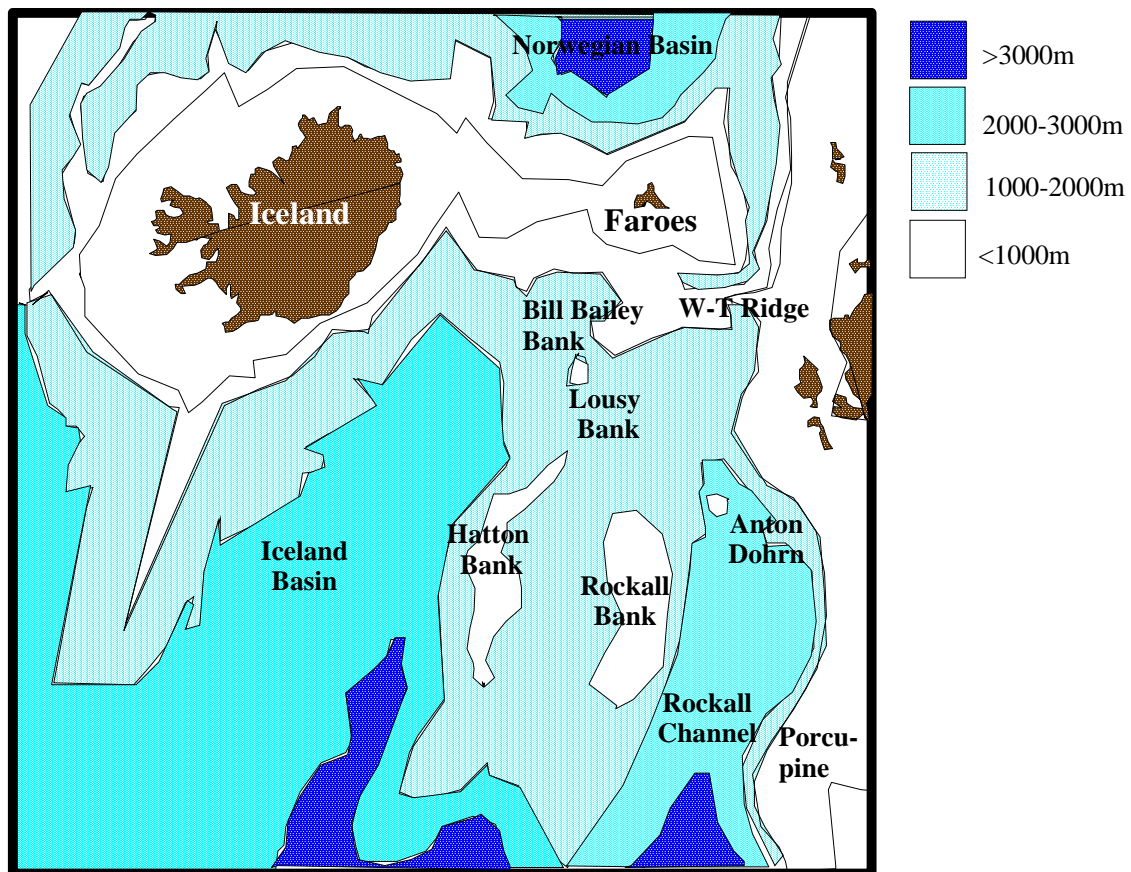

Figure 3. Bathymetry of the SEA 7 region showing key features mentioned in the text (redrawn from Hansen (2000)).

Away from the shelf area, the oceanic region is dominated by the northward flowing shelf edge current that brings saline and warm water to the north-west European shelf. The Rockall Channel is a closed basin below 1200m, but above that there is a broad northward flow of warm saline water. Flow around the seamounts and the Rockall and Hatton Banks is generally anticyclonic, and the Iceland Basin (the main route of the North Atlantic Current) contains relatively cooler and fresher waters. The whole region is subject to deep winter mixing (~600m) that can bring deep nutrient-rich waters back to the surface following the previous summer phytoplankton production.

Offshore waters in the region can become stratified during the summer months with warm buoyant waters overlying denser cold waters. This essentially creates a physical barrier to the phytoplankton which rapidly utilize the available inorganic nutrients and decline in abundance. When waters off the shelf-break meet with the tidally mixed waters on the shelf a seasonal front can develop that can produce local upwelling events providing additional nutrients to surface waters thus enhancing local primary production in such areas. Similarly, when water masses with differing surface temperatures meet, fronts can develop again stimulating planktonic production.

1.3 Nutrient Salts.

In order for a phytoplankton population to be successful, certain micro-nutrients are required in high enough concentrations to support population growth. In the marine environment, nitrogen is generally considered to be the limiting micro-nutrient although phosphorus and silicon are also required in varying quantities by certain phytoplanktonic groups. The following section briefly outlines the seasonal and geographical distributions of dissolved available inorganic nitrate (DAIN), phosphorus (DAIP) and silicate in the SEA7 region.

For the purpose of this exercise two data-sets were employed for the seasonal analysis of nutrient salts in the SEA 7 region. The ICES nutrient data set was the most extensive, data from the BODC archive was also used for comparison. The region was split into three geographic provinces (Figure 4).

1) Waters to the east of 10˚W representing waters on the continental shelf.
2) Waters to the west of 10˚W representing waters of the open Atlantic away from the continental shelf.
3) The 'Clyde Sea box' representing waters discharging from the Northern Irish Sea and the Firth of Clyde.

The justification for creating a sub-set of the Clyde Sea area within the continental shelf waters was due to the differing origins and character of waters within this area. The Clyde Sea box receives waters exiting the Irish Sea via the North Channel as well as waters discharging from the Firth of Clyde that are preferentially enriched with nutrients from anthropogenic sources.

For the purpose of examining the nutrient data-sets only samples from the top 30m of the water column were used, these being waters having the greatest influence upon the phytoplankton within each of the three sub-regions.
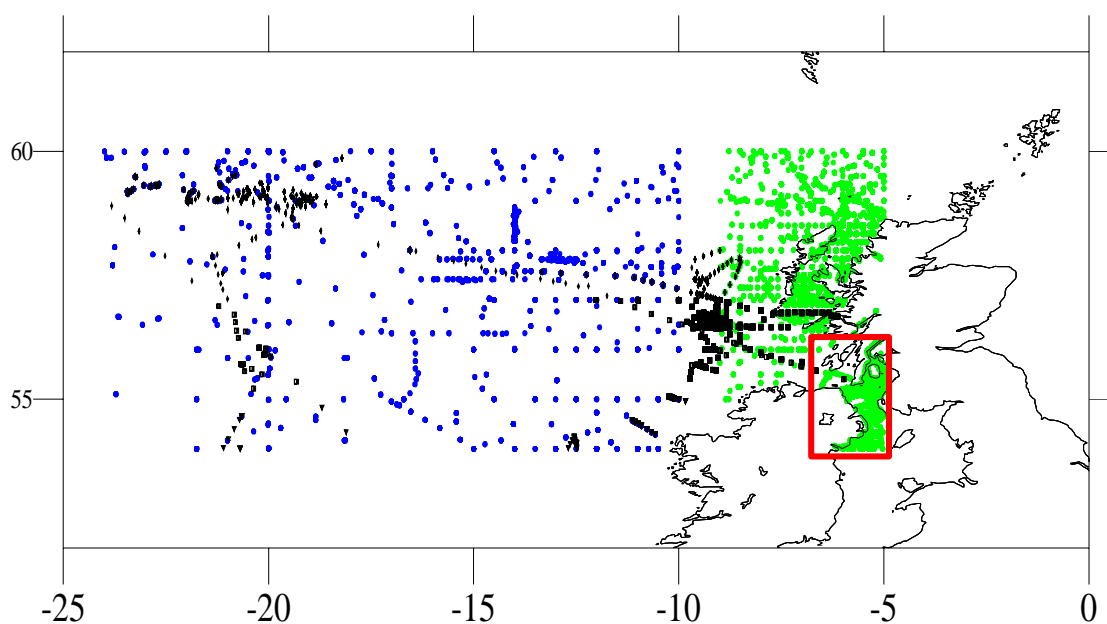
Figure 4. Sample locations of the ICES and BODC nutrient data-bases used in this study. Blue identifiers – ICES offshore stations, green identifiers – ICES on-shelf locations, black identifiers BODC stations.

2 NUTRIENT DYNAMICS IN SEA7

2.1 Nutrients on the Shelf

This section aims to review the processes governing the nutrient salt regimes in waters extending from the sea lochs of the western Scottish coastline out to approximately 10˚W. This region covers a broad geographical area with many different hydrographic provinces. As such this review looks primarily at the hydrographic and biogeochemical processes affecting the distribution of nutrients in two broad domains; the sea lochs and open coastal waters.

Sea lochs on the western Scottish coast are fjordic sytems with a net seaward flux of freshwater entering the loch via the head and a saline inflow at the mouth. Both the freshwater and saline inputs supply dissolved inorganic nutrients to the system. The distribution of these nutrients is governed by physical, chemical and biological processes operating both within the water column and the sediments.

The Clyde Sea box represents waters of the northern Irish Sea and the Firth of Clyde. These waters have been shown to be influenced by relatively high anthropogenic nutrient loads (Grantham & Tett, 1993; Jones *et al*., 1995; Allen *et al*., 1998; Gowen & Stewart 2005; Gowen *et al*., in prep.) and as such are discussed separately from other waters on the continental shelf. The Clyde Sea is the largest fjordic system on the Scottish west coast (Edwards *et al.,* 1986). Nutrients from agricultural land and the densely populated and industrialised Glasgow conurbations enter via the rivers, through sewage outflows and via direct industrial discharges. Such nutrient inputs

have been shown to cause localised enhancement of chlorophyll standing crop in the area (Jones *et al.*, 1995). Grantham & Tett (1993) examined the relationship between nutrients and salinity in the Clyde Sea and showed that the saline end member concentration of nitrate was of the order of 6.8µM, whilst the freshwater end member concentration reached 100µM. Grantham & Tett (1993) also reported high N:Si ratios indicating possible enrichment of DAIN by sewage.

Water exchange between the Irish Sea North Channel and the Clyde Sea is restricted by a shallow sill. Rippeth & Jones (1996) demonstrated how during the summer months nitrate accumulates in the surface layers of the Clyde Sea owing to the reduced cross-sill exchange during this time. During winter this water is then pumped out into the North Channel when cross-sill exchange increases. In addition to the accumulation of riverine nitrate within the Clyde Sea, nitrate is also introduced from outside of the sill during the early spring owing to deep-water renewal and increased cross-sill exchange during this time. The fate of waters discharging from the Clyde Sea are to become entrained into waters exiting the Irish Sea via the North Channel with the net movement of these waters being in a northward flow. These waters are of particular significance as it has been postulated that much of the nutrient fuelling production in the sea lochs of the west of Scotland originates in the Clyde Sea/Irish Sea area (Rippeth & Jones, 1996).

Many processes are common to most of the west coast sea lochs though there may be variations in the magnitude and timings (etc) of these processes. The Clyde Sea is different to most of the other west coast lochs in that the majority of nutrients entering the system do so via runoff from land.

There are a number of small shallow lochs such as Loch Ardbhair on the northwest coast of Scotland that remain unstratified and have flushing times of approximately 1 day (Gowen *et al.*, 1983), other waters such as Loch Creran and Killary Harbour have higher inputs of freshwater and are normally well stratified (Ross *et al.*, 1994) and have slightly longer flushing times. There are also deeper lochs such as Loch Etive or Loch Linne, which both discharge into the Firth of Lorne. These lochs have two or more basins, with the lower basin being similar in character to Loch Creran, whilst the upper basins are much deeper (~150m) and have flushing times of between 1-2 weeks (Tett 1986).

Whilst the Scottish sea lochs can be shown to differ with regard to such hydrographic processes, broad comparisons of the nutrient regimes of these northern sea lochs (excluding the Clyde) can be made. It has been estimated that the source of saline waters entering Loch Linnhe (via the Firth of Lorne) consists of approximately 75% Irish Sea/Clyde Sea water and 25% Atlantic Water (Mackay *et al.*, 1986). Watts *et al.* (1998) confirmed in a study of Loch Linnhe that the main source of all nutrients in the upper basin was from saline inflow (Table 1). These waters entering the Loch via the sea are denser than the receiving waters, as such the saline inflow can under certain hydrographic conditions sink thus making the nutrients dissolved within them less available to the photic zone than those of freshwater origin. These deep, saline and nutrient-rich waters can be returned to the photic zone during renewal events which in Loch Linnhe have been shown to be governed by tidal excursions, river run-off rates and wind direction (Allen, 1995).

Millimoles m^{-3} s^{-1}	Minimum saline flux (springs)	Maximum saline flux (springs)	Minimum freshwater flux	Maximum freshwater flux
Nitrate	9542	21 883	125	1800
Phosphate	1120	2594	46	184
Silicate	8844	14 740	689	2756

Table 1. The relative fluxes of each micro-nutrient to the upper basin of Loch Linnhe from saline and freshwater sources (after Watts *et al..*, 1998).

During winter the open North Atlantic is mixed to depths of several hundreds of meters and the water column over the shelf is mixed to the bottom. Stratification on the shelf starts during the spring bringing with it the potential for the development of fronts between the mixed and thermally stratified shelf waters especially around the islands of western Scotland or near the shelf break. The development of stratification on the outer shelf waters can cause frontal systems to migrate inshore during the spring and offshore during the autumn (Longhurst, 1998). Productivity at these fronts is often greater than the surrounding regions as a result of nutrient enhancement via upwelling and diffusion processes.

2.2   Nutrients in Open Atlantic Waters off the Shelf Edge

The offshelf region of SEA7 occupies waters from the shelf edge (here taken as waters to the west of 10°W) to the northern half of the Rockall Trough with water depths down to 2500m and westwards to the Icelandic basin. The region receives surface waters from several sources. One source originates from the Iceland Basin and travels southeast along the Rockall and Faeroes Banks. Another major source is the slope current entering the region from the southwest. The relative contribution of either of these waters to the region at any time is governed by atmospheric pressure anomalies between Iceland and the Azores commonly know as the North Atlantic Oscillation (see section 10). Bottom waters in the region can originate from sources further a field such as the Mediterranean and Norwegian Seas or even Antarctica, these waters can be rich in nutrients such as silica.

Silica plays an important role in the development of the spring diatom bloom of the region. In a recent study Brown *et al.* (2003) demonstrated how diatom dominance of the phytoplankton population decreased when silicate concentrations fell below 2μM Si l^{-1}.

Nutrient dynamics of these offshore waters during the summer months are strongly influenced by "zones of remnant water" which are colder and denser than those surrounding. These dense cold waters can become trapped during periods of strong stratification essentially locking-out the nutrients from the photic zone. As the summer season passes, increased wind strengths gradually turn-over the water column replenishing the surface waters with nutrients from depth.

Within this region there are several bathymetric features of ecological and geological interest including the Anton Dhorn seamount in the middle of the Rockall Trough. Seamounts have been shown to be ecological features that are governed by hydrographic and nutrient processes of the waters above and adjacent to them. Enhanced primary production has been observed around seamounts. One explanation for this may be the doming effect of waters over the seamount (Rogers, 1994), this enables deep nutrient-rich water to rise over the seamount where, given the right conditions of light and water column stability phytoplankton growth is enhanced. White *et al.* (2004) however suggest that such localised increases in production are fuelled primarily through deep winter mixing processes over the seamount.

3 SEASONALITY OF DISSOLVED NUTRIENT SALTS

The seasonality plots presented below are derived from monthly averaged data from the ICES nutrient database 1970-2000

3.1 Dissolved Available Inorganic Nitrogen (DAIN)

It can be seen from Figure 5 that the concentration of DAIN is generally highest in waters off the shelf edge. In this region concentrations reach a seasonal maximum of approximately 12μM during March/April and become depleted thereafter following the onset of the spring phytoplankton bloom. DAIN concentrations continue to decline throughout the summer months with lowest concentrations (~2μM) being recorded during September. Following this DAIN minimum, concentrations increase owing to deep-water mixing as wind strength increases during the winter months. The seasonality of DAIN concentrations in open shelf waters shows a similar profile to that of the Clyde box region throughout the year and are recharged during the winter months primarily through deep winter mixing although waters to the south of the region may be influenced by Irish Sea/Clyde Sea discharges. Peak concentrations (~10μM) occur earlier at these coastal sea areas as a result of the earlier development of the spring bloom. The recharge of DAIN in the more inshore Clyde Sea location begins earlier than the shelf sea region possibly as a result of enhanced anthropogenic loading into the Clyde Basin from land-based discharges. These results support those of Jones *et al.* (1995) although these authors suggested that DAIN concentrations fall to near undetectable levels within the inner Clyde during the summer months. This disparity between the current study and that of Jones *et al.* (1995) is due to the inclusion of data from outside the Firth of Clyde extending from the NW Irish Sea to the north of the North Irish Sea Channel in the present study.

The northern sea lochs of the western Scottish seaboard (e.g. Loch Creren) record lower concentrations of DAIN in comparison with the other regions. This reflects the significant input of freshwaters entering these lochs which have low nutrient concentrations as a consequence of reduced anthropogenic loadings and characteristics of the local geology.
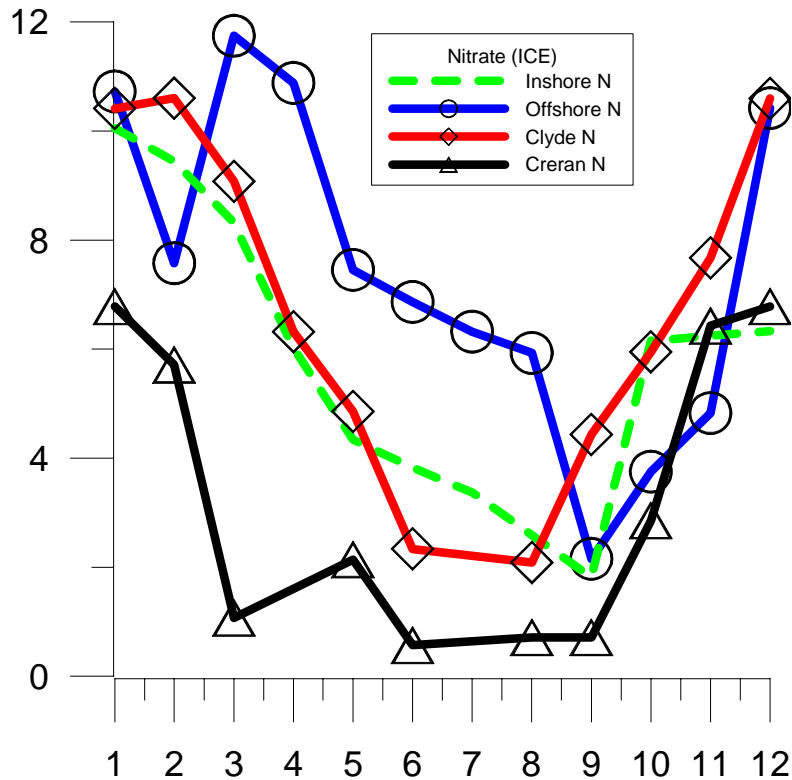
Figure 5. Average seasonality of Dissolved Available Inorganic Nitrogen (as µMoles) in offshore (blue), shelf sea (green), Clyde Box (red) and Creran Loch (black) regions of SEA area 7. Data from the ICES data-base 1970-2002, Data for Loch Creran from Watts *et al.* (1996)).

3.2 Dissolved Available Inorganic Phosphate (DAIP)

Figure 6 shows the seasonality of DAIP for the three regions. It can be seen that with regard to this nutrient-salt the Clyde Sea region has the highest concentration of the three regions with peak concentrations (~1.1µM) being recorded during December/January. Concentrations decrease throughout the spring and summer months with minimum concentrations (~0.4µM) being recorded during August. Waters extending from the coast to the shelf break show a similar seasonal profile as to that of the Clyde Sea region although concentrations are generally lower in this region than either the Clyde Sea or offshore regions. Highest concentrations (~0.7µM) on the shelf edge occur during January and decline through the spring and summer reaching minimum concentrations (~0.25µM) during August. The seasonality of phosphate for waters off the shelf edge shows a different profile to those discussed for the Clyde and coastal water regions. Highest concentrations (~0.9µM) are recorded during March and decline throughout the spring and summer reaching a minimum during October (~0.25µM) before being recharged by deep water mixing during the winter months.
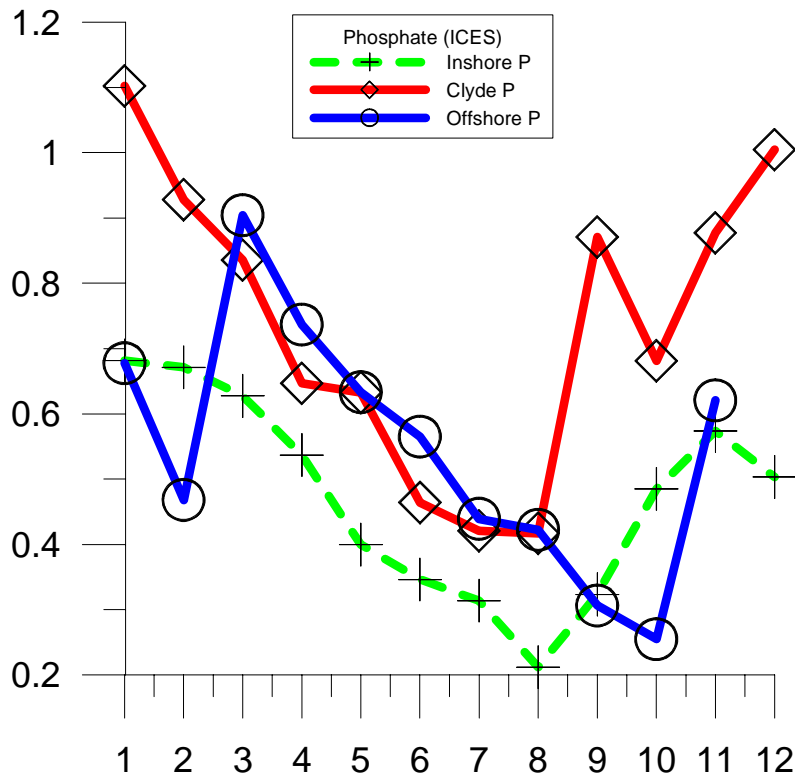
Figure 6. Average seasonality of Dissolved Available Inorganic Phosphorus (as µMoles) in offshore (blue), shelf sea (green) and Forth of Clyde (red) regions of SEA area 7. Data from the ICES data-base 1970-2002.

3.3   Silicate

The seasonality of silicate for the three regions is shown in Figure 7. It can be seen from this figure that highest winter concentrations occur within the Clyde Sea box with maximum concentrations (~8.5µM) occurring between December and January. Concentrations of silicate are rapidly utilised by the diatom flora during the spring bloom and lowest values (~2µM) occur during July, after which recharge steadily occurs as a result of increased run-off from land and the dissolution of silica frustules from sedimented diatomaceous material. The seasonality profile of silica in waters on the shelf edge is similar to that reported for the Clyde Sea box. However, winter concentrations are considerably lower reaching a maximum of ~6µM during February.

Waters off the shelf show a slightly different seasonal profile with maximum concentrations (~6µM) occurring approximately two months later than the more inshore regions. This reflects the later development of the diatom spring bloom and lower diatom production in such waters. Minimum concentrations occur between July and September with concentrations similar to those recorded for waters on the shelf edge (~1µM).
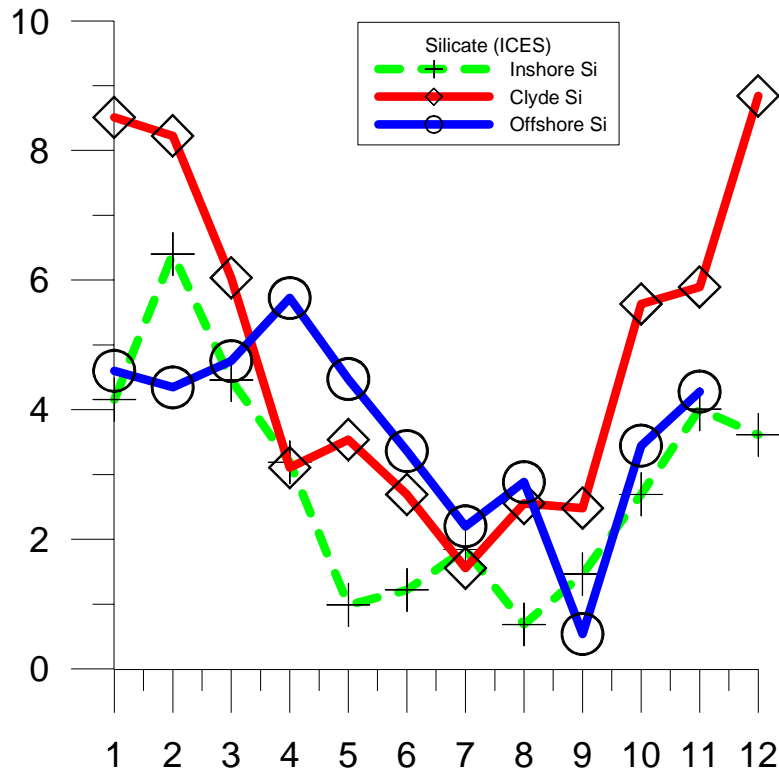
Figure 7. Average seasonality of Dissolved Silica (as μMoles) in offshore (blue), shelf sea (green) and Forth of Clyde (red) regions of SEA area 7. Data from the ICES data-base 1970-2002.

4   PHYTOPLANKTON

4.1   Bulk Chlorophyll Analysis

The phytoplankton are plants and just as with their terrestrial counterparts they contain chlorophyll. Thus the chlorophyll content of marine waters is a useful proxy of phytoplankton biomass. Figure 8 gives the monthly mean chlorophyll concentrations for different water-masses in the SEA7 area. It can be seen from this figure that highest concentrations of chlorophyll are to be found in inshore waters and generally decreases offshore. The Clyde Sea box has highest overall chlorophyll concentrations of all the regions studied and reflects the high anthropogenic loadings of nutrient salts to this region. The northern coastal sea lochs can also record high chlorophyll concentrations during the spring months, this is generally driven by other processes such as water column stability and a favourable light regime although as mentioned previously can be influenced by the northward flowing coastal current carrying with it nutrients originating in the Irish/Clyde Sea. The Clyde Sea box also records elevating chlorophyll concentrations during the late summer/autumn as a consequence of the breakdown of stratification and re-supply of nutrients to the surface waters.

Chlorophyll concentrations during the spring decrease offshore with waters on the coastal-shelf being approximating half of that recorded in the sea lochs. The

phenology of the spring bloom on the shelf and in the sea lochs are similar with maximum concentrations being recorded during April. However, unlike the sea lochs the autumnal production on the shelf is reduced and is more similar in character to production in more offshore waters. Mean chlorophyll concentrations during the spring in waters off the shelf edge are significantly lower than those recorded on the shelf or in the sea lochs and the spring bloom occurs approximately one month later during May in these waters.
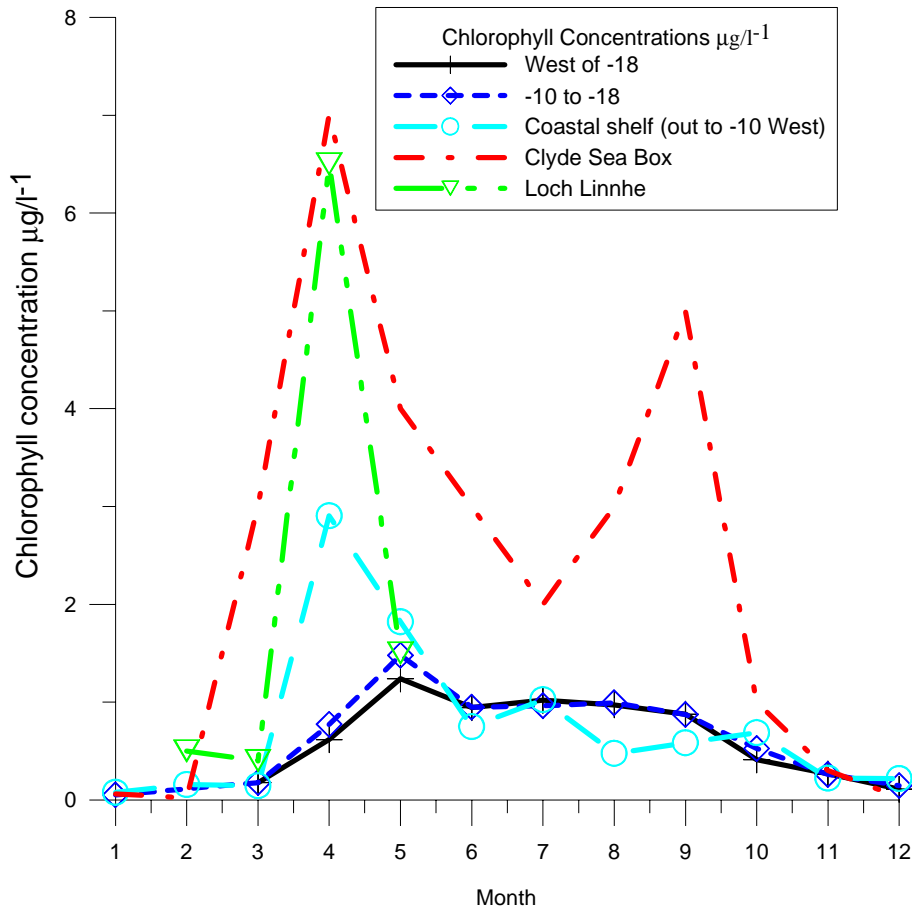

Figure 8. Seasonality of chlorophyll concentrations for different waters masses in the SEA 7 region. Data for the off-shelf and shelf regions are monthly mean concentrations from the ICES data-sets 1970-1996. Data for the Clyde Sea are from Jones *et al*., 1995 and for Loch Linnhe are from Watts *et al*., 1998.

Data from the continuous plankton recorder surveys for the region show a broad-scale similarity with the data discussed above (Figure 9). It can be seen that the phytoplankton colour index, another proxy indicator for phytoplankton biomass is generally highest in coastal waters and decreases offshore. However, it can be seen from Figure 9 that there is some considerable variation in the colour index in offshore waters, this is most likely an artefact of the relative position of frontal systems which are known to stimulate primary production through processes such as upwelling.
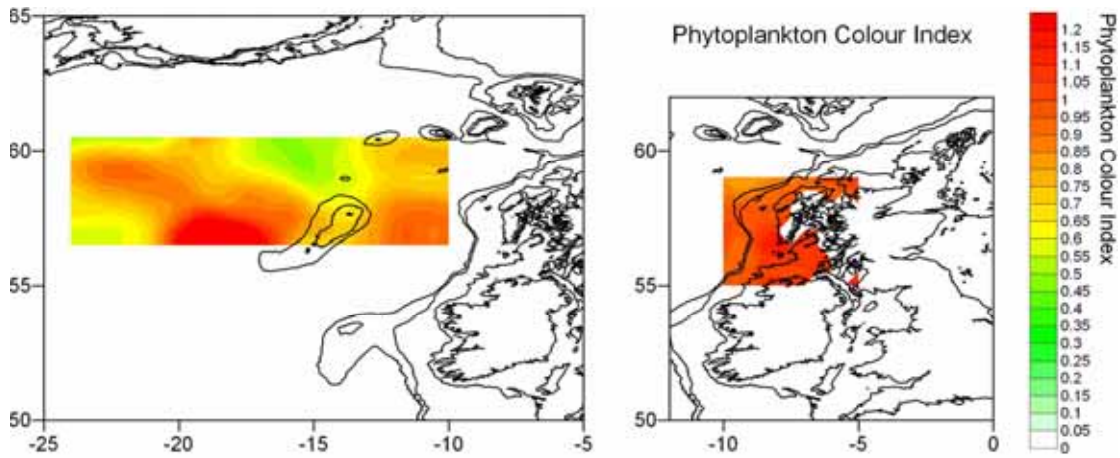
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Figure 9. The phytoplankton colour index from the CPR averaged for the years 1970-2000

Figure 10 below shows a typical depth integrated profile of the water column chlorophyll concentrations along a transect (the Ellett line) extending from Scottish coastal waters out to the Rockall Basin during May 2001. The figure clearly demonstrates how chlorophyll concentrations are highest in coastal shelf waters. Increased concentrations of chlorophyll are also recorded in offshore waters associated with the development of the seasonal thermocline that extends to several tens of meters during this time of year.

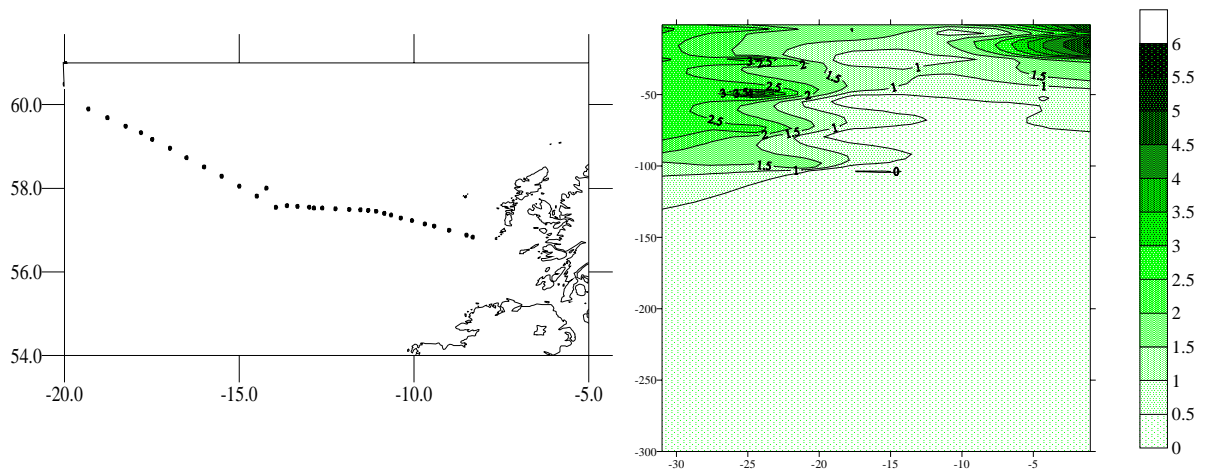

Figure 10. Depth integrated chlorophyll concentrations (µg/litre, bottom) along a transect extending from the coastal shelf to the Rockall Basin (the Ellett Line, left) during May 2001 (Data courtesy of Penny Holliday, NOC, Southampton).

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5   REGIONAL VARIATION IN PHYTOPLANKTON ECOLOGY

5.1   Phytoplankton Composition On the Shelf

Scottish coastal and shelf-sea waters provide a wide variety of pelagic environments. As has been previously mentioned there are subtle variations in the nutrient budgets and hydrographic regimes between the coastal and offshore regions and to a certain degree these are reflected in the composition and abundance of the phytoplankton communities found. The phytoplankton composition and seasonality of Scottish coastal waters conform to the so-called light-nutrient-mixing theory (Tett, 1992). The potential bloom state of a phytoplankton community can be restricted by the shortage of nutrients, by turbulent mixing and/or by grazing pressure. The annual cycle of phytoplankton in northern temperate waters is governed by the interplay between variations in light, stratification and the relative effects of stratification upon nutrient supply. Stratification in Scottish coastal waters is governed by both wind-stirring, surface heating and also by riverine run-off and tidal mixing. In the northern Sea lochs during periods of high freshwater loading, stratification is driven by haline effects. During periods of low freshwater flow the sea lochs generally remain mixed owing to wind and tidal stirring. Thermal stratification in these waters tends to be short-lived and is restricted to periods of fine weather during high summer.   High riverine flow into these waters can affect the plankton flora in several ways, by enhancing growth via increased nutrient inputs and also by extending the season of phytoplankton growth.

Waters of the northern sea lochs during spring are dominated by the diatoms and to a lesser degree the phytoflagellates. Wood *et al*. (1973) studied the seasonal plankton composition of Loch Etive and reported the dominance of the chain forming diatom *Skeletonema costatum*. This species accounted for up to 90% of the biomass during the spring phytoplankton peak in 1971 and regularly accounts for up to 50% of the phytoplankton biomass between March and June (Wood *et al*., 1973; Tett *et al*., 1985; Tett, 1992). The same diatom has been shown to dominate the spring bloom in sea lochs from Loch Striven to Loch Creran (Wood *et al*., 1973; Tett *et al*., 1981). Tett *et al*. (1986) in a study of the Firth of Clyde sea lochs suggest that the dominance of this species during the spring is governed by the stabilizing effects of reduced near-surface salinities. During the early summer months the continued replenishment of silicate to these sea lochs can prolong diatom dominance and other diatoms such as *Rhizosolenia* spp. and *Chaetoceros* spp. can be an important component of the early summer phytoplankton assemblage in the sea lochs and further offshore in regions such as the Islay Front (Simpson *et al*., 1979). Other species typically found in these northern sea lochs during the spring bloom are diatoms of the genera *Thalassiosira, Leptocylindrus* and *Chaetoceros*. On occasions small thecate Gonyaulacoid dinoflagellates can also be abundant during the late spring early summer (Lewis, 1985).

During the summer months the phytoplankton assemblage in Scottish coastal waters is generally dominated by the dinoflagellates. In the Firth of Clyde large dinoflagellates such as *Ceratium* spp. are abundant during July and August (Tett, 1992). The same genus was also shown to be abundant in the Minch during July 1982 possibly as a result of fine weather conditions (Gowen *et al*., 1983). Heterotrophic dinoflagellates such as *Protoperidinium* spp. show a marked seasonal cycle in abundances in the

Firth of Clyde with peak abundances found during the summer months (Tett, 1971). Other dinoflagellates dominating at this time of year include *Gymnodinium* spp and *Scripsiella* spp. (Tett *et al*., 1986). Diatoms can also be a significant component of the plankton flora during the summer months in some sea lochs, Tett *et al*. (1986) reported high concentrations of the chain forming diatom *Leptocylindrus danicus* in Lochs Striven and Fyne during July 1980. The high abundances of this species at this time were associated with strongly salinity stratified surface waters and may be utilizing the elevated nutrients associated with riverine discharge.

Dodge (1995) studied the seasonal cycle of armoured dinoflagellates in Loch Eriboll in north Scotland and reported that the most abundant dinoflagellates during the early summer months were heterotrophic species such as *Protoperidinium ovatum*. As the summer progressed autotrophic species such as *Ceratium* spp become the dominant forms in the Loch.

Month	Species
March	*Skeletonema costatum, Thalassiosira* spp., *Gonyaulax* spp.
April	*S. costatum, Lauderia* sp., *Thalassiosira rotula, T. nordenskioldii, Chaetoceros* spp., μ-flagellates.
May	*Rhizosolenia deliculata, Chaetoceros* spp., *Lauderia* sp., *S. costatum, Cerataulina pelagica, Thalassiosira* spp., *Leptocylindrus* spp., *Heterocapsa triquetra, Gymnodinium* spp. μ flagellates.
June	*C. decipiens, R. deliculata, C. pelagica, Thalassiosira* spp., *S. costatum, Leptocylindrus* spp., *Ceratium furca, C. lineatum, C. fusus, Heterocapsa triquetra, Protoperidinium divergens, Protoperidinium* spp., *Gymnodinium* spp, *Gonyaulax* spp. μ-flagellates.
July	*C. decipiens, Leptocylindrus danicus, Chaetoceros* spp., *S. costatum, Gonyaulax* spp., *Gymnodinium* spp., *Scripsiella* spp.,*Ceratium* spp. μ-flagellates.
August	*Ceratium* spp., *Protoperidinium* spp, *Gonyaulax* spp., *Chaetoceros* spp, *Guinardia* spp, μ-flagellates
September	*Ceratium fusus, Gymnodinium* spp., *Gyrodinium aureolum* (=*Karenia mikimotoi*), *Chaetoceros* spp., μ-flagellates
October/Nov	*S. costatum, Gymnodinium* spp., *Thalassiosira decipiens, Cylindrotheca closterium*, μ-flagellates.

Table 2. Species lists of typical dominant members of the phytoplankton in Scottish coastal waters throughout the seasons. (Produced from information in Gowen *et al*. (1983); Tett *et al*. (1986), Boney (1986) & Dodge (1995))

It can be seen from Table 2 above that throughout the year the smaller nano-plankton can be a significant component of the phytoplankton community. Boney (1986) highlighted the relative contribution of this group of organisms to the total phytoplankton biomass of the Firth of Clyde. These microbial organisms showed less seasonal variation when compared with the population changes of the microphytoplankton. There is evidence that nanophytoplankton can be food for smaller copepods, microzooplankton and fish larvae and as such are an important component of the coastal marine food-web. Of the many classes observed by Boney (1986) it was the green flagellates (Prasinophyceae) that were most abundant during spring, summer and autumn. Other nanoplankton species included the prymnesiophyte *Phaeocystis pouchetii* which had peak abundances in early spring and the coccolithophorids *Emiliana huxleyi* and *Kephyrion* spp. which were present during summer and autumn.

To the west of the islands and fjordal systems of the Scottish coast the phytoplankton community becomes more influenced by species more commonly associated with open Atlantic waters (see below) and the community composition is governed by the dynamic interplay between the Scottish coastal currents and waters moving onto the shelf from the open Atlantic.

5.2   Phytoplankton Composition Off the Shelf

Figure 11 below shows the seasonal composition of the major phytoplankton groups for offshore waters in the SEA7 region derived from the BODC database for the years 1972-2002. It can be seen from this illustration that during the early spring diatoms dominate the phytoplankton assemblage. By June however, the coccolithophorids are numerically dominant although diatoms still contribute significantly to the assemblage during this time. As the summer progresses all groups decline in abundance with coccolithophorids, diatoms and dinoflagellates co-dominating the assemblage between July and September. Small flagellated algae reach maximum abundances during July but remain less abundant than the other plankton groups during this time. Late summer blooms of coccolithophorids are well documented in the northeastern Atlantic Ocean and are especially frequent bordering the coastal boundary biomes, such as over the Rockall Channel (Longhurst, 1998). The spring diatom bloom is thought to be limited by silica, which has been shown to be reduced to limiting values before nitrate limitation. Typical dominating diatom species at this time tend to be larger forms such as *Rhizosolenia, Fragillariopsis, Thalassionema, Thalassiosira* and *Nitzschia*. After silicate limitation the smaller flagellated algae of the coccolithophorids become numerically dominant.
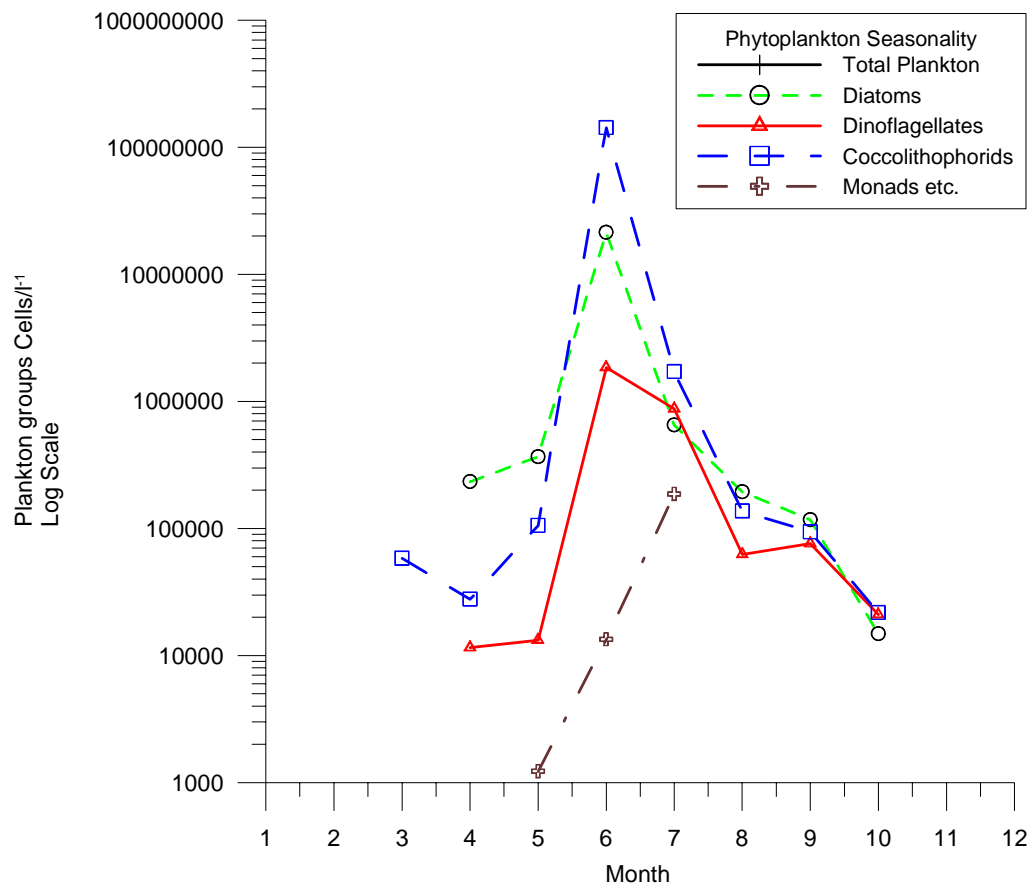
Figure 11. Seasonality of major phytoplankton groups in the SEA7 region. Data from the BODC archive 1972-2002).

In the temperate north Atlantic *Emiliana huxleyi* is the most abundant coccolithophore (Okada & McIntyre, 1979), with *Coccolithus pelagicus* and *Cyclococcolithus leptoporus* also common in the water column (e.g. Turner *et al*., 1988). Numerous sampling trips from ships have enabled the oceanographic community to understand more of the spatial and temporal distributions of *E. huxleyi*. In more recent years such studies have been augmented by satellite telemetry (e.g. AVHRR, CZCS, SeaWIFS etc.) in conjunction with real-time ground-truthing studies. This has enabled the scientific community to trace the development of the north Atlantic coccolithophore bloom and track the movements of these species in open Atlantic waters (Brown & Yoder, 1993; Holligan *et al*.,1993). These blooms tend to be most intense to the south of Iceland (see Figure 12) and Holligan *et al*. (1993) showed how the coccolithophore bloom in 1991 extended from south of Iceland through to the Rockall Trough and east to the shelf waters west of Scotland.
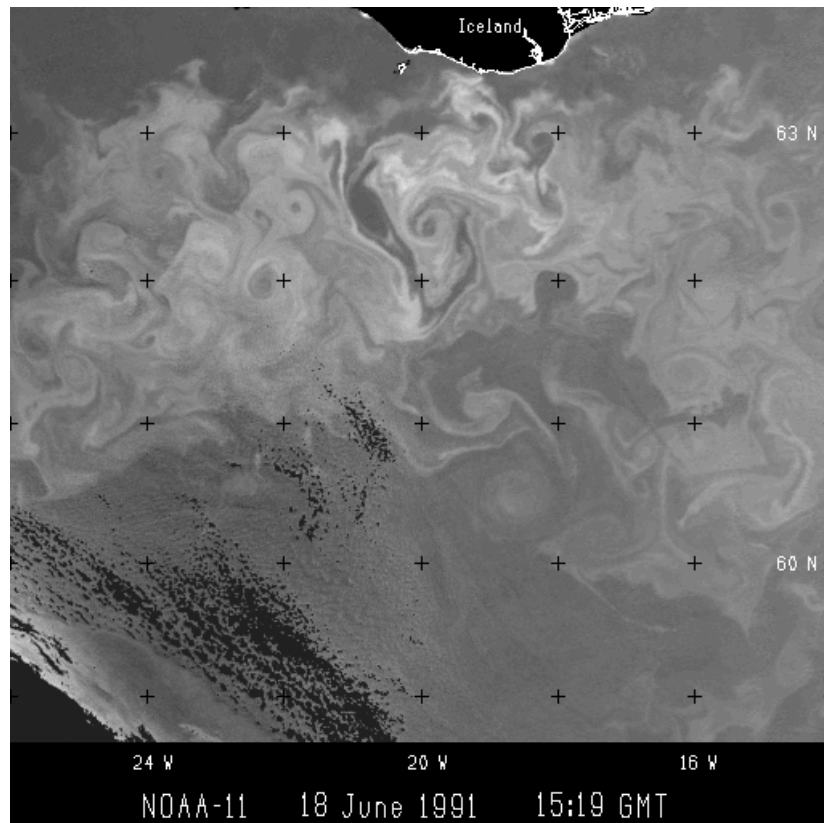
Figure 12. AVHRR satellite images of a bloom of the coccolithophore *Emiliana huxleyi* in open Atlantic Waters to the west of SEA 7 during June 1991. Image shows high reflectance (coccolith light scatter) as light shades. (The AVHRR data were received by the NERC Satellite Receiving Station Dundee and processed by the NERC Remote Sensing Data Analysis Service Plymouth, image courtesy of Dr. S. Groom, Plymouth Marine Laboratory)

Data from the continuous plankton recorder shows that typical summer dinoflagellate species from the SEA7 offshore region include *Ceratium furca, C. fusus, C horridum, C. lineatum, C. longipes, C. macroceros, Dinophysis* spp.,*Gonyaulax* spp., *Oxytoxum* spp. and *Protoperidinium* spp. (Barnard *et al.*, 2004).

6   PHYTOPLANKTON BLOOMS, HARMFUL ALGAL EVENTS AND TOXIN PRODUCING ALGAE

It has been estimated that there are approximately three thousand species of phytoplankton described from marine waters (Sournia *et al.*, 1991). Of these approximately 50 species are known to have harmful properties, these properties include the production of toxins such as domoic acid, okadaic acid, yessotoxins and saxitoxins. These toxins released by certain phytoplankton can bioaccumulate and as such can cause illness and even deaths of higher marine organisms and humans via the consumption of fish and shellfish contaminated after feeding upon toxic phytoplankton. Many species such as *Alexandrium* spp. and *Dinophysis* spp. can be toxic to organisms even when population densities are low and as such, toxic algal events can occur outside of bloom-state conditions.

Other phytoplankton species can be regarded as harmful not because they form toxins but because they can occur in such high densities that they may remove oxygen from the water column and sediments after the population dies and is subsequently attacked by microbes. Sometimes the population of a species may reach such high proportions as to cause the discolouration of seawater and are often referred to as red, brown or white-tides. Other phytoplankton groups such as the diatom *Chaetoceros* spp. when in bloom state can cause mechanical damage to other organisms e.g. the scratching of gill surfaces of fish caused by microscopic spines (setae) associated with this diatom genus.

Harmful algal events, phytoplankton blooms and toxic phytoplankton species have been reported from Scottish coastal waters within the SEA7 area, however, blooms of toxic phytoplankton are rare. One of the most dramatic events occurred during the summer of 1980 when a red-tide of the dinoflagellate *Gymnodinium aureolum* (= *Karenia mikimotoi*) was reported from sea lochs in the Firth of Clyde. This red-tide was responsible for the death of over 3000 salmon from a fish farm in Loch Fyne, the deaths were thought to be a result of a gill-damaging toxin produced by this species (Jones *et al*., 1982). This species bloomed extensively in 1996 along the Scottish west coast causing the deaths of finfish, shellfish and other invertebrates (Kelly & MacDonald, 1997). This dinoflagellate was also abundant in waters extending out to the shelf break in the summer of 1996 (Smith, 1999).

A known vector species for Paralytic Shellfish Poisoning (PSP) is *Alexandrium tamarense*. This species was reported from Loch Creran, the Sound of Jura and Loch Sunart during the 1980's (Lewis (1985) reported in Tett & Edwards (2002)). Results from the monitoring programme for toxin producing algae in Scottish coastal waters for 2003 and 2004 (Fraser *et al*., 2004) suggest this species is now present throughout the spring and summer months in waters extending from the Firth of Clyde to Loch Laxford on the Scottish north coast. A survey undertaken of major commercial shellfisheries in the 1970's showed no toxicity outside of north-east England, however, the cysts of this species were recorded during the 1980's in Loch Creran on the Scottish west coast. Tett & Edwards (2002) suggested the possibility of two genetic strains of this species with populations on the east coast of Britain being toxic whilst those on the west and south coasts of the UK being a non-toxic subspecies. These authors also suggest that this species may have spread northwards in recent decades, however owing to insufficient data collection prior to the 1980's such assumptions must be taken with caution.

Dinophysis spp. a genus known to produce okadaic acid, the cause of Diarrhetic Shellfish Poisoning (DSP) has also been reported in Scottish coastal waters. *Dinophysis* spp. have been recorded from the Firth of Clyde, Loch Etive, Loch Creran, Loch Striven, the Minch and from the Malin Shelf (Tett & Edwards, 2002). This genus has also been identified in waters off the shelf break (BODC unpublished data). In 1979 and 1982 mass mortalities of farmed salmon and trout were associated with blooms of an unidentified flagellate, ('flagellate X' possibly a species of *Chatonella*, *Olisthodiscus* or *Heterosigma akashiwo*) in Scottish west coast sea lochs (Tett *et al*., 1980; Gowen *et al*., 1982; Gowen, 1987).

The potentially toxic diatom genus *Pseudo-nitzschia* is also commonly reported from Scottish coastal waters. *Pseudo-nitzschia* spp. are known producers of domoic acid a

causative agent of Amnesic Shellfish Poisoning (ASP). Monitoring for ASP toxins in cultivated and wild populations of shellfish from Scottish coastal waters only began in 1998. Some harvesting closures were implemented in 1998 as a result of high domoic acid concentrations, however, in 1999, the majority of king scallop (*Pecten maximus*) fisheries from the Scottish west coast were closed due to domoic acid toxicity (Gallagher *et al*., 2001). More recent studies have shown this species to be abundant along the western Scottish coastline extending from the Clyde to Loch Laxford and out to the shelf edge (Fraser *et al*., 2004).

Diatoms of the genus *Chaetoceros* are a common constituent of the spring/summer plankton flora and the blooming of at least one species of this genus (*C.wighami*) has been documented as being responsible for the deaths of farmed salmon in west Scotland with an estimated economic loss of approximately £0.5million during July 1998 (Treasurer *et al*., 2003).

Certain prymnesiophyte algae although non-toxic can be regarded as nuisance species. Species such *Phaeocystis pouchetii* have the ability to form dense blooms which cause foaming along shorelines. *P. pouchetii* was recorded in the Firth of Clyde during the 1970's (Boney, 1986) and again in more recent years (Tett & Edwards, 2002).

Species	**Toxin/Impact**
Alexandrium tamerense	Paralytic shellfish Toxin
Karenia mikimotoi	Hemolytic, Ichthyotoxin
Dinophysis accuminata	Diarrhetic Shellfish Toxin
D. acuta	Diarrhetic Shellfish Toxin
D. norvegica	Diarrhetic Shellfish Toxin
D. dens	Diarrhetic Shellfish Toxin
Phalacroma rotundata	Diarrhetic Shellfish Toxin
Prorocentrum lima	Diarrhetic Shellfish Toxin
Lingulodinium polyedrum	Yessotoxin
Protoceratium reticulum	Yessotoxin
Protoperidinium spp.	Potential Azaspiracid producers (ASA)
Pseudo-nitzschia seriata	Amnesic Shellfish Toxin (Domoic acid)
P. australis	Amnesic Shellfish Toxin (Domoic acid)
P. fraudulenta	Amnesic Shellfish Toxin (Domoic acid)
P. multiseries	Amnesic Shellfish Toxin (Domoic acid)
P. pungens	Amnesic Shellfish Toxin (Domoic acid)
Chaetoceros wighami	Physical damage to gill structures etc.
Flagellate X (=Heterosigma akashiwo?)	?
Phaeocystis pouchetii	Foaming, anoxia
Cheatoceros spp.	Physical damage to gill structures etc.

Table 3. Species list of potentially toxic/harmful algal strains reported from Scottish coastal waters (after Tett & Edwards (2002) and Fraser *et al*. (2004)).

7   ZOOPLANKTON

Zooplankton are the animal constituent of the plankton, some are herbivores, feeding upon phytoplankton, while others are carnivorous, feeding upon other members of the zooplankton. Some members of the zooplankton community, particularly copepods (small crustacea), are of importance to higher trophic levels (i.e. food for fish larvae). The zooplankton community contains a wide range of organisms and this chapter is an overview of some of the more abundant taxa found in the SEA 7 area, as taken from Continuous Plankton Recorder data. The area is split into two, on shelf (0° to 10° West), and on shelf (10° to 24° West), to allow examination of the two communities (Figure 13).
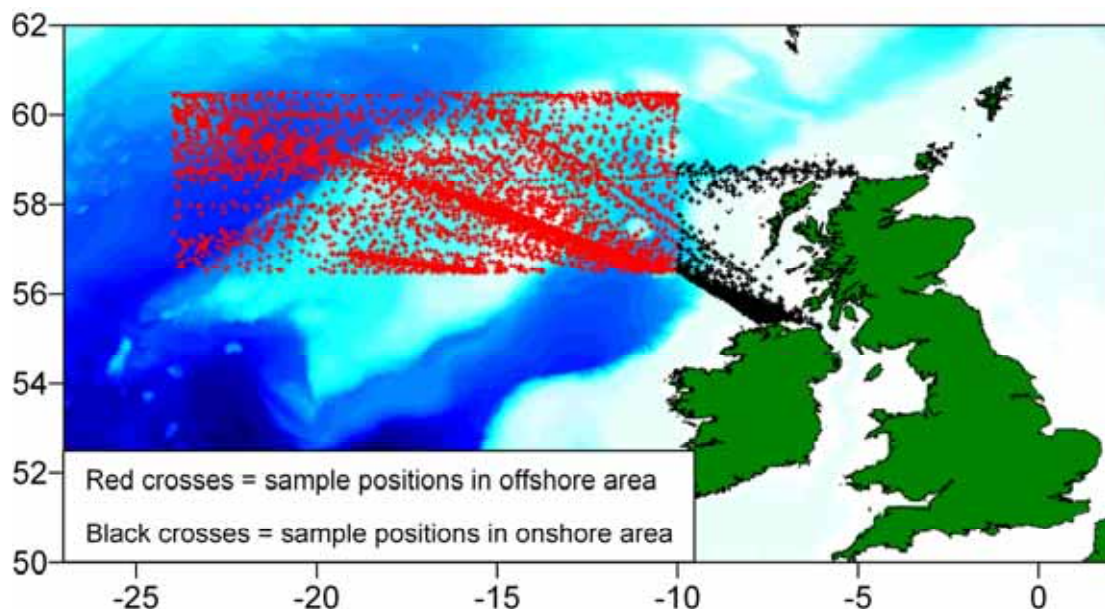

Figure 13. Sample locations from the continuous plankton recorder surveys used in this study. Red crosses are offshore sample positions, black crosses are inshore sample positions

7.1   Community composition

Table 4 shows the zooplankton community composition (taxa occurring on over 1% of samples) for both on and off shelf areas. The on shelf area is dominated by Calanoid copepods, in particular the smaller taxa *Para-pseudocalanus*, as well as the two large *Calanus*, *helgolandicus* and *finmarchicus*. Off shelf, the most frequently recorded taxa are Euphausiids (which have a high abundance to the far west of the SEA 7 area), with lower numbers of Calanoid copepods.

% occurrence	On Shelf		% occurrence	Off Shelf
51	*Para-pseudocalanus* spp.		38.6	Euphausiacea
49.7	*Calanus finmarchicus*		35.3	*Acartia* spp.
49.5	*Calanus helgolandicus*		30.8	*Calanus finmarchicus*
40.8	*Acartia* spp.		27.6	*Metridia lucens*
39.8	Euphausiacea		26.8	*Oithona* spp.
34.9	*Calanus* stage i-iv		24.7	*Para-pseudocalanus* spp.
34.9	*Metridia lucens*		20.1	Hyperiidea
33.8	*Oithona* spp.		17.6	*Calanus* stage i-iv
33.7	Decapoda larvae		13.5	*Pleuromamma robusta*
28.5	Thecosomata		12.1	*Evadne* spp.
22.2	Chaetognatha		9.4	Thecosomata
21.7	Fish larvae		9.3	*Euchaeta norvegica*
15.7	*Centropages typicus*		9.2	Decapoda larvae
15.2	Hyperiidea		7.9	*Calanus helgolandicus*
13.4	Echinodermata larvae		7.5	Fish Larvae
13.0	Larvacea		6.1	Chaetognatha
11.4	*Evadne* spp.		5.7	Larvacea
8.7	*Candacia armata*		3.8	*Podon* spp.
8.5	*Podon* spp.		3.5	Tomopteris
7.5	*Temora longicornis*		3.3	*Centropages typicus*
5.1	Lamellibranch larvae		3.1	Harpacticoida
4.9	Cyphonautes larvae		3.1	Sergestiid
4.6	Tomopteris		2.5	Echindodermata larvae
4.3	Cirripede larvae		2.1	*Pleuromamma borealis*
3.2	*Euchaeta hebes*		1.8	*Rhincalanus nasutus*
2.9	*Pleuromamma robusta*		1.3	*Clausocalanus* spp.
2.3	*Euchaeta norvegica*		1.2	Thaliacea
2.1	*Clausocalanus* spp.		1.2	*Pleuromamma gracilis*
1.9	*Corycaeus* spp.		1.1	*Clione limacina*
1.7	*Eucalanus crassus*		1.0	Ostracoda
1.6	*Clione limacina*			
1.4	Sergestiid			
1.3	*Rhincalanus nasutus*			
1.1	Harpacticoida			

Table 4. Community composition of on and off shelf SEA 7 area.

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7.2 Calanoid copepods

Copepods, such as *Calanus*, constitute a major food resource for many commercial fish species, such as cod and herring (Brander, 1992). Changes in their populations are therefore of considerable importance, be it natural or anthropogenically forced. The dominant copepod genus in the North Atlantic is *Calanus*, which represents a major resource to the higher trophic levels, and is itself a strong grazer on phytoplankton (Planque, 1996). In the SEA 7 area, the dominant species are *Calanus finmarchicus* and *Calanus helgolandicus*, these species have been extensively studied for many years, *C. finmarchicus* was first identified in 1770 by Gunnerus, but was not separated from *C. helgolandicus* as a different species until 1958. The community of both areas (particularly on shelf) are dominated by calanoid copepods, and a number of these are examined in more detail. Spatial distribution maps and graphs of seasonal abundance are plotted.

7.2.1 *Calanus finmarchicus*
Spatial maps : Figure 14a Present throughout the SEA 7 area, but abundant off shelf area around Rockall and to the far West. Also high abundance values on shelf.

Seasonality: Figure 14b On and Off shelf areas similar, with peak in abundance in May and a tailing off through the summer months. November to March values are the lowest.

7.2.2 *Calanus helgolandicus*
Spatial maps: Figure 14c Virtually absent from the off shelf area, the species appears confined to the shelf area, with greatest abundance to the south.

Seasonality: Figure 14d On shelf the species has a peak in seasonal cycle during June, but with values high from April to October (a suggestion of a secondary peak). Abundance drops during November and December, with lowest values January to March. The peak in abundance off shelf is similarly in June, with again a suggestion on secondary peaks during late summer – autumn months.
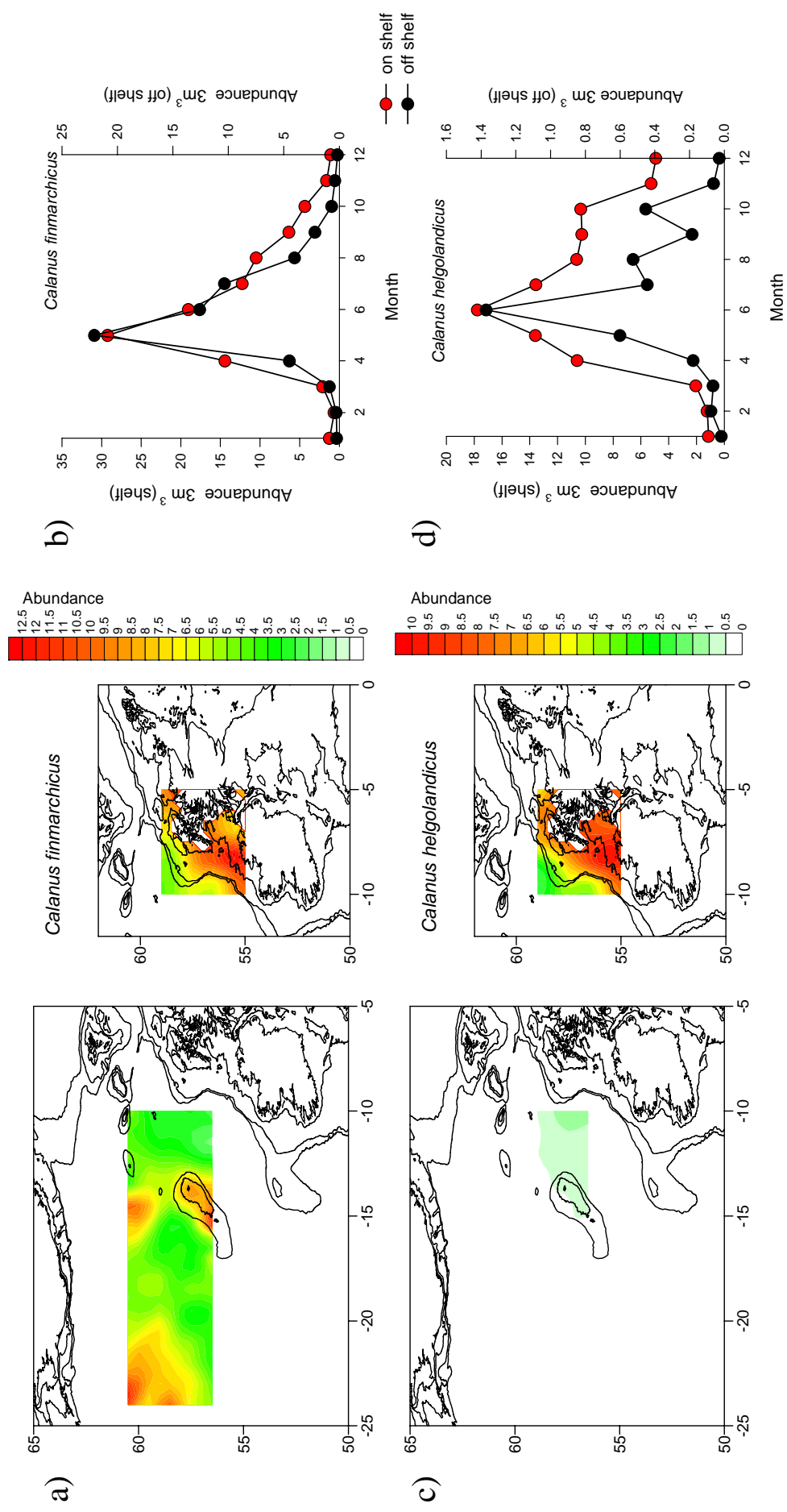
Figure 14. On- and off-shore, spatial and seasonal abundance diagrams for *C. finmarchicus* (a & b respectively) and *C. helgolandicus* (c & d respectively).

7.2.3 *Acartia* spp.

Spatial maps: Figure 15a *Acartia* spp. appears to be most abundant between just off the shelf edge, and slightly to the west of Rockall, but is present throughout the study area.

Seasonality: Figure 15b There appears to be a lag of one month between on and off-shelf seasonal cycle, with a distinct on shelf peak in July followed by a off shelf peak in August.

7.2.4 *Centropages* spp.

Spatial maps: Figure 15c Highest abundance of *Centropages* spp. occur on shelf mainly and slightly off shelf, with lower abundance further to the west.

Seasonality: Figure 15d Highest values occur off shelf in August, with a month lag to a peak in September on shelf. Lowest values occur December to March.

7.2.5 *Temora* spp.

Spatial maps: Figure 16a *Temora* spp. are confined to the on shelf area, mainly to the extreme south and north, abundance is low compared to the other small copepods.

Seasonality: Figure 16b With the low abundance, seasonal cycles are not clear, particularly off shelf. On shelf there is a distinct peak in June, with medium values from April to September. Off shelf, there appears to be a initial increase in July, followed by an absence of the taxa in August and a distinct peak in October.

7.2.6 *Para – Pseudocalanus* spp.

Spatial maps: Figure 16c The most abundant of the small copepods, greatest numbers are found on shelf (particularly to the north), with abundance falling westwards off shelf.

Seasonality: Figure 16d Seasonal cycle is similar on and off shelf, with a peak in June. There appears to be a secondary peak in August off shelf and in September on shelf.

7.2.7 *Oithona* spp.

Spatial maps: Figure 17a This taxa is common throughout the study area, both on and off shelf, but with lower abundance over Rosemary Bank, and high abundance on shelf and centred around 16° West.

Seasonality: Figure 17b Seasonal peak occurs first off shelf during May and June, followed by a peak on shelf during July. On shelf there is a secondary peak in September.
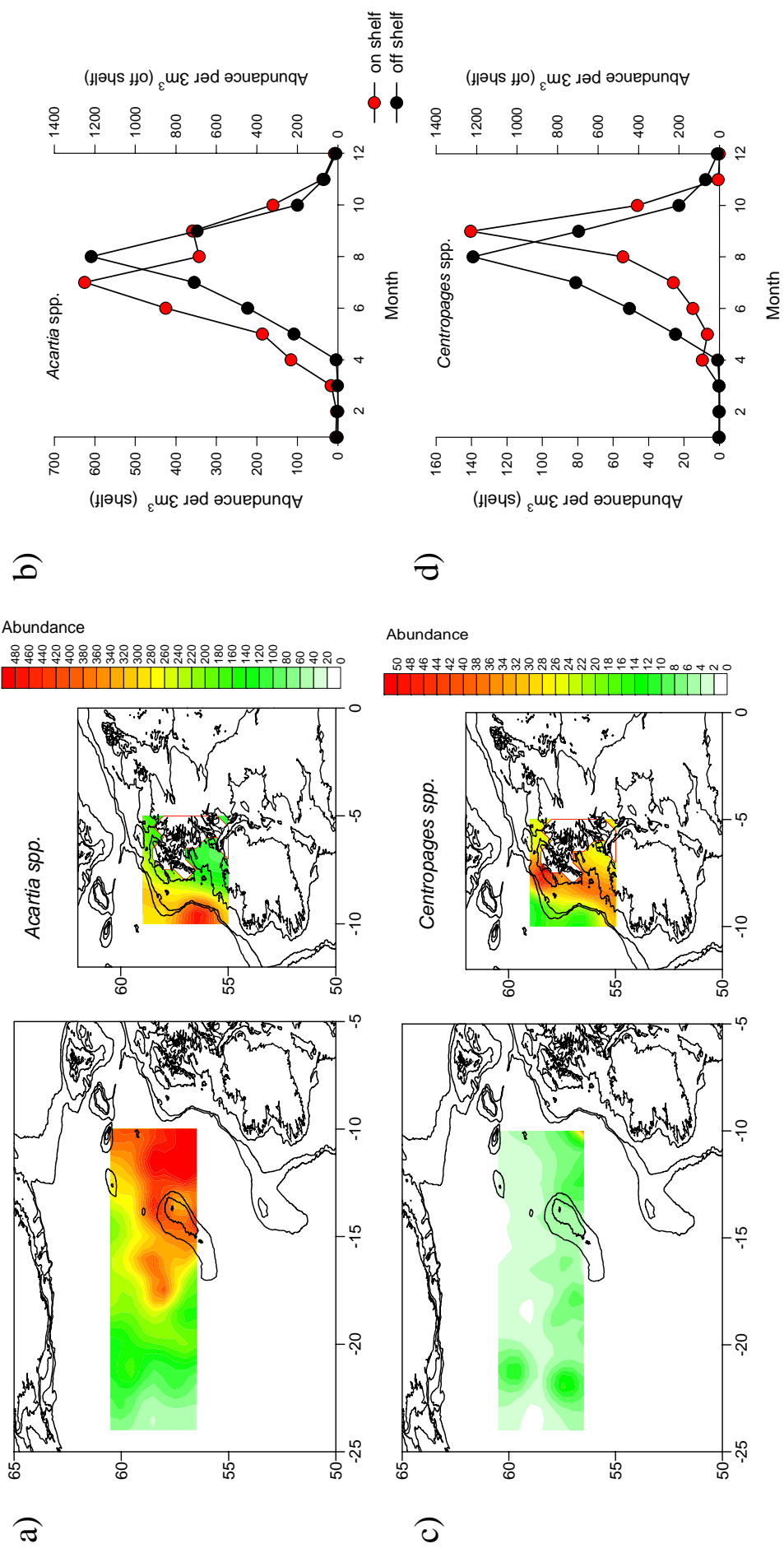
Figure 15. On- and off-shore, spatial and seasonal abundance diagrams for *Acartia* spp. (a & b respectively) and *Centropages* spp. (c & d respectively).
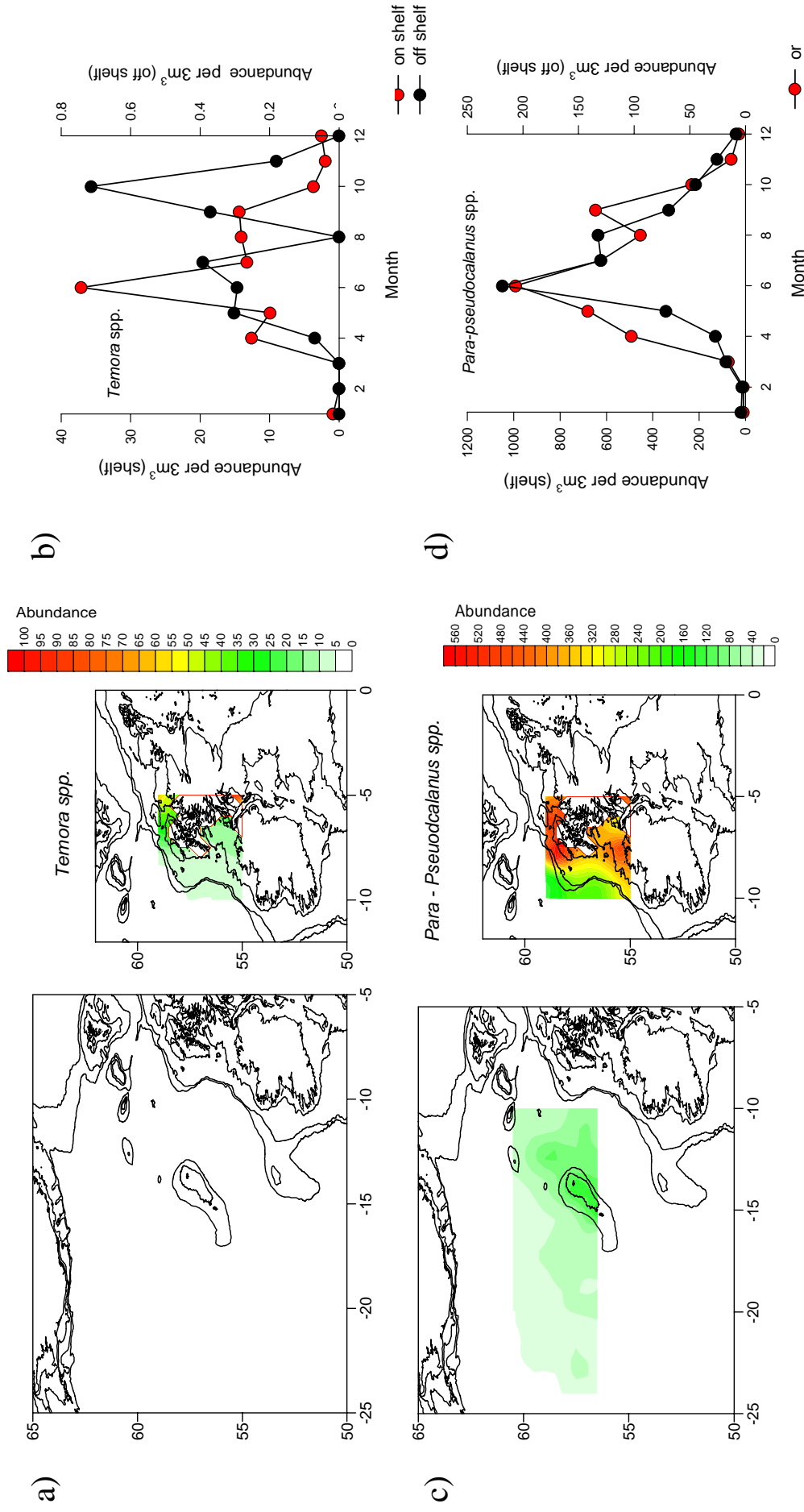
29

Figure 16. On- and off-shore, spatial and seasonal abundance diagrams for *Temora* spp. (a & b respectively) and *Para – Pseudocalanus* spp. (c & d respectively).
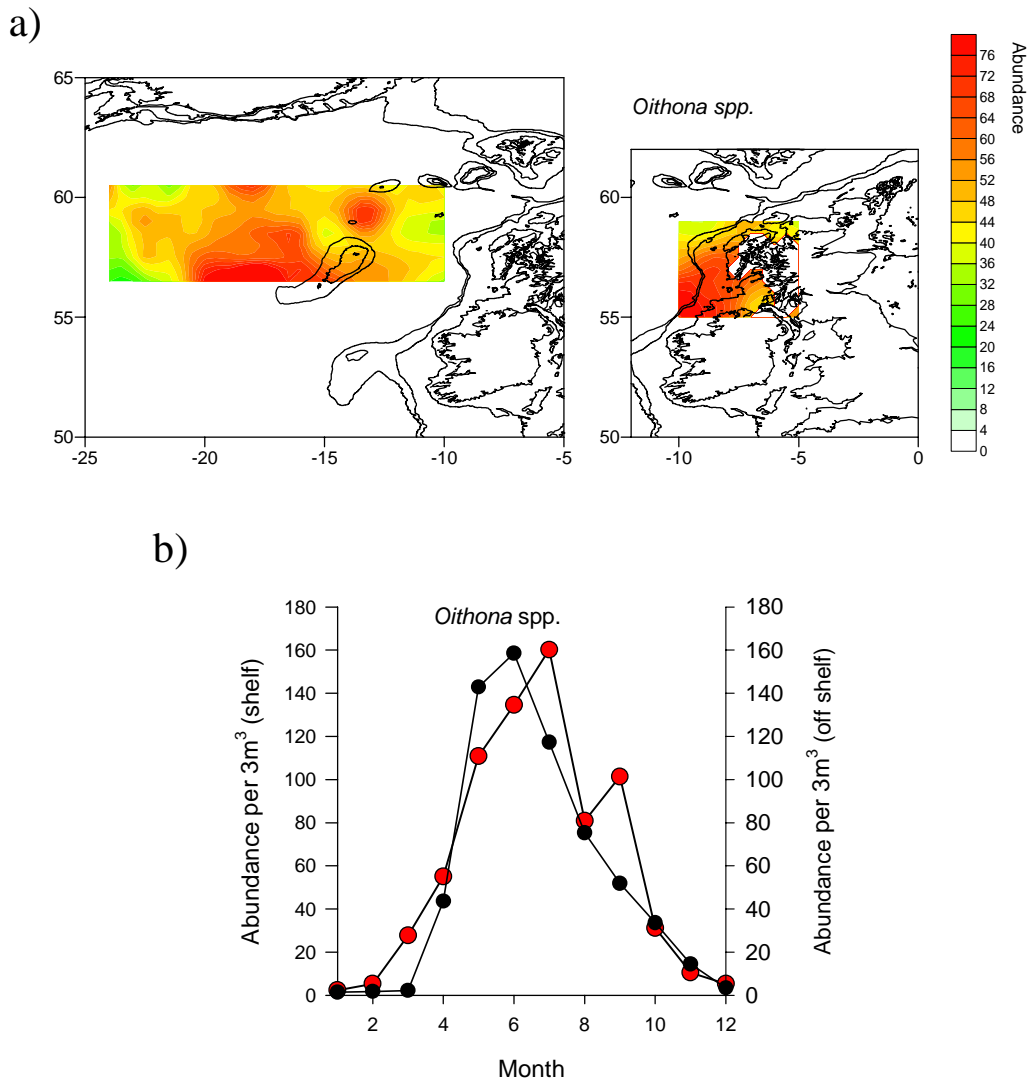
30

a)

b)

Figure 17. On- and off-shore, spatial (a) and seasonal abundance (b) diagrams for *Oithona* spp.

7.3 Total Amphipoda

Spatial maps: Figure 18a Amphipoda appear to be concentrated to the far west of the SEA 7 area, this is most probably Hyperiidea. Low values are found throughout the rest of the area, except on and to the north of Rockall.

Seasonality: Figure 18b Off and on shelf peaks occur during September, but with an initial increase during the summer (July and August). Lowest values occur off shelf from November to April, with low on shelf numbers during February, March and April.

7.4 Decapoda larvae

Spatial maps: Figure 18c Decapoda appear to be confined to the on shelf area, in fact in the most shallow part of the SEA 7 area.

Seasonality: Figure 18d A peak in abundance occurs off shelf during May, with an on shelf peak in June (although there is a smaller increase on shelf in March). Lowest values occur in both area from October to February.
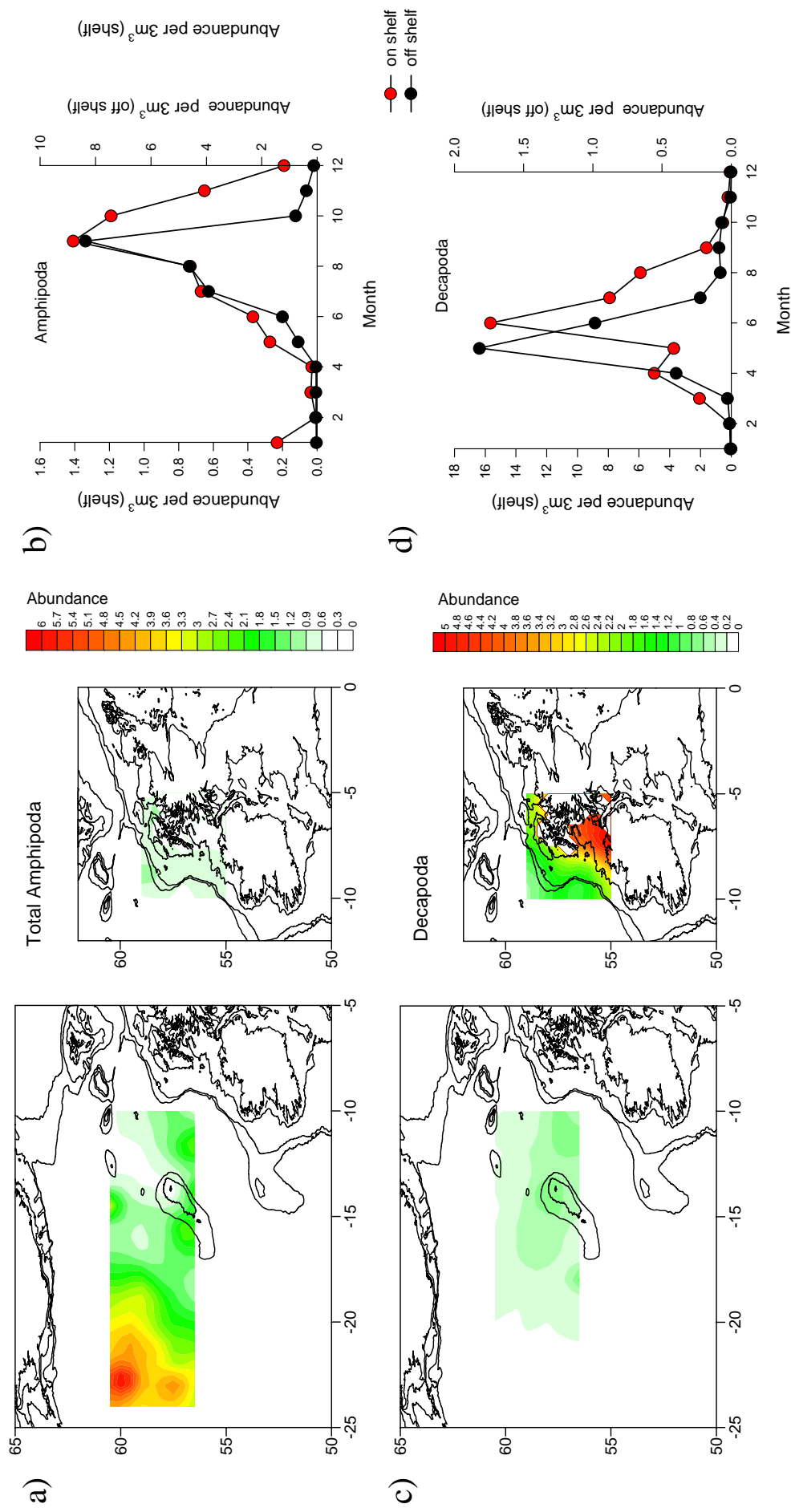
31

Figure 18. On- and off-shore, spatial and seasonal abundance diagrams for Total Amphipoda (a & b respectively) and Decapoda (c & d respectively).

7.5 Euphausiacea

Spatial maps: Figure 19a This taxa occurs mainly to the extreme west of the SEA 7 area (west of 17°), with lower numbers found throughout the rest of the area.

Seasonality: Figure 19b Both on and off shelf areas display similar seasonal cycles, with a peak during May (and June off shelf). There is a secondary increase on shelf during autumn months.

7.6 Total Cladocera

Spatial maps: Figure 19c This group is most abundant off shelf, west of the shelf break, out to approx. 23 ^{o} West. There appears to be low abundance on shelf, and to the far northwest of the SEA 7 area.

Seasonality: Figure 19d On shelf there is a peak in May and June, with a secondary increase in August and September. Off shelf the peak is delayed, occurring in June and July, but with no secondary increase.

7.7 Mollusca

Spatial maps: Figure 20a This group (which is dominated by Thecosomata), is more abundant on shelf, particularly in the south of the area. There are low abundances in the off shelf area.

Seasonality: Figure 20b On shelf this group peaks in abundance during the summer months of June and July, and to a lesser extent August and September. Abundance on shelf are considerably higher than off shelf, where the seasonal peak is in September.

7.8 Echinodermata larvae

Spatial maps: Figure 20c Echinoderm larvae are mostly confined to the northern part of the on shelf area. Off shelf they are less common, put occur around the Rockall area.

Seasonality: Figure 20d On shelf Echinoderm larvae peak seasonally in August, with numbers higher during Summer and Autumn months. Off shelf, where numbers are much lower, the seasonal peak is earlier in May and June, but with a small secondary peak in September.

7.9 Larvacea

Spatial maps: Figure 21a Larvacea occur extensively throughout the whole SEA 7 area (both off and on shelf), but with highest values in the immediate on shelf location.

Seasonality: Figure 21b On shelf seasonal peak is in June, but abundance increases from March through to July. Off shelf seasonal cycle has a more distinct peak in May, with a smaller secondary peak in August.

7.10 Chaetognatha

Spatial maps Figure 21c: Chaetognatha occur predominately on shelf, but with lower numbers throughout the SEA 7 area.

Seasonality Figure 21d: On shelf there is a peak during July, but with raised abundances during late Autumn and Winter (October to January). Off shelf the seasonal peak occurs in September.
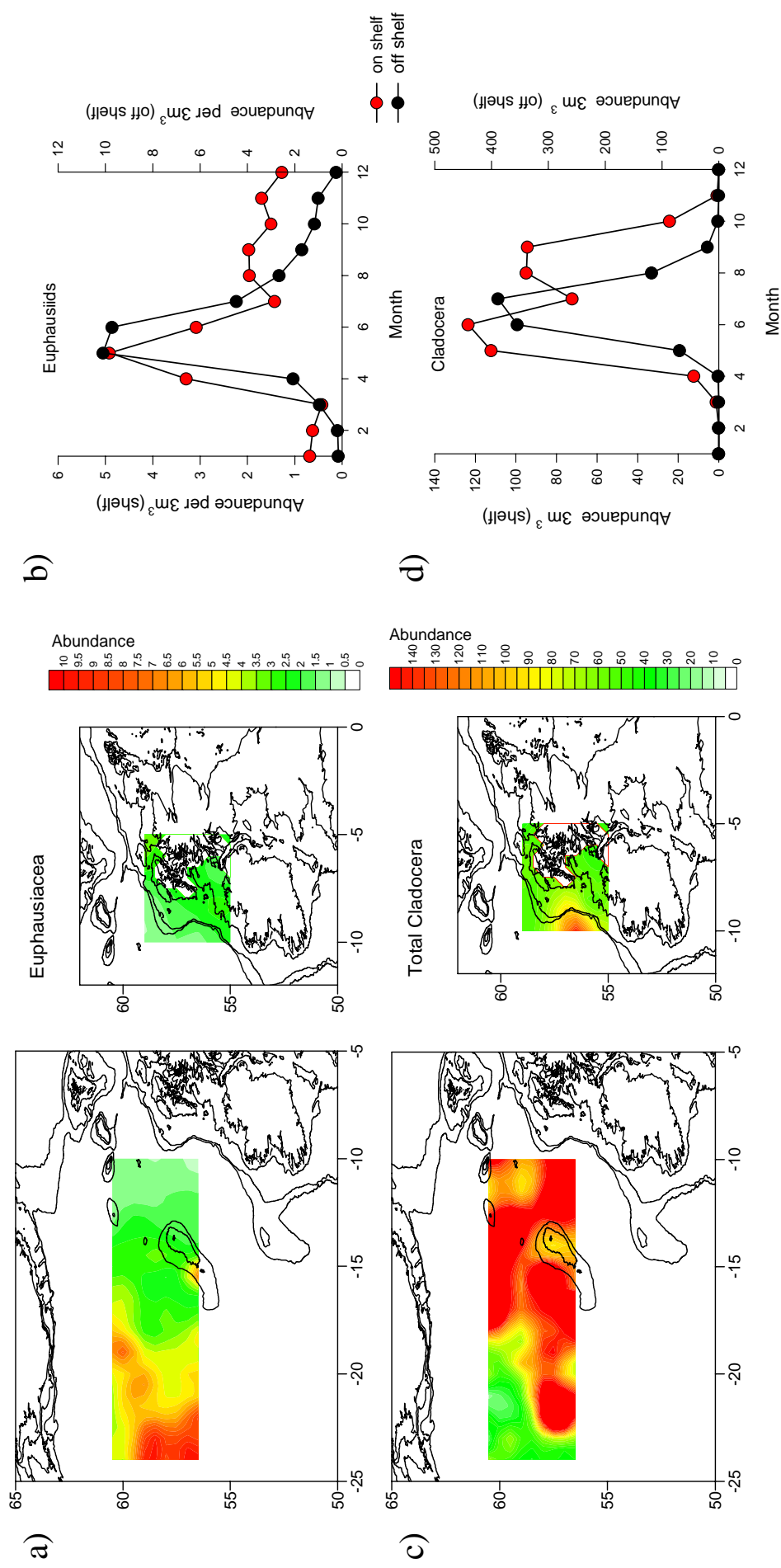
Figure 19. On- and off- shelf, spatial and seasonal abundance diagrams for Euphausiidea (a & b respectively) and Cladocera (c & d respectively).
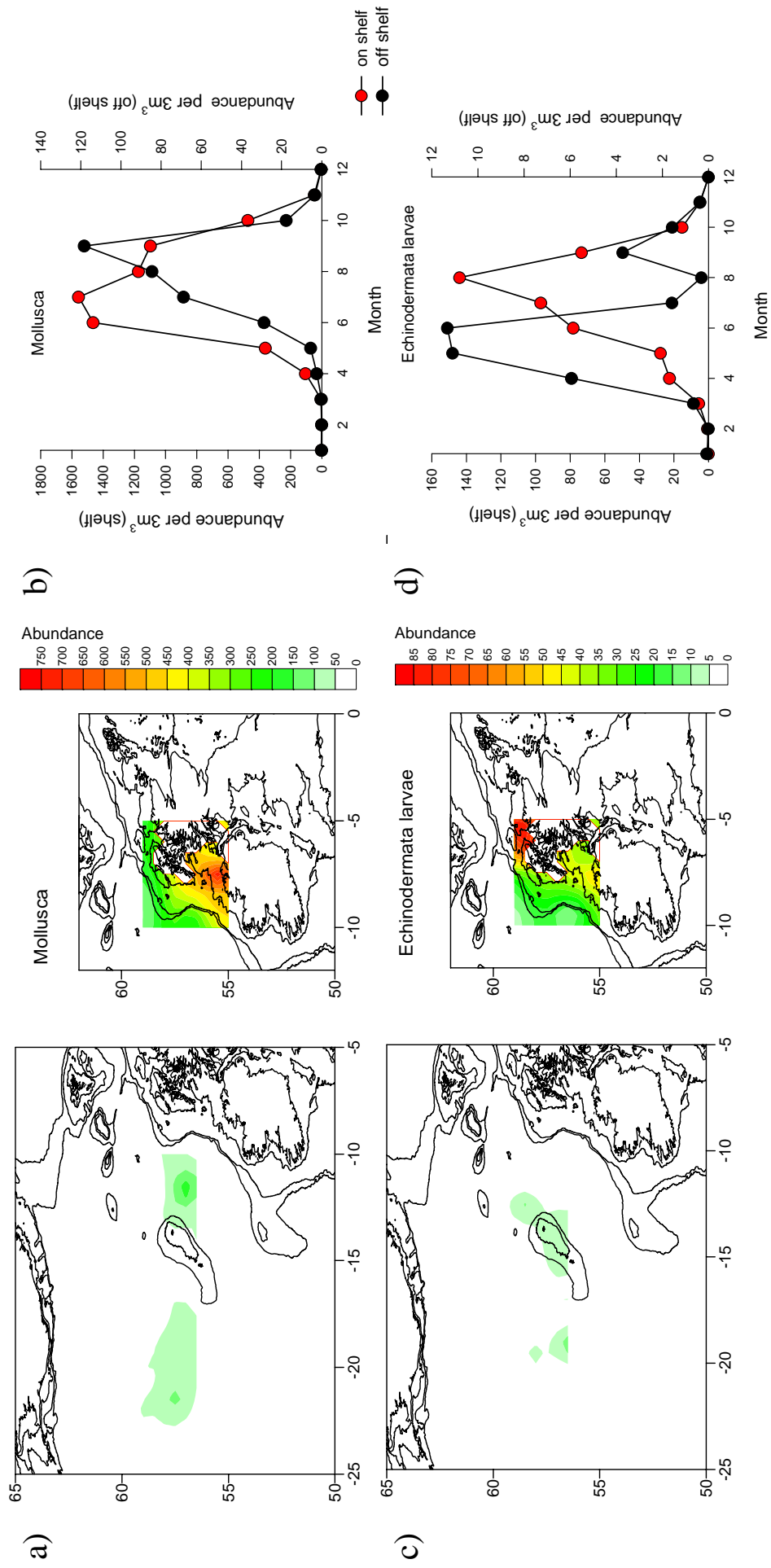
34

Figure 20. On- and off- shelf, spatial and seasonal abundance diagrams for Mollusca larave (a & b respectively) and Echinodermata larvae (c & d respectively).
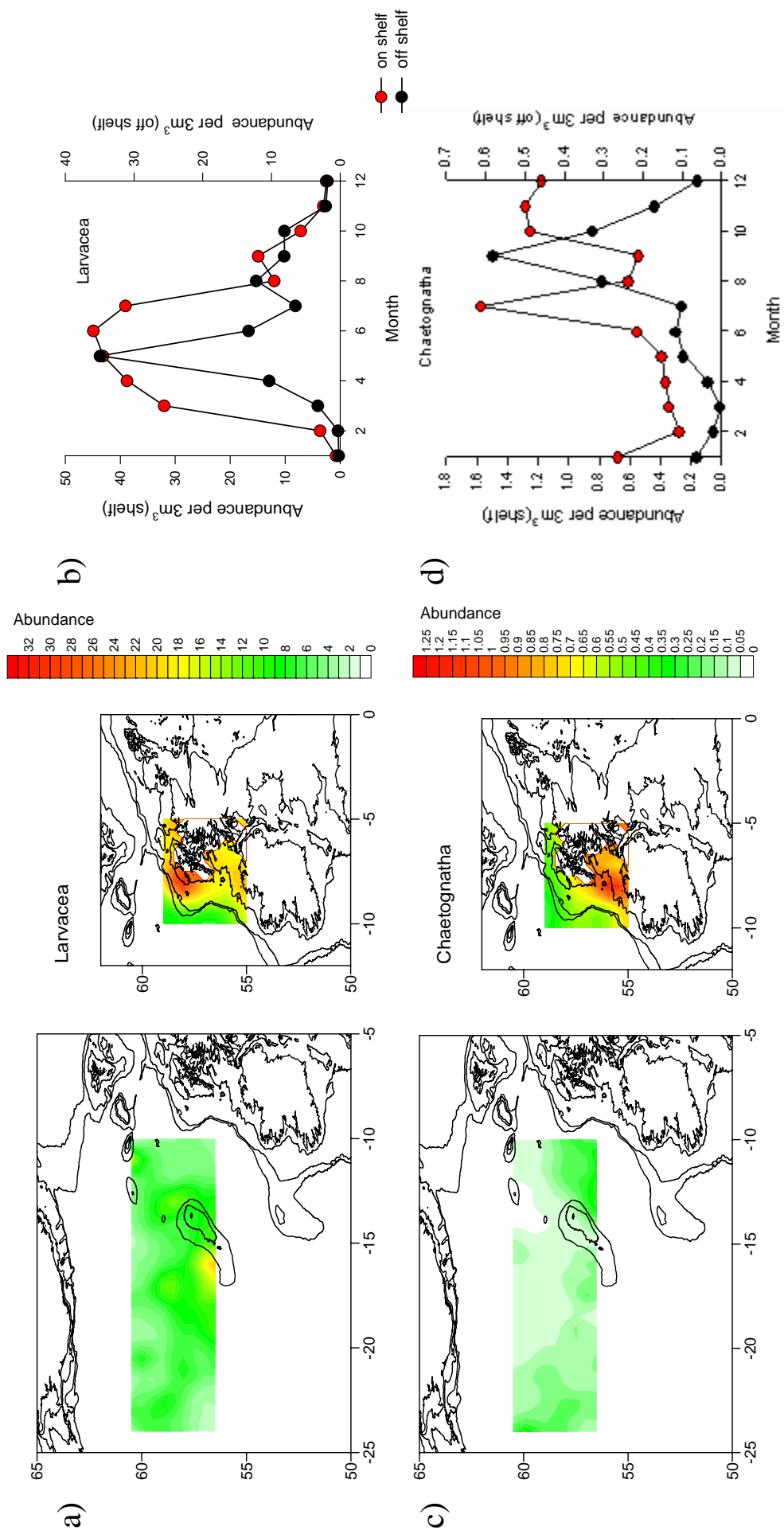
35

Figure 21. On- and off- shelf, spatial and seasonal abundance diagrams for Larvaceans (a & b respectively) and Chaetognaths (c & d respectively).
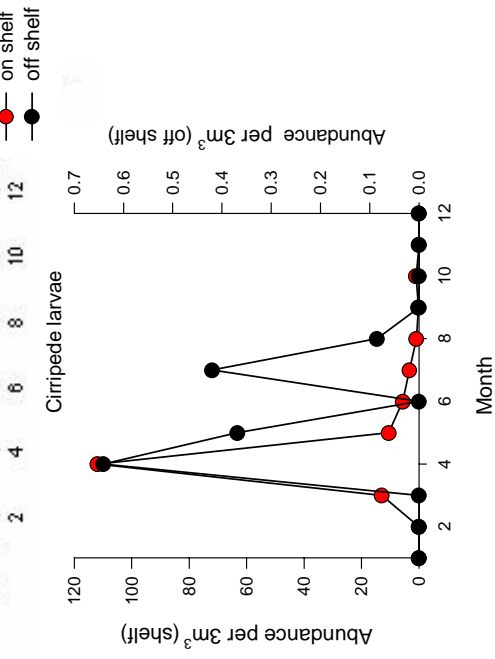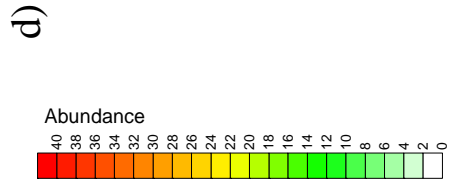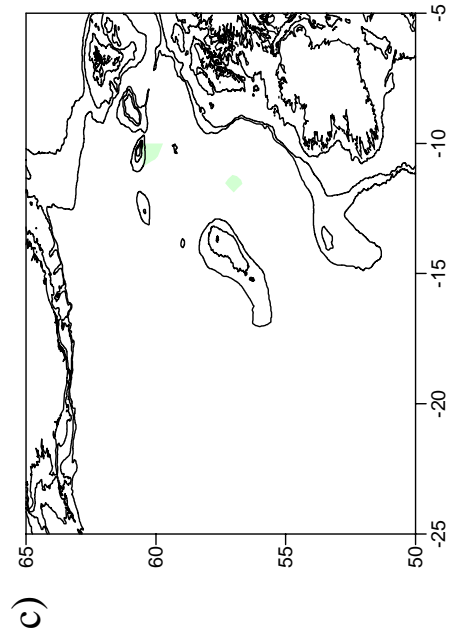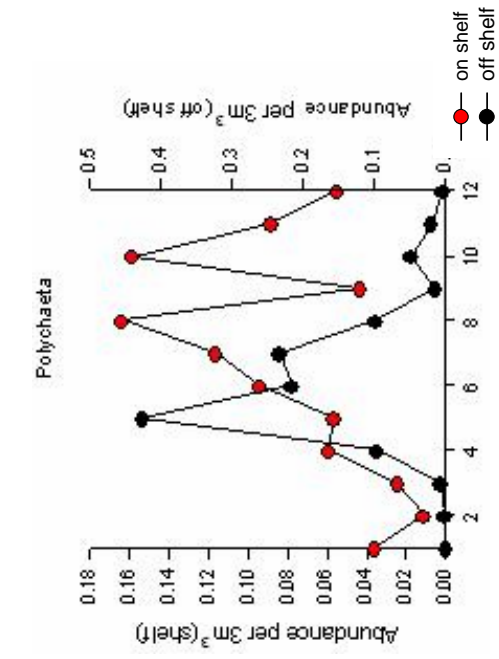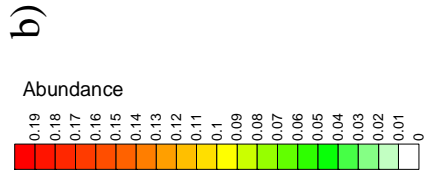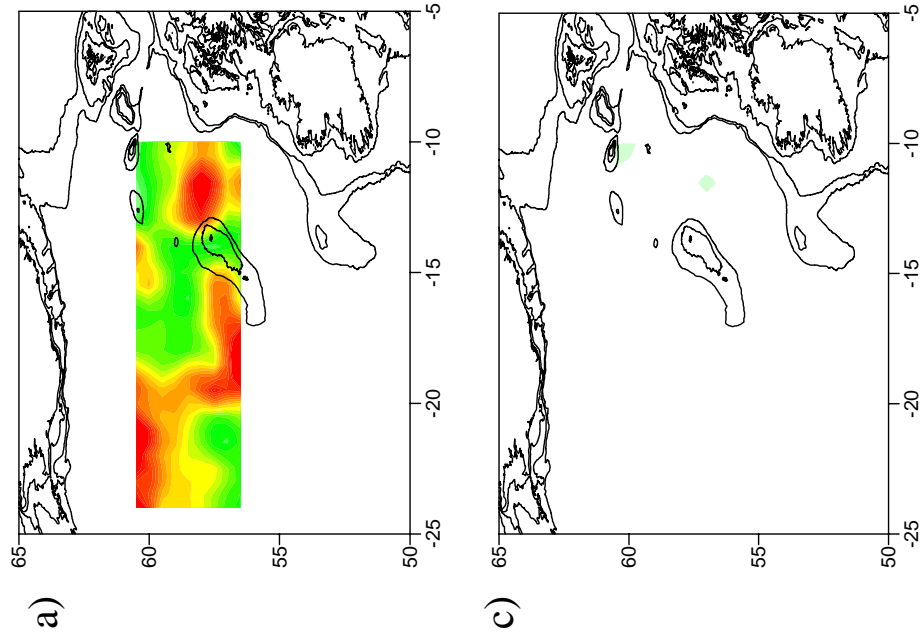
36

Figure 22. On- and off- shelf, spatial and seasonal abundance diagrams for Polychaeta (a & b respectively) and Cirripede larvae (c & d respectively).

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7.11 Polychaeta

Spatial maps Figure 22a: This group occurs throughout the study area, but in very low numbers. Areas of higher abundance include immediately on shelf, to the east and west sides of Rockall, and to the northwest of the area.

Seasonality Figure 22b: Seasonal graphs show that abundance is very low, with a peak off shelf in May, and higher values on shelf in August and October.

7.12 Cirripede larvae

Spatial maps Figure 22c: The spatial maps show an almost complete lack of cirripede larvae off shelf, they are found on shelf (to the extreme north and south of the area).

Seasonality Figure 22d: On shelf abundance peaks in April, with low numbers during the rest of the year. Off shelf numbers are very low, but there is an identifiable peak during April, plus a secondary peak during July.

8   GELATINOUS ZOOPLANKTON

The gelatinous zooplankton cover the coelenterates and ctenophores which can be regarded as macro/megaplankton due to their relative large size. Of all the zooplankton groups it is the gelatinous forms which have received the least study for the region and the most comprehensive work on the distribution and biology of this group of organisms in UK waters is that of Russell (1953) to which the reader is referred.

Jellyfish such as the moon jellyfish (*Aurelia aurita*) are commonly reported in the inshore lochs of the western Scottish coast and can reach bloom proportions. The carnivorous medusae of this species are produced via an over-wintering benthic polyp in the spring and grow rapidly during the summer months. *A. aurita* can be entrained in water currents and transported from these lochs where the pelagic phase develops to more offshore locations (Tett 1992). The ctenophores or sea gooseberries can also be abundant in the coastal waters of the SEA7 region with *Pleurobrachia pileus* and *Bolinopsis infandibulum* being the most commonly recorded.

Data on the distribution and occurrence of coelenterates and ctenophores is lacking for more offshore regions of the SEA7 region. Data from the continuous plankton recorder (CPR) gives us some indication of coelenterate abundance by analysis of the % coverage of coelenterate material recorded from the CPR silks (Figure 23). The coastal zone (with the exception of the Clyde box) is poorly represented by the CPR data and as such is not included in this analysis. It can be seen from figure 23 that the highest coelenterate index scores are recorded from the Clyde region. Offshore the distribution is more patchy with highest concentrations being recorded from waters to the extreme south and north of the region possibly associated with frontal activity.

Not mentioned above are the siphonophores, these are another order of the phylum Coelenterata. These are not individuals as such but a colony of several kinds of well-integrated polymorphic hydroid and medusoid individuals, the most notorious being *Physalia physalis*, the Portuguese Man-o'-War (Newell & Newell, 1977). Relatively few species are found in British waters although *Velella velella* (By-the-Wind Sailor) is occasionally seen in large numbers in the Clyde. Both these species are native to warmer waters and it is likely that their distribution will increase to more northern

waters if sea temperatures rise. As with other members of the zooplankton community, jellyfish and their relatives are prone to climatic shifts (see section 10 later) and it has recently been shown that the abundances of two species (*A. aurita* and *Cyanea capitella)* recorded over a 15 year period in waters to the north of Scotland were positively correlated with the North Atlantic Oscillation (Purcell. 2005).
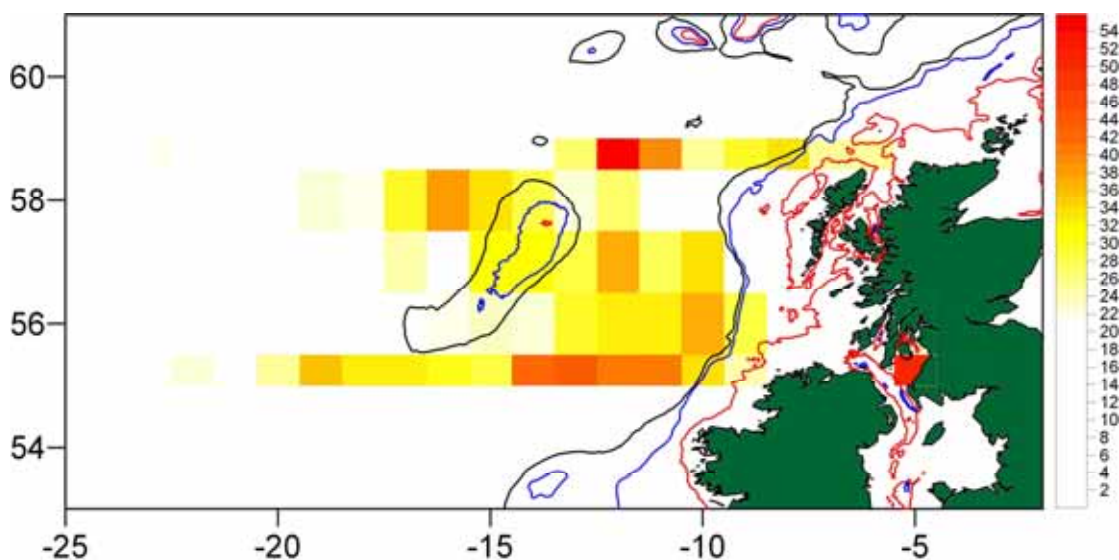

Figure 23. The distribution of Coelenterates in the SEA7 region as a function of % coverage of CPR silks with coelenterate material.

9   RESTING STAGES IN SEDIMENTS AND BALLAST WATERS

9.1   Sediments

Certain phytoplankton and zooplankton species can produce resting stages as part of there lifecycle. In the zooplankton most information comes from copepods of which 44 species have been shown to produce two types of eggs, the normal or subitaneous eggs and resting or diapause eggs. The production of these diapause eggs is caused by a change in environmental conditions and is induced by high population densities or a combination of shortening day length and temperature reduction. Once formed these diapause eggs do not develop immediately but sink to the seabed. If buried in the sediment the duration of the resting stage is increased and in some species can remain viable for as long as 40 years. However, in general the resting stages are a seasonal occurrence and hatch-time is measured in months, triggered by a period of cooling. (see review in Mauchline (1998))

Dinoflagellates such as the potentially toxic *Alexandrium* spp. produce cysts which rapidly sink out of the water column and can remain dormant in the sediments for several years. Once reintroduced into the water column and given the right combination of environmental conditions these cysts can act as an inoculum for future populations.. These cysts are formed due to either adverse environmental conditions or following sexual reproduction. As with diapause eggs these cysts sink to the seabed

but due to their hydrodynamic properties cysts tend to be concentrated in fine rather than coarse sediments (Marret & Scourse, 2002). These cysts can be transported a considerable way by water currents, especially during the winter months due to storm re-suspension events (Reid, 1975; Marret & Scourse, 2002).

Diatoms also produce resting stages known as auxospores. The development of diatom auxospores can result from environmental stress of population, as such auxospores provide a mechanism by which a dormant (benthic) population can be maintained until more favorable conditions return.

9.2   Ballast waters

The realisation that planktonic organisms can survive ships pumps has been known since the 1890's where a number of biologists used ship seawater systems to collect plankton samples. However, it was Ostenfeld (1908) who first proposed shipboard transportation of an organism as an explanation concerning the occurrence of the Asian diatom *Odontella* (*Biddulphia) sinensis* into the North Sea in 1903 (review in Carlton (1985)).

During transport in ballast tanks organisms have to put up with hostile conditions with a lack of light, varying temperatures, and reduced food availability (Carlton, 1985). However, as some planktonic organisms can produce resting stages, there survival in even the harshest conditions and subsequent hatching is of no surprise.

A study in Australia (Hallegraeff & Bolch, 1992) surveyed cargo boat ballast tanks and showed 65% were carrying significant amounts of silt in the bottom of their ballast tanks. All of these sediments contained diatoms and diatom auxospores and 50% contained dinoflagellate resting spores that were not endemic to Australian waters. As well as transport in the sediment, Williams *et al*. (1988) found 22 zooplankton species and 45 other planktonic taxa in ballast water, in cargo vessels operating between Japan and Australia. Therefore, it can be assumed that sediments and water in ballast tanks are an important vector for the spread and introduction of planktonic species. Introduction of such species can lead to the problem of genetic mixing of different stocks and the introduction of new species to an environment (Carlton, 1985).

It is also noted that the transport of these organisms can also occur on a smaller scale in domestic traffic, which can rapidly move nuisance species and increase the distributional ranges of species (Lavoie *et al*., 1999).

With specific reference to the SEA7 region little information is available, but it must be assumed that introductions of new species to the Irish Sea, North Sea and English Channel may also be represented in the SEA 7 area.

The introduction of a new species can have unfavourable effects and one such introduction reported for European waters is the non-indigenous diatom *Coscinodiscus wailesii* originally from the Pacific and Sea of China. It was first reported in the English Channel in January of 1977 and by June/July of 1978 was found in the eastern Irish Sea and now has a sizable population and is regularly

recorded from UK waters (Edwards *et al*., 2001). Although non-toxic, blooms have been reported to produce large quantities of mucilage which attracts sediment particles causing problems to fishermen, such as the clogging and breaking of fishing nets (Boalch & Harbour, 1977).

The introduction of new marine species from ballast waters has increased from the 1960's and is now thought to be responsible for about 20% of all new species introduced to the marine environment in Britain (for a full review of all species identified see Eno *et al*., (1997)).

10 THE INFLUENCE OF CLIMATE FORCING UPON PLANKTONIC COMMUNITIES IN THE SEA 7 REGION

The influence of climatic processes upon plankton community dynamics within the SEA 7 region are complex since the region covers a large geographic area with a variety of hydrographic provinces. Owing to the size and nature of the water-mass under examination, the majority of data available for the analysis of climate change impacts for the SEA 7 region comes from the continuous plankton recorder (CPR) data-base. This section is meant as an introduction to the potential impacts of climate change upon hydrographic processes that govern plankton production in the region.

The northern Atlantic Ocean plays a key role in the global circulation of water. It is in this region that the deep water mass characteristics of the global ocean are determined and the interaction between climate and the oceans are at their most dynamic. The climate of the SEA 7 region is dominated by the so-called North Atlantic Oscillation which determines the strength and direction of winds blowing over the UK and western Europe. The NAO is governed by the relative differences in Atmospheric pressure between the low pressure region centered around Iceland and the high pressure region located near the Azores. It is the fluctuations in these low-high pressure regions that determine the frequency and severity of storms and the amount of rainfall that falls within the SEA 7 region. Fluctuations in the severity and duration of winter storms have several implications for the plankton community of these waters.

During periods when the winter high atmospheric pressure cells over the Azores are intensified there is a general strengthening of winter southwesterly winds over the North East Atlantic. During such times the maritime regions of western Europe receive increased amounts of precipitation. Increased precipitation falling on land will invariably increase both the amount of dissolved available nutrients and sediment load entering the coastal waters. This can have several implications for the phytoplankton community. Firstly, increased nutrient loading to the system during the winter months can be responsible for elevated phytoplankton growth during the spring and summer. Secondly, increased sedimentary loads to the coastal zone can limit the depth of the photic zone potentially limiting phytoplankton growth via light limitation. In more offshore waters the timing of the spring bloom are linked to the onset of stratification of the waters column. If wind strengths remain high during the early spring then stratification can be delayed due to wind-driven mixing processes, this in turn can delay the spring bloom as the phytoplankton require relatively stable waters and a favourable light climate for bloom development. As phytoplankton are the base of the

marine food-web such climatically modified processes can have a knock on effect throughout the food chain.

Time-series analysis of phytoplankton abundances within offshore regions of the SEA 7 region have shown that waters to the north of the region have declined in abundance in recent years whilst those to the south have increased in abundance (Edwards *et al.*, 2001). These perturbations have been linked with changes of north Atlantic current regime shifts and climate (Reid *et al.*, 1998).

Richardson & Schoeman (2004) analysed CPR data collected over a twenty-year period for the whole of the northeast Atlantic, these authors suggested that waters of the study region fell into two turbulent-nutrient regimes associated with temperature. The first are turbulent-nutrient-rich cool waters where warming is likely to boost phytoplankton metabolic rates as well as increase stratification both of which will boost primary production. Secondly, stratified- nutrient-poor-warm waters where warming may reduce phytoplankton abundance due to enhanced stratification, ultimately leading to a microbial dominated community. Richardson & Schoeman (2004) also showed how such changes at the base of the foodweb were tightly coupled to the zooplankton community indicating very strong bottom-up control of the plankton community in such regions.

In other waters of the Northeast Atlantic Ocean the influence of climate forcing on the abundances of toxic phytoplankton species has been evaluated. Belgrano et al. (1999) evaluated a time series of primary production, chlorophyll and toxic phytoplankton species for the years 1986-1996 in the Gullmor Fjord, Sweden. These authors were able to demonstrate that certain phytoplankton species were related to changes in the North Atlantic Oscillation. Time-series of toxic forms in the SEA 7 region are as yet too short for statistical evaluation. However, it is probable that climate drivers like the NAO may have a significant impact upon the abundance of toxic forms in this region also.

11   REFERENCES

Allen, G. (1995) *Inflows, Mixing and the Internal Tide of Upper Loch Linnhe*. Ph.D. Thesis, University of Wales, 125pp

Allen, J. R., Slinn, D.J., Shammon, T.M., Hartnoll, R.G. & Hawkins, S.J. (1998). Evidence of eutrophication of the Irish Sea over four decades. *Limnology & Oceanography*, 43, 1970-1974.

Barnard *et al*.,(2004) Continuous Plankton Records:Plankton Atlas of the North Atlantic Ocean (1958–1999). II. Biogeographical charts. *Marine Ecology Progress Series* Supplement 11-75

Belgrano, A., Lindahl, O. & Hernroth, B. (1999) North Atlantic Oscillation primary production and toxic phytoplankton in the Gullmar Fjord, Sweden (1985-1996) *Proceedings of the Royal Society London* (B) 266, 425-430

Boalch & Harbour, 1977. Unusual diatom off the coast of south-west England and its effect on fishing. *Nature.* **269**, 687 - 688

Boney, A.D. (1986) Seasonal studies on the phytoplankton and primary production in the inner Firth of Clyde. *Proceedings of the Royal Society of Edinburgh. Section B (Biological Sciences)*. 203-223.

Brown, C. W., and Yoder, J. A. (1994), Distribution pattern of coccolithophorid blooms in the western North Atlantic, *Cont. Shelf Res.* 14:175-

Brown, L., Sanders, R., Savidge, G. & Lucas, C.H. . (2003) The uptake of silica during the spring bloom in the northeast Atlantic Ocean. *Limnology and Oceanography.* 48 (5), 1831-1845

Bunn, N.A., Fox, C.J. and Webb, T. (2000), A literature review of studies on fish egg mortality: Implications for the estimation of spawning stock biomass by the annual egg production method. *Sci. Ser. Tech. Rep., CEFAS, Lowestoft.* **111:** 37.

Carlton, J.T. (1985), Transoceanic and interoceanic dispersal of coastal organisms: The biology of ballast water. *Oceanogr. Mar. Biol. Ann. Rev.* **23:** 313-371.

Dodge, J.D. (1995) A seasonal analysis of the armoured dinoflagellates of Loch Eriboll, Scotland. *Journal of the Marine Biological Association of the UK*. 75, 219-235

Edwards, A., Baxter, M.S., Ellett, D.J., Martin, J.H.A., Meldrum, D.T. & Griffiths, C.R. (1986). Clyde Sea Hydrography. *Proceedings of the Royal Society of Edinburgh* 90B. 67-83

Edwards, M., John, A.W.G., Johns D.G. & Reid, P.C(2001). Case History of the non-indigenous diatoms Coscinodiscus Wailsii in the northeast Atlantic. *Journal of the Marine Biological Association of the United Kingdom,* 81., 207-211

Edwards, M, Reid, P.C & Planque, B. (2001). Long term and regional variability of phytoplankton biomass in the northeast Atlantic 1960-1995. *ICES Journal of Marine Science,* 58. 39-49.

Eno, N.C., Clark, R.A. and Sanderson, W.G. (1997), *Joint Nature Conservation Committee: Non-native marine species in British waters: a review and directory*. Joint Nature Conservation Committee. Peterborough. pp: 136.

Fraser, S, Bresnan, E & Moffat, C. (2004). Monitoring programme for toxin producing phytoplankton in Scottish coastal waters. *Fisheries Research Services Contract Report No* 12/04. FRS Aberdeen.

Gallagher, S., Howard, G. Hess, P., MacDonald, E. Kelly, M.C., Brown, N, MacKenzie, P., Gillibrand, P. & Turrell, W.R. (2001) The occurrence of amnesic shellfish poisons in shellfish from Scottish waters. In Hallegraeff et al. eds. Harmful Algal Blooms 2000. *Proceedings of the ninth international conference on harmful algal blooms.* Hobart, Australia Feb 2000. pp 30-33

Gowen, R.J., Lewis, J.M. & Bullock , A.M. (1982)A flagellate bloom and associated mortalities of farmed trout and salmon in upper Loch Fyne. *Scottish Marine Biological Association Internal Report* 71. 15pp

Gowen, R.J. Tett, P. & Jones, K.J. (1983) The hydrography and phytoplankton ecology of Loch Ardbhair: A small sea-loch on the west coast of Scotland. *Journal of Experimental Marine Biology and Ecology*. 71, 1-16

Gowen, R.J. (1987) Toxic phytoplankton in Scottish coastal waters. *Rapports et Procés-verbaux des Réunions Counseil International pour l' Exploration de la Mer.* 187, 89-93

Gowen, R.J. and Stewart, B.M. (2005) The Irish Sea: Nutrient status and phytoplankton. *Journal of Sea Res.* 54. 36-50

Gowen, R.G., Tett, P., Kennington, K.,Mills, D.K., Shammon, T.M.,Greenwood, N., Stewart, B.M., Devlin, M. & Wither, A. (2006 in prep) Is the Irish Sea Eutrophic?

Grantham, B & Tett, P. (1993) The nutrients status of the Clyde Sea in winter. Estuarine, *Coastal & Shelf Science*, 36, 449-462

Hallegreff, G.M. and Bolch, C.J. (1992), Transport of diatom and dinoflagellate resting spores in ships' ballast water: implications for plankton biogeography and aquaculture. *J. Plank. Res.* **14:** 1067-1084.

Hansen, B. 2000. Havið. Føroya Skúlabókagrunnur, Torshavn, 232 pp.

Holligan PM, Fernandez E, Aiken J, Balch WM, Boyd P, Burkhill PH, Finch M, Groom SB, Malin G, Muller K, Purdie DA, Robinson C, Trees CC, Turner SM and van der Wal P (1993) A biogeochemical study of the coccolithophore Emiliania huxleyi in the north Atlantic. *Global Biogeochem. Cycles,* 7: 879-900.

Jones, K.J., Ayres, P., Bullock, A.M., Roberts, R.J. and Tett, P. (1982), A red tide of *Gyrodinium aureolum* in sea lochs of the Firth of Clyde and associated mortalities of pond reared salmon. *Journal of the Marine Biological Association of the United Kingdom.* **62:** 771-782.

Jones, K.J., Grantham, B., Ezzi, I., Rippeth, T. & Simpson, J. (1995) Physical controls on phytoplankton and nutrient cycles in the Clyde Sea, a fjordic system on the west of Scotland. In. *Ecology of Fjords and Coastal Waters.* Skjoidal et al eds. Elselvier. 93-104

Kelly, M. & MacDonald,E (1997) SOAEFD Toxic algal bloom report, 1 January 1996 to 31 December 1996. Marine Laboratory, Aberdeen, *FRS Rep*ort 2/97 11pp

Lavoie, D.M., Smith, L.D. and Ruiz, G.M. (1999), The potential for intercoastal transfer of non-indigenous species in the ballast water of ships. *Estuar. Coast. Shelf Sci.* **48:** 551-564.

Lewis, J., Tett, P. & Dodge, J. D. (1985). The cyst-theca cycle of *Gonyaulax polyedra (Lingulodinium machaeophorum)* in Creran, a Scottish west coast sea-loch. In *Toxic Dinoflagellates*, ed. Anderson, White, & Baden. Elsevier Science Publishing Co., 85-90.

Longhurst, A.R. (1998) Ecological Geography of the Sea. Academic Press. California. p 398

Mackay, W.A., Baxter, M.S. Ellett, D.J., & Meldrum, D.T. (1986) Radiocaesium and circulation patterns west of Scotland. *Journal of Environmental Reactivity.* 4, 205-232.

Mandali de Figueiredo, G. (2003), Trophodynamics of the planktonic community in the coastal areas of the central Irish Sea, with emphasis on fish larvae and their prey. PhD Thesis, Liverpool. pp: 186.

Marret, F. and Scourse, J. (2002), Control of modern dinoflagellate cyst distribution in the Irish and Celtic Seas by seasonal stratification dynamics. *Mar. Micropaleont.* **47:** 101-116.

Mauchline, J. (1998), *Advances in marine biology: The biology of calanoid copepods.* J.H.S. Blaxter, A.J. Southward, P.A. Tyler (eds). Academic Press Ltd. London. **33:** pp: 710

Okada, H. & McIntyre, A. (1979) Seasonal distribution of modern coccolithophorids in the western N. Atlantic Ocean. *Marine Biology.* 54. 319-328

Purcell, J.E. (2005) Climatic effects on formation of jellyfish and ctenophore blooms: a review. Journal of the Marine Biological Association of the United Kingdom. Volume 85, 3. 261-477

Richardson.A.J. & Schoeman. D.S (2004). Climatic Impact on Plankton Ecosystems in the Northeast Atlantic. *Science* 305. 1609-1612.

Rippeth, T.P and Jones, K.J. (1996) The seasonal cycle of nitrate in the Clyde Sea. *Journal of Marine Systems*. 12, 299-310

Reid, P.C. Edwards, M, Hunt, H.G. & Warner, A.J. (1998) Phytoplankton change in the North Atlantic. *Nature*, 391, 546.

Rogers, A.D. (1994) The biology of seamounts. *Adv.Mar Biol*. 30:305-350.

Russell, ,F.S. (1953) *The Medusae of the British Isles*. CUP. Cambridge UK. 2 vols.

Simpson, JH; Edelsten, DJ; Edwards, A; Morris, NCG; Tett, PB (1979)The Islay Front: Physical Structure and Phytoplankton Distribution. *Estuarine and Coastal Marine Science* Vol 9, No 6, p 713-726

Smith, P. S. D. (1999). Bio-optical observations at the Hebridean shelf edge. PhD, University of Wales, Bangor, Menai Bridge.

Tait, R.V. (1992), *Elements of marine Ecology*. Butterworth-Heinemann Ltd. Oxford. pp: 356.

Tett, P.B. (1971) The relationship between dinoflagellates and the bioluminescence of sea water. *Journal of the Marine Biological Association of the UK*. 51, 183-206.

Tett, P. Phytoplankton and fish kills in Loch Strivan. *Scottish Marine Biological Association, Internal Report* 25. 110 pp1980

Tett, P., Drysdale, M. & Shaw, J. (1981) Phytoplankton in Loch Creran during 1979, and its effects upon the rearing of oyster larvae. *Scottish Marine Biological Association Internal Reports*. 52. Oban: SMBA

Tett, P., Heaney, S.I. & Droop, M.R. . (1985) The redfield ratio and phytoplankton growth rate. *Journal of the Marine Biological Association of the United Kingdom*. 65, 487-504.

Tett, P. The ecology of plankton in Scottish coastal waters. (1992). Proceedings of the Royal Society of Edinburgh. 100B. 27-54

Tett, P. Gowen, R. Granthem, B. & Jones, K. (1986). The phytoplankton ecology of the Firth of Clyde sea lochs Striven & Fyne. *Proceedings of the Royal Society of Edinburgh*. Section B (Biological Sciences). 223-239

Tett, P. (1986) Physical exchange and the dynamics of phytoplankton in Scottish Sea Lochs. The role of freshwater outflow in coastal marine systems. Berlin, May 1985, ed. Skreslet, S. Springer Verlag. NATO ASI series, G7, 205-218

Tett, P & Edwards, V. (2002) Review of Harmful Algal Blooms in Scottish Coastal Waters. *Report to SEPA June 2002*. Napier University. Edinburgh 120p

Treasurer, J.W., Hannah, F. & Cox, D. (2003) Impact of a phytoplankton bloom on mortalities and feeding response of farmed Atlantic salmon, Salmo salar, in west Scotland. *Aquaculture* 218, 103-113

Turner, S.M. Malin, G., Liss, P.G., Holligan, P.M. & Harbour, D.S. (1988) The seasonal variation of dimethyl sulfide and dimethylsulfoniopropionate concentrations in nearshore waters. *Limnology and Oceanography*. 33, 364-375

Watts, L.J., Rippeth, T.P. & Edwards, A. (1998) The roles of hydrodrographic and biogeochemical processes in the distribution of dissolved inorganic nutrients in a Scottish sea loch: Consequences for the spring phytoplankton bloom. *Estuarine, Coastal and Shelf Science*. 46, 39-50.

White, M., Mohn, C., de Stigter, H., and Mottram, G. 2004: Deep water coral development as a function of hydrodynamics and surface productivity around the submarine banks of the Rockall Trough, NE Atlantic. In press: *Deep water corals and ecosystems*. Procs 2nd International symposium on deep water corals,. Eds. A. Freiwald and M. Roberts. Erlangen, Germany

Williams, R.J., Griffiths, F.B., Van der Wal, E.J. and Kelly, L. (1988), Cargo vessel ballast water as a vector for the transport of non-indigenous marine species. *Estuarine, Coastal and Shelf Science* **26:** 409-420.

Wood, B.J.B., Tett, P.B. & Edwards, A. (1973) An introduction to the phytoplankton primary production and relative hydrography of Loch Etive. *Journal of Ecology*, 61. 569-585