The Role of Kelp in the Marine Environment

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DEPARTMENT OF THE ENVIRONMENT, HERITAGE
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The Role of Kelp in the Marine Environment

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Preface

National Parks & Wildlife Service (NPWS) at the Department of Environment, Heritage and Local Government (DoEHLG) is responsible for the conservation of natural habitats and species and the protection of biological diversity in Ireland; it is also responsible for providing advice to Licensing Authorities in that regard.

In recent years, the national kelp resource has come under increasing pressure from coastal developments and industrial expansion and diversification. The most significant of these is a proposal to develop a mechanical kelp harvesting industry in Ireland. Following a preliminary examination, it was apparent that a significant corpus of knowledge existed to indicate that kelp species play a varied and valuable role in the structure and function of inshore habitats and communities.

To ensure the continued provision of high quality advice, NPWS commissioned an expert review of the role of kelp in the marine environment with an assessment of the likely threats that may arise from a possible mechanical harvesting industry. These reviews focussed specifically on marine birds, fish, invertebrates, flora and productivity. Contributing authors were also requested to outline areas of research that would address conspicuous gaps in information and provide a summary of their conclusions. Rather than produce five separate reports, the contributions were edited into a single reporting format, in consulatation with the respective authors to ensure there was no misrepresentation of each individual’s views.

No part of this publication should be taken as a statement of NPWS policy. The views expressed by individual contributors with regard to their respective areas of expertise are not necessarily those of NPWS or other contributing experts.

Dr Eamonn Kelly

Executive Summary

Kelp forests have been described as one of the most ecologically dynamic and biologically diverse habitats on the planet. In response to proposals to develop a mechanical kelp harvesting industry in Ireland, a series of expert reviews were commissioned to describe the various ecological roles of kelp in the marine environment and particularly in relation to marine productivity, flora, fauna, fish and birds. *Laminaria digitata* and *L. hyperborea* are the only species that form extended monospecific kelp beds in Ireland and constituted the primary target species of this review.

The primary production of kelp per unit area is amongst the highest known in aquatic ecosystems. Kelp primary production results in the production of new biomass, detrital material shed from the blade tip, mucus and other dissolved inorganic material and spores, as well as internal respiration. The production of dissolved organic matter by kelp although very difficult to determine in the field is also considered an important part of kelp production. The importance of kelp not only as a habitat but as a food resource has been highlighted by numerous studies; in some cases, up to 60% of carbon found in coastal invertebrates is attributable to kelp productivity. It may be consumed directly or colonised by bacteria that in turn are preyed upon by consumers.

The holdfast, stipe and fronds of kelp plants present available substratum for colonisation by marine flora and invertebrates. The holdfasts tend to host strongly associated communities of epiphytes and marine invertebrates. Kelp contributes directly and indirectly to the food resource of suspension and deposit feeding invertebrates that in turn serve as prey to more mobile invertebrates such as polychaetes, cnidaria and larger decapods. Kelp derived detritus on the shore is also consumed by invertebrates and bird species.

The rich fauna of mobile invertebrates in kelp beds makes this an important habitat in the diet of fish species. Seasonal and temporal changes in the abundance of prey species reflected in the diet of some fish species would suggest a degree of opportunism. As invertebrate abundance has also been related to the age and size of the plant within kelp species, there may be some interspecific variation between kelp species in the feeding opportunities available to fishes.

Kelp forests provide a foraging habitat for birds due to the associated and diverse invertebrate and fish communities present. Three sub-components, the surface canopy, mid- and bottom- areas, and fringe areas were distinguished in this regard. Accumulations of drift kelp in open water provide a valuable roosting site for birds, particulary as they often transport potential prey items. Many marine and terrestrial bird species are directly dependant on kelp detritus washed up on the shore as wrack due to the densities of resident larvae and invertebrates. Kelp wrack also benefits birds via its role in providing organic matter to coastal marine ecosystems.

Some invertebrate and fish species exhibit egg attachment and nest-building, respectively, in kelp habitats while others such as juvenile gadoids and salmon utilise kelp habitats as important nursery and refuge grounds. The under-storey habitats created by the kelp plants also give rise to microniches that support a somewhat similar community of species, particularly large decapods. The effective extension of the substratum into the water column increases shelter, or refugia, available to fishes while also providing habitat for the prey species used as a forage base by reef fishes. This contribution to diversity is more pronounced in otherwise relatively 2-dimensional environments.

The potential impacts that may arise from mechanical kelp harvesting are reviewed and significant gaps in information are identified.

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Introduction

Kelp species represent the largest and structurally most complex brown algae and comprise different genera referred to as the Order Laminariales. Kelps are the most prominent constituents of the lower intertidal and subtidal of Atlantic and Pacific rocky shores of temperate regions of both the Northern and Southern Hemisphere. As canopy algae they often form dense beds, referred to as kelp forests, supporting a rich understorey flora and fauna. Worldwide, kelp forests sustain a huge diversity of fish and are the source of raw material for the alginate industry. Major factors in determining the biogeographical distribution of kelp species are the winter and summer seawater isotherms that set the limits for survival and reproduction. Five kelp species are indigenous to Ireland: *Saccorhiza polyschides* (Lightfoot) Batters; *Alaria esculenta* (L.) Greville; *Laminaria hyperborea* (Gunnerus) Foslie; *Laminaria digitata* (Hudson) J.V. Lamouroux; and *Laminaria saccharina* J.V. Lamouroux. They differ in various aspects, such as morphology, ecophysiology and longevity, and show distinct patterns of vertical distribution on the shore. *L. digitata* and *L. hyperborea* are the only species that form extended monospecific kelp beds and are the target species of this review.

The basic structure of kelp consists of a holdfast (mostly branching root-like structures that anchor the kelp to the substratum), a long flexible stipe and a frond (also called a blade or lamina). The vertical distribution or zonation of kelp species on subtidal rocky substrata results from their responses to a number of factors such as light penetration, wave exposure, competition, grazing and tolerance to emersion. The extension of *Laminaria digitata* beds into greater depths of the shallow sublittoral zone is restricted by the occurrence of *L. hyperborea* (Lüning, 1990). This species is less adapted to the strong wave impact of the upper sublittoral zone. The 1 – 2 metres long rigid upright stipe lifts the large digitate blade of *L. digitata* above the bottom and thus allows maximal exposure of the frond to light while shading all other understorey algae allowing only shade loving algae to florish. Dense *L. hyperborea* forests are formed down to depths, which obtain 5% of surface light (e.g., a depth of 30 m in Ireland). An additional advantage of *L. hyperborea* with respect to its competitiveness is its longevity. Individuals may reach an average age up to 15 years, whereas other laminarian species of the upper sublittoral zone generally live no longer than 3 - 4 years (Lüning, *op. cit.*) although Gunnarson (1991) reported 25 years old *L. hyperborea* plants from Iceland.

The biological cycle and growth of the Laminariaceae is well documented. The life cycle of *Laminaria digitata* has been known since Sauvageau (1918). *Laminaria* plants have a two stage life cycle in which a large diploid thallus (comprising holdfast, stipe and blade) produce haploid spores which germinate to produce a nearly microscopic plant (the gametophyte) that in turn produces haploid male and female gametes. Fusion of the gametes gives rise to the diploid or sporophyte phase. The overwhelming bulk of primary production in the species is produced by the sporophyte. Reproduction is from July until the end of the year/spring. The spores are produced in visible dark patches on the blade termed sori (single = sorus). Flagellate zoospores are shed in two seasonal peaks one in July and one in November. The sporophyte becomes mature after 18 months, reaching maximum fertility at 3 years. Plants can live for 5 years in sheltered places. *L. hyperborea* can live for more than 12 years with an average of 8 years; they reach maturity after two years and are fertile during winter.

Growth in all *Laminaria* species is meristematic. The meristem (or cell division area) is located between the stipe and blade. The stipe always exhibits positive growth while the blade of *L. digitata* increases in the first six months of the year but decreases in length during the last six months due to apical erosion (Cosson, 1978 as cited in Arzel, 1989). In other words *net growth in length is a balance between blade growth at the basal meristem and erosion at the blade tip*. However, on balance, blade growth exceeds apical blade erosion during the first three years of the plant's life. Maximum length is reached during the third year while blade erosion exceeds growth in year four. The blade disappears by year five. In *L. hyperborea* and *L. saccharina*, the old blade is shed annually after sporulation. Prior to shedding, a constriction or waist appears in the blade dividing the older from the younger part. The part that detaches is where the sori have developed and then sporulated. Following shedding, regeneration of the blade occurs in both *L. hyperborea and L. saccharina*.

Each year the kelp plant renews its blade or lamina while the stipe increases in size. However kelp stipes cannot be compared to wood as a carbon storage mechanism and by far the greater part of kelp annual production is released back into the ecosystem each year, as the blade decays. A comparison of blade growth rate, measured as increase in length by means of marker holes or tags, with actual blade size shows the time of maximum tissue shedding. As might be expected the greater part of detritus production occurs in late summer with the loss of old blade material. In addition, old plants are removed by winter storms. Further detritus is formed in late spring when *L. hyperborea* sheds its old fronds. However the high production to biomass (P/B) ratio of kelp beds suggests that shedding of old or damaged tissue may occur at other periods as well.

Kelp forests of cold-temperate regions around the world represent highly diverse, dynamic and complex ecosystems (Mann 1982; Dayton 1985). The biodiversity of kelp forests is extraordinarily high in comparison to other algal communities. Through their three-dimensional structure kelp species provide additional substrata for a broad spectrum of macro and micro flora and fauna. The diversity and number of individuals, however, is higher in *Laminaria hyperborea* beds than in *L. digitata* stands (Schultze *et al.*, 1990). This might be attributed to the effects of higher mechanical impact as *L. digitata* grows in shallower water and is therefore more exposed to surf and occasional emersion. Additionally, the smooth and flexible stipes of *L. digitata* are generally not colonised by other species.

Ecological Role

Kelp forests have been described as one of the most ecologically dynamic and biologically diverse habitats on the planet (Birkett *et al.*, 1998). Kelp species are considered as *Keystone Species* or species whose presence affects the survival and abundance of many other species in the ecosystem. Their removal is likely to result in 'a relatively significant shift in the composition of the community and perhaps in the physical structure of the environment' (Wilson, 1992). Clearly the removal of kelp species will have obvious negative effects on the invertebrate species that live in the holdfast, the stipe or fronds or under the fronds. Additionally, material that is continually being lost from kelp forests fuels a complex recycling system of bacteria, herbivores, direct and indirect suspension feeders and eventually carnivores.

As in all plants, primary production results in the manufacture of new biological matter by combining light energy with carbon dioxinde (CO_2) and water (H_2O) to form carbohydrate and subsequently other more complex material through the inclusion of nitrogen (N), phosphorus (P) and other inorganic elements. In unicellular plants, plants grow by cell division but in more complex multicellular plants cell division is confined to certain meristematic areas. In *Laminaria*, cell division occurs at the junction of the stipe and lamina (or blade). However growth is often counterbalanced by erosion of the blade tip. In addition, kelps produce mucus and other extracellular matter and also discharge spores into the surrounding water. Thus, it is not possible to equate yearly production with the net increase in plant weight over the growing season, i.e., the primary production of *Laminaria* is more than the simple increase in thallus weight.

Estimates of the total primary production of kelp beds are surprisingly high. Mann (1982) suggested figures of 1000-2000 g carbon (C) m^2 per year based on reviews of several previous studies (by comparison, coastal plankton is thought to produce 150-300 g C per year). However, Mann's (*op. cit.*) measurements in Nova Scotia of 2000 g C m^{-2} were not replicated by some subsequent workers (Chapman, 1987). Nevertheless, it is generally accepted that primary production is high in kelp beds with reports of 1000 g C m^{-2} per year (Mohammed & Fredriksen, 2004). A recent estimate (Birkett *et al*., 1998) of subtidal macroalgal productivity for Strangford Lough, Co. Down gave a figure of 68,582 tonnes C for the lough. The area of Strangford is 15,398 ha.; dividing total production by area gives a figure of 440 g C per m^2 per year, on the unrealistic assumption that the entire lough is covered with kelp forest. A more realistic guesstimate that 25% of the area is kelp forest gives a production 4 times greater of 1600 g C per m^2 per year.

In ecosystem modeling, macroalgal production is estimated by means of a production to biomass ratio (P/B). Several authors suggest P/B ratio for kelp forest of 4-10, i.e., production is 4-10 times average standing crop. Birkett *et al*. (1998) give a standing crop in Strangford of 276,281 wet tonnes or approximately 15,000 tonnes of C giving a P/B of about 4. Werner and Kraan (2004) report a standing crop of 3.4-19.5 kg wet weight of kelp per m^2 in Galway Bay. Using the ratio of tonnes C produced to wet tonnes standing crop of 0.248 presented by Birkett *et al*., (*op. cit.*) suggests a production of 843-4,800 g C per m^2. As the average yearly biomass is used in P/B calculations, a figure of about 2000 g C seems appropriate. This figure agrees with other estimates for kelp forest, e.g., in Norway, *L. hyperborea* reaches recorded densities of 15 kg. wet weight per m^2 at depth from 5-15 metres (Arzel *et al*., 1990).

In a review of kelp forest ecosystems of the north west Atlantic, Steneck *et al.* (2004) identify three distinct and sequential phases in their trophic structure in the Gulf of Maine based on archaeological, historical, ecological and fisheries data. Phase 1 is characterised by top predators such as cod, haddock and wolffish and lasts ca. 4,000 years; Phase 2 is characterised by herbivorous sea urchins and extended from the 1970’s to the mid-1990’s. Phase 3 is dominated by crabs and has only developed since 1995. The factor that brings about such changes is reported as fishing pressure. When the populations of the top level fish predators had been reduced by severe overfishing in the 1960’s and ‘70’s, predation pressure on lower trophic levels decreased and this probably lead to the increase in urchins and other benthic invertebrates within the kelp beds (Steneck *et al*., *op. cit.*). They state that locally this transition could happen rapidly although regionally it took decades. By the mid-‘70’s and early ‘80’s, kelp forests reached an all time low in their distribution and abundance throughout the region due to intensive urchin grazing pressure giving rise to the so called “urchin barrens”. Coralline algal crusts (which are not preyed upon by urchins) dominated the benthos and due to their flat, two dimensional nature, they do not provide the same range of microhabitats for taxa such as crustaceans and polychaetes. Fishing of the urchins commenced in 1987 and the population was quickly depleted so that by the mid-1990's local re-establishment of macroalgal beds had occurred. Steneck *et al*. (*op. cit.*) also state that the top predators in the kelp beds at present are crab species such as *Cancer* and *Hyas*.

Even though modern fishing pressures in inshore Irish coastal areas have been ongoing for many decades, increases in urchin populations such as *Echinus, Psammechinus* and *Paracentrotus* have not been recorded. Steneck *et al.* (2002) report that sea urchin-induced kelp deforestation were reported in Ireland by Kitching and Ebling (1961) and Ebling *et al* (1966). However, examination of these papers made no mention of laminarians although Kitching and Ebling (*op. cit.*) do refer to *Enteromorpha, Chylocladia, Polysiphonia, Ceramium* and *Ectocarpus*.

The bulk of research on relationships between fish fauna and kelp species has been carried out in North America and Australasia. Numerous studies have been conducted on the ecology of the giant kelp forests, *Macrocystis pyrifera* and *Nereocystis* spp. distributed along the western coasts of the United States and Canada, with considerable emphasis on related fish species associations and biodiversity (e.g., Quast, 1968ab; Miller and Geibel, 1973; Russel, 1977; Leaman, 1980; Ebeling *et al*., 1980; Ebling and Laur, 1988; Laur *et al*., 1988). A number of studies have researched the fish species diversity in kelp habitat relative to non-vegetative habitats (Larson and DeMartini, 1984; Stephens *et al*., 1984; Murphy *et al*., 2000) whilst some studies have specifically investigated the effects of kelp removal and harvesting on associated fish communities (Limbaugh, 1955; Bodkin, 1988). There has also been a considerable amount of research conducted in New Zealand on herbivorous fish associations in kelp forests (Zemke-White and Clements, *in press*) as well as studies on fish diversity associated with kelp habitat (Shears and Babcock, 2003).

Most of the research on fish species associated with kelp habitat in Europe has been conducted in Norway. Høisæter and Fossa (1993) compiled a list of fish species found in Norwegian kelp forests and investigated the diet of a number of species, whilst Fossa (1995) reported the distribution of fishes closely linked to kelp habitat.

Other researchers have highlighted the importance of the habitat for particular species, e.g., Sjøtun and Lorentsen (2003) recently demonstrated the importance of *Laminaria hyperborea* forests as important habitats for juvenile gadoids. Studies in Northern Ireland (Erwin *et al.*, 1990), England (Moore, 1972; 1973), Scotland (Abbott and Perkins, 1977; Perkins *et al.*, 1978) and Helgoland (Schultze *et al.*, 1990) have been primarily concerned with invertebrate fauna of the kelp habitat with only coincidental records of benthic fishes reported. For example, Abbot and Perkins (*op. cit.*) found *Pholis gunnellus* (butterfish) eggs in the holdfast of *L. hyperborea*, whilst Erwin *et al*. (*op. cit.*) only recorded one fish species, *Ctenolabrus rupestris* Goldsinny Wrasse, in their survey of the *L. hyperborea* communities around the coast of Northern Ireland. Only one study in Scotland was devoted to the study of fishes in kelp habitat and this was concerned with the biology of some small fishes living in the holdfasts of *Saccharina polyschides* (Gordon, 1983).

The available literature on fish species associated with kelp habitat in Ireland is limited. The few studies that have focused on kelp habitat fauna have been mainly concerned with the benthic invertebrate community with little consideration given to the nektonic component (e.g., Edwards, 1980; McGrath, 1997; Picton and Costello, 1998). Some records are available through review of the BIOMAR project's database on biotopes in Ireland (Picton and Costello, 1998) and through review of the wider literature on the biology and ecology of fish species (e.g., Dunne, 1981, Miller, 1986, Erwin and Picton, 1990, Varian, 1998). However, there does not appear to have been a study that has focused specifically on kelp habitat associations and preferences in fishes. To that end, a list of fish species that may be associated with kelp habitat in Ireland is presented in Appendix 1. Records of fish species observed in similar habitat elsewhere in Europe were included due to the limited amount of information available on kelp habitat species associations in Ireland. It should be noted that this list can only give an indication of the species that may *potentially* be associated with kelp habitats in Ireland, as there may be significant local variation in the species composition of associated communities depending on geographical factors (Erwin *et al*., 1990; Murphy *et al*., 2000). For example, Erwin *et al*. (*op. cit.*) found significant variation in the species composition of *Laminaria hyperborea* communities on different areas of the coast and this was attributed both to the exposure gradient along the coastline and a change in water clarity.

Viewing the kelp forest as a simplified food chain (Figure 1), it is apparent that kelp species form the basis of the grazing food chain (i.e., through primary production) and are a major contributor to the detrital food chain. Birds and fish are examples of carnivores (or predators) within this food chain but neither are necessarily the apex consumers in the system as each in turn may be predated upon by higher level carnivores.

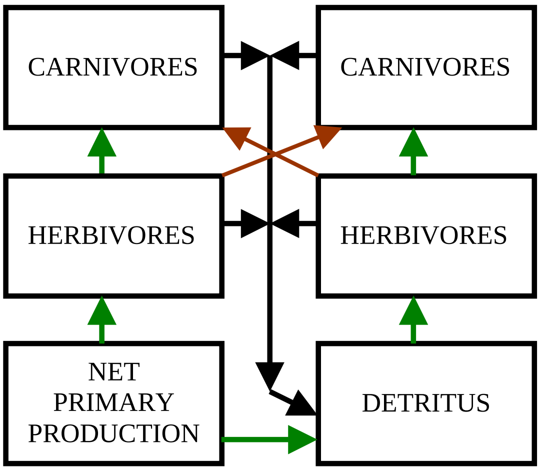


Figure 1 Simplified Food Chain.

While previous studies of kelp forest food chains have been undertaken, relatively little attention has been given to the higher predatory levels (e.g., birds). One exception is Fredriksen (2003) who studied a Norwegian kelp forest food web using stable isotope analysis based on $\delta\ ^{13}$Carbon and $\delta\ ^{15}$ Nitrogen. This method allows the carbon (food) source to be traced for each of the food web components and also allows the identification of trophic relationships (i.e., feeding relationships). Two bird species were studied and the results found that 37% and 49% of the carbon of Cormorants *Phalacrocorax carbo* and Common Eiders *Somateria mollissima* originated from kelp, considerably greater for example, than for particle (filter) feeders whose carbon signal was intermediate between kelp and phytoplankton (Figure 2). The two seabird species however were found to occupy two different trophic levels relating to their different food sources within the kelp forest (Cormorants – fish; Eiders – invertebrates).

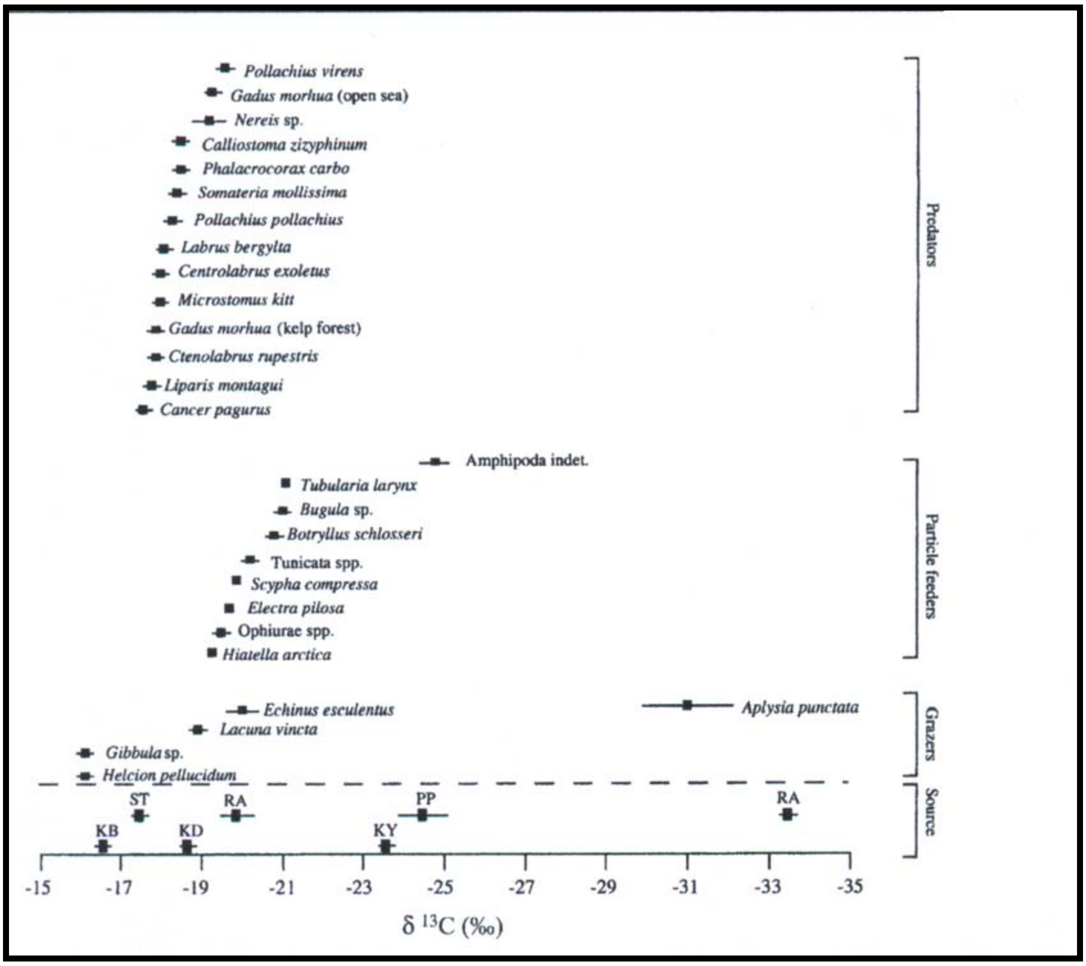


Figure 2 δ ^{13}C values from the different carbon sources and animals representing three principal feeding modes within the kelp forest ecosystem (From Fredriksen, 2003).

1. Production

A. Spatial and temporal growth patterns

Kelp forests occur from the sub-littoral fringe downward on hard substrata. It is generally agreed that the maximum depth reflects the extent of light penetration with kelp found at 30 m in very clear Atlantic water but at less than 2 m in turbid water, for example, the Shannon Estuary. Several physical factors interact in kelp growth. Differences recorded between plants growing on the low intertidal and those from the subtidal are not due to variation in the ionic composition of the water since the action of wind, tidal currents and waves result in an homogeneous salt concentration at the surface and down to 4 m deep. The reasons are found in differences in the infrared, red and ultra-violet radiation penetration coefficient of the water column and in absorption by plant pigments. Irradiation intensity and temperature determine growth rate, especially at the spore and pro-thalli stage of the kelp life cycle. As a result, the performance of plants growing in the intertidal depart from the growth optimum experimentally recorded for *Laminaria digitata* gametophytes by Pérez (1971) of 1,500–4,000 lux and highest fertility at 13°C (Fig. 3). Growth of the plantlets is optimal at 11°C-13°C (Pérez, *op. cit.*).

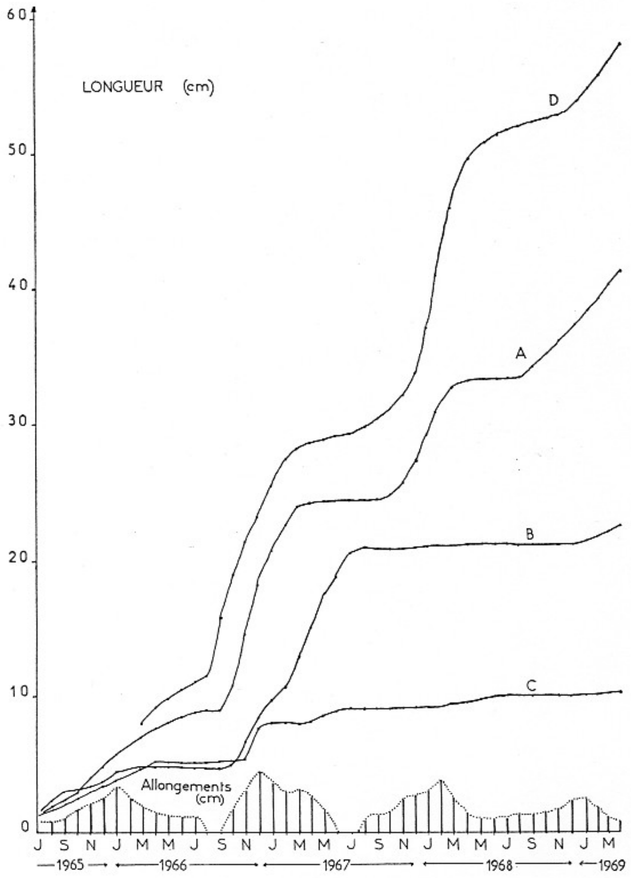


FIG. 13. — *Evolution de la longueur du stipe au cours de la vie de* Laminaria digitata *à différents niveaux bathymétriques.* Courbes B et C : thalles vivant à l'extrême limite de l'étage infralittoral ; courbe A : ceux vivant légèrement en dessous du niveau des plus basses mers ; courbe D : ceux vivant par 4 m de fond ; les allongements mensuels portés à la base du graphique se rapportent à la courbe A.

Figure 3 Growth in length of the stipe in *Laminaria digitata* at different depths, B and C: lowest shore, A: just below extreme low water springs, D: -4 m O.D. Monthly increase in length for curve A is shown at base of graph (Pérez, 1971).

Kelps tend to grow fastest in the cooler part of the year with maximum biomass occurring in early Autumn. In Galway Bay, Werner and Kraan (2004) found this pattern for both *Laminaria digitata* and *L. hyperborea*. The weight evolution of a kelp population was estimated by Arzel (1998) who showed variation from 10 kg of *L. digitata* wet weight per m^2 in July and August in Brittany down to 3 kg per m^2 at the end of August and early September when equinoctial storms occurred. A similar pattern was observed by Chapman (1984) and by Werner and Kraan (*op. cit.*) in Galway Bay.

B. Nutrients

The growth pattern in kelp mirrors the distribution of N and P in coastal waters with a winter peak in nutrients followed by a summer minimum. The link between kelp growth and nutrient availability is complex. In phytoplankton ecology, it is known that nutrient shortage affects algal growth and eutrophication results in a greater phytoplankton biomass. It is not certain that increased nutrients directly increase kelp production. Several studies report that smaller more ephemeral algae respond to nutrient increase rather than kelp in coastal ecosystems. However, aquaculture experience shows that kelp growth is limited by nutrient shortage. It is also noticeable that the world's kelp forests only occur in areas with high seasonal N and P availability. Some workers report maximum growth during periods of high nutrient concentrations while Mizuta (2003) suggests that growth stops in Summer in *Laminaria japonica* when internal P falls below a critical level. Kelps have a capacity to store N and P in their tissue and make it available for later growth, thus buffering the plant against external nutrient shortage. Accordingly, growth in summer may be limited either by nutrient shortage or, if sufficient stored nutrient is available, by light shortage caused by overcrowding. There is also evidence that, as in many higher plants, growth is not directly linked to external conditions but controlled by internal regulation.

C. Age and production

In Canada, the natural mortality of *Laminaria digitata* and *L. longicruris* sporophytes is approximately 50% of the population per year (Chapman 1986).

Table 1 *Laminaria digitata* survival over time in Brittany, France as presented in Pérez (1971).

Date	Nombre de survivants
Juillet 65	100
Juillet 66	36,0
Juillet 67	13,1
Juillet 68	4,6
Juin 69	

In *L. digitata* in Britany only 4.6% of a cohort survived to year 4 (Table 1). In terms of population dynamics, *L. digitata* exhibits a high population turnover. Growth is meristematic with new cells produced from the stipo-frontal zone. The stipe always exhibits positive growth while the blade increases in the first six months of the year but decreases in the last six months due to apical erosion (Cosson, 1978 as cited in Arzel, 1989). However, on balance blade growth exceeds apical blade erosion during the first three years of the plant's life. Maximum length is reached during the third year while blade erosion exceeds growth in year four (Figure 4). The blade disappears by year five. Age vs. length ratio is not very significant because of the great variation from one sampling site to another. Different cohorts in different regimes produce different weight estimations.

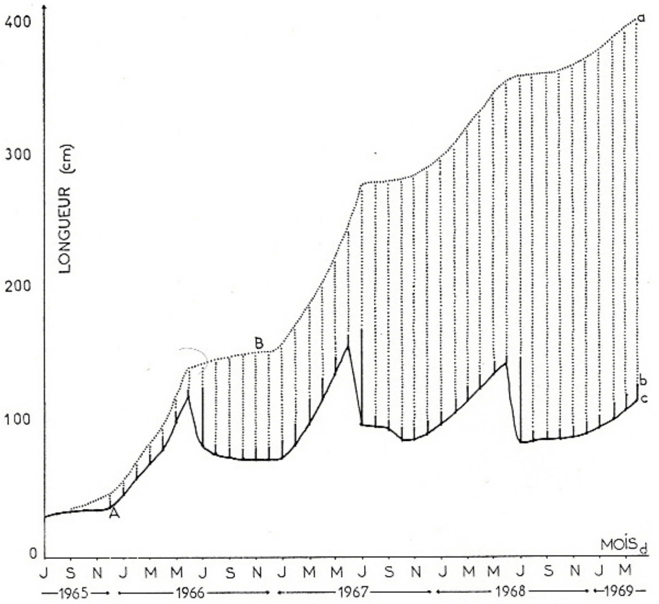


FIG. 7. — *Croissance en longueur de la lame.* La courbe A représente l'évolution réelle de la longueur de la lame ; la courbe B l'évolution de cette longueur s'il n'y avait pas d'usure apicale ; la distance *ab*, la somme des pertes apicales des mois précédents ; *bc*, la perte du mois présent.

Figure 4 Growth in length of the lamina of *Laminaria digitata*. The lower curve shows the actual measured length, the upper curve shows potential length in the absence of apical erosion. The difference between curves is the cumulative amount lost to erosion, the lower heavy black line is the amount lost in that month (Pérez, 1971).

Age vs. weight vs. length indicates that the maximum weight of a cohort is reached on year 1 (Table 2). This is also corroborated in a study conducted in Norwegian *Laminaria hyperborea* (Arzel *et al*., 1990). In terms of resource management and at first sight this means that fallowing in *Laminaria digitata* harvesting would be of no use. However, this conclusion depends on whether mortality is density dependent (i.e., due to competition between plants) or density independent due to storms, predation, etc.

Table 2 Age, weight and length data of *Laminaria digitata* as presented in Pérez (1971).

Year	Size (cm)	Wet Weight (g)	Number of individuals	Total weight (kg)
1	30	50	1275	13.750
2	120	100	97	9.7
3	190	260	37	9.62
4	140	130	18	2.34
5	90	70		

D. The forms of productivity in kelps

Blade and stipe growth

Kelp primary production results in the production of new biomass, detrital material shed from the blade tip, mucus and other dissolved inorganic material and spores, as well as internal respiration. Each year the kelp plant renews its entire blade or lamina while the stipe increases in size. However, kelp stipes cannot be compared to wood as a carbon storage mechanism and by far the greater part of kelp annual production is released back into the ecosystem each year as the blade decays. A comparison of blade growth rate, measured as increase in length by means of marker holes or tags, with biomass shows the time of maximum tissue shedding. As might be expected the greater part of detritus production occurs in late summer with the loss of old blade material. In addition, old plants are removed by winter storms. However, the high P/B ratio of kelp beds suggests that shedding of old or damaged tissue occurs at other periods as well.

Regeneration of the blade naturally occurs in both *Laminaria hyperborea and L. saccharina*. In *L. hyperborea*, the whole thallus disappears after sporulation. In *L. saccharina*, the major part of the thallus is seasonally detached from the plant (from November in Brittany). The part detached is that where the sorus has developed. Blade regeneration is possible in *L. digitata* when the meristematic zone is preserved by cutting at 5 cm above the stipe. Regeneration time varies depending on the season when removal occurs; it is of 5 months if cut before the growth peak but of 10 months if cutting occurs at the beginning of the low growth phase. Blade regeneration also varies with the age of the plants. If the meristem is preserved, four successive regenerations are possible.

In Connemara, large quantities of kelp are cast ashore. In Winter, whole plants are removed by storms and the cast up stipes of *Laminaria hyperborea* are known as *slatai mhara* (sea rods). In May, the old shed fronds of this species are washed up and called *scotach* (May weed). In Brittany, a significant biomass of *L. digitata* drifts ashore every year in September. This kelp "wreckage" is well known by local populations who have used this seaweed as soil fertilizer for centuries. A reason for this seasonal shedding is that kelps have reached their seasonal optimum in length and weight and the thin calcareous layer under increasing wave action in winter no longer maintains their holdfasts. A consequence of this cyclical and natural kelp removal is to allow more space and light for the recruitment generated by the previous June and July sporulations. Another reason for this significant weight reduction per square meter in autumn is the loss of tissue due to sporulation. In *L. digitata*, which is a perennial species, the blade tends to break after sporulation at the level of the most developed sori. Arzel (1998) observed that in this species the sorus accounted for a small patch on the blade on year two, then for 50% of the blade surface on year three and over 80% on year 4 and even more thereafter should the plant survive. In *L. saccharina* and *L. hyperborea* the seasonal loss in tissue is also due to constriction in the blade at the level of the sori.

Shed spores

Spores constitute part of kelp production. Chapman (1984) reports that a *Laminaria digitata* plant produces 6 thousand million spores per year. This gives a density of 600 spores per ml in a 10m deep water column above the plant (assuming 1 plant per square m). Such a density is comparable to phytoplankton densities but as spores only remain viable for a few days the spore population is very transient. Allowing a spore to have a dry weight comparable to a single *Skeletonema costatum* cell, this corresponds to 150 g dry weight or about 70 g C. 70 g C is a small percentage of a possible kelp primary production of 1000-2000 g C per m^2 per year but an appreciable fraction of planktonic primary production of 100-300 g C m^2 per year. If these figures are more than guesstimates, algal spores may be quite important as food in the immediate vicinity of kelp beds. As kelp species shed spores in winter as well as late summer the shed spores may augment the sparse winter plankton. Spores probably have a lower C to N and P ratio than other tissue so their food value is also greater. In situations where more than one *L. digitata* plant occurs per m^2, then estimates will be even higher.

Dissolved Organic Matter (DOM)

While it is accepted that algae produce DOM, the exact amount is difficult to determine in the field. Khailov and Burlakova (1969) suggest that up to 3 kg dry weight per m^2 is produced by *Laminaria saccharina* in the Barents Sea but this includes cell contents of old fronds. Mann (1988) quotes a figure of almost 30% of kelp production being in the form of DOM in a South African kelp bed. Very recently, Mohammed & Fredricksen (2004) in a careful 3-year study of *L. hyperborea* estimated a total annual production of 4,129 g C m^{-2} per year of which no less than 1,129 g was in the form of dissolved organic carbon (POC). These figures demonstrate that DOM is an important part of kelp production.

E. The proportion of total primary production in coastal waters due to kelp

The primary production of kelp per unit area is amongst the highest known in aquatic ecosystems. Lower but comparable figures have been estimated for the intertidal fucoids. Planktonic primary production per unit area is much lower, rarely exceeding 300 g C per m^2. The extent of these three biotopes is a function of coastal landforms and morphology. Consequently, the ratio of kelp productivity to other forms of primary production in a given bay depends ultimately on geomorphology.

At one extreme a linear steeply shelving coast will have proportionately small kelp beds. In contrast in an almost enclosed rocky bay, kelp will be the dominant producer. Two Irish examples illustrate this contrast. In Killary Harbour, a narrow steeply shelving shore has a total area of about 23 ha, compared to a surface area of 770 ha, or about 3% of the total area. Allowing a production of 1,000 gC m^2 this gives 230 tonnes C per year compared to the measured planktonic production of 1,306 tonnes (McMaon and Patching quoted in Rodhouse and Roden, 1987). Strangford Lough, in contrast, has large intertidal and shallow subtidal areas and Table 3 illustrates that over 66% of primary production derived from subtidal macroalgae *(Laminaria digitata, L. saccharina* and *L. hyperborea).*

Table 3 Primary production as tonnes of carbon in Strangford Lough.

	Intertidal	Sub-tidal <10m	>10m	TOTAL
Intertidal macroalgae	24,098			24,098
Subtidal macroalgae		68,582		68,582
Phytoplankton	812	5,952	3,394	10,158

F. The fate of kelp production

It is agreed that little kelp production is grazed directly but enters the food chain as detritus (e.g., Mann, 1988). The Blue Rayed Limpet grazes kelp and is known to cause some older plants to detatch by weakening the holdfast but in general little of the living plant is consumed. This may reflect the low nitrogen content of macroalgae. Phytoplankton differs from kelp in their C:N ratios. Plankton typically has a ratio of 106:16:1 C:N:P but *Laminaria* is recorded as 239:13:1 and 384:25:1. That is, *Laminaria* tissue is deficient in N and P compared to plankton and consequently is less nutritious for consumers.

Laminaria detritus can be consumed directly or colonized by bacteria which use the material as an energy source and absorb inorganic N to form protein. In turn, the bacteria-detritus aggregate can be consumed by invertebrates. However, some mussel species can digest kelp detritus directly. An interesting result is that only 23% of kelp detritus carbon was available to invertebrate filter feeders (the rest was metabolized by the bacteria) but nearly all the N from the kelp was available. This suggests that nitrogenous compounds limited the ecosystem rather than energy stored in carbohydrate. It also suggests that comparisons based solely on carbon production may overestimate the value of kelp as a food source relative to phytoplankton. A second pathway to invertebrate consumers lies in the flocculation or formation of particulate organic carbon (POC) from DOC that is then colonized and metabolized by bacteria. As DOC can constitute a substantial proportion of kelp production, this pathway may be of importance to higher trophic levels.

Several studies have demonstrated the importance of kelp as a food source. Duggins (1989) in a study of kelp beds in the Aletutian Islands found that 40 – 60 % of carbon found in coastal invertebrates could be traced to kelp photosynthesis. Fredrikson (2003) also showed that kelp (*L. hyperborea*) carbon was incorporated into invertebrates and birds off Norway. Indirect evidence also shows the importance of kelp in coastal ecosystems. Duggins *et al*. (*op. cit.*) showed that filter feeders grew considerably slower off islands where the kelp forest had been destroyed by sea urchins. Dugan *et al*. (2003) showed that biodiversity of birds and invertebrates on sandy Californian beaches could be correlated with the quantity of drift kelp washed ashore and left to decay.

As the total removal of the kelp forest not only removes it’s contribution to primary production but also destroys the habitat of many of the species which live on this production, it is difficult to separate the effect of removing a food source from that of destroying a habitat. But as kelp primary production does not accumulate in the ecosystem and it is so intense relative to normal planktonic production, it is reasonable to assume that much of it is consumed by other species. This assumption is supported by the studies noted above.

2. Available Substratum

A. Flora

All parts of kelps (holdfast, stipe and blade) function as substrata, and with increasing age of kelp plants the number of both individuals and species of kelp associated flora increases significantly (Rinde *et al.*, 1992). The epiphytic flora, generally found on the stipes of *Laminaria hyperborea*, comprises mainly red algal species, such as *Palmaria palmata, Phyllophora* spp. and *Delesseria sanguinea* (Whittick 1983). Along with these leafy species, a substantial number of filamentous, branched species, such as *Polysiphonia* and *Ceramium* species, and coralline encrusting algae, such as *Lithothamnion* spp., can also be found.

No peer-reviewed studies have been carried out in Ireland on the epiflora specifically associated with kelp even though its physical structure provides a perfect and convenient sampling unit that can be aged and measured with some degree of accuracy. Most epiphytic algae are not host specific (Luning, 1990) although there is evidence to suggest the presence of a strongly associated holdfast community in *Laminaria hyperborea* (Evertsen, 2003). Its stiff and upright stipe provides substratum for a number of macroalgae. More than 40 species of epiphytic algae can be found, of which the rhodophytes are dominant (Christie *et al.*, 1998). Evertsen (*op. cit.*) reported 15 species of epiflora on *L. hyperborea* stipes, which are presented in Table 4. The distribution of different species and groups can be patchy within kelp leading to a sometimes extremely varied floral species profile between two kelp holdfasts of the same species, from the same depth at a common site (Sommerfield and Warwick, 1999).

Table 4 Species of epiphytic flora found in a study by Evertsen (2003).

Chlorphyceae	Rhodophyceae	Phaeophyceae
Ulva sp.	*Corallina officinalis*	*Dictyota dichotoma*
	Ceramium spp.	*Laminaria spp.*
	Delesseria sanguinea	*Himanthalia elongata*
	Cryptopleura ramosa	*Halurus siliquosa*
	Plocamium cartilagineum	
	Polysiphonia spp.	
	Palmaria palmata	
	Gracilaria spp.	
	Ptilota plumosa	
	Gymnogongrus crenulatus	

B. Invertebrates

Christie *et al.* (2003) provide a suite of references that record the large numbers of invertebrate species and individuals that occur in kelp forests. Appendix 2 includes the invertebrate species recorded from various Irish sources, e.g., Edwards (1980), Ball *et al.* (1995) and Healy and McGrath (1998) from kelp holdfasts and within kelp forests. Farran (1915) and Southern (1915) include notes on kelp fauna but due to considerable changes in taxonomy, the taxonomic status of some of these records is difficult to establish. Christie *et al.* (*op. cit.*) and Wagge-Nielsen *et al.* (2003) between them provide lists of species from various phyla for Norwegian waters and record 238 taxa (including fish) from 58 plants examined with an average density of 8,000 individuals per laminarian. Both publications agree that amphipods and gastropods were the most diverse and numerically dominant groups present but both these sources underestimate the numbers of polychaete species (see Healy and McGrath (1998) for a more extensive listing of polychaetes). Birkett *et al.* (1998) provide figures for classes and higher taxa and these total to ca. 1,260, some 173 of which are polychaetes. These same authors list three species of ctenophores; however, as ctenophores are exclusively planktonic, they cannot be regarded as living in/on (or dependant upon) kelp forests. Edwards (*op. cit.*), working in Bantry and Dunmanus Bays in the south west Ireland, noted that decreases in diversity and depths to which plants could grow were related to levels of suspended solids. Open water forests could live in deeper depths and had greater numbers of associated species whereas inshore kelp communities, living at the ends of bays where freshwater inflow and wave action increased turbidity, were restricted to ca. ≤ 10 m depth and had few species. He also noted that suspension feeders dominated these inshore communities, a feeding group that would benefit from higher levels of suspended material. Moore (1973) had earlier identified turbidity as an important ecological factor regulating growth of laminarians.

In contrast, Steneck *et al.* (2004) observed that kelp forests off the Gulf of Maine are naturally low in species diversity with only 15 taxa recorded. There are no records of sponges, coelenterates, polychaetes, cirripeds, isopods, bryozoans or tunicates, all of which are highly associated with kelp forests in Ireland. Their absence in western Atlantic kelp forests is hard to understand and pressure from urchin grazing cannot be used to explain this.

Jones (1973), working off the north east coast of Britain where water quality is seriously compromised by pollution, found that holdfast communities were less diverse than at open water sites with ca. 45% of the species complement being absent from these polluted sites. Species that were rare at the open water sites were absent from the polluted site, and no new species were recorded at the polluted sites. However, Abbott and Perkins (1977) and Perkins *et al.* (1978) report that successive sampling of laminarian holdfasts over a 6 year period between 1971 and 1976 collected off the Cumbrian coast right beside two outfalls carrying industrial wastes failed to reveal any reduction in species numbers. They state that the effluent released from the pipes are “not inimical” to a healthy biota in the receiving area.

Christie *et al.* (2003) and Jørgensen and Christie (2003) note that the three distinctive areas of the alga, i.e., holdfast, stipe and frond, support three different faunal groupings. The three dimensional holdfast with its internal spaces provides a refuge area for mobile species of polychaetes, e.g., *Anaitides, Eulalia, Harmothoe, Hediste, Kefersteinia, Lagisca, Lepidonotus,* crustaceans, e.g., *Bodotria, Idotea, Apherusa, Jassa, Melita, Porcellana* and echinoderms e.g., *Amphipholis, Asterina, Ophiothrix, Asterias, Psammechinus, Pawsonia* and *Ocnus* while the lower part of the stipe with its well-developed epiphyte community also supports a variety of polychaetes, e.g., *Amblyosyllis, Brania, Pionosyllis, Trypanosyllis* crustaceans, e.g., *Caprella, Pariambus Ammothelia, Anoplodactylus*, molluscs e.g., *Onoba*, *Tricolia*, *Elysia* and echinoderms e.g., *Echinus, Psammechinus, Henricia*. The frond supports the lowest numbers of species while the holdfast was found to support the highest (Christie *et al., op. cit.*). These authors found that species abundance in the stipe was highest in Summer although there were large variations between sites and seasons from a small number of individuals to more than 80,000 per stipe. Furthermore, season or habitat volume was not related to species diversity but was related to species abundance.

3. Food & Feeding

A. Invertebrates

With regard to the kelp as a direct food source for invertebrates, gastropods e.g., *Patella* and *Helicon* and some echinoderms, e.g., *Echinus* and *Psammechinus* are known to browse on kelp and these same group of species will also use other algae present within the kelp forest. Indirectly (through particulate organic matter), the kelp and associated algal species contribute to the food resource of suspension and deposit feeders (Dugan *et al.*, 2003) to feeding groups that are abundant in kelp forest, e.g., sponges, many polychaete families such as terebellids, sabellids, serpulids and spirorbids, bivalves, cirripeds, bryozoans and echinoderms such as holothurians and crinoids and tunicates. These in turn, along with the browsers (and other sources such as phyto and zooplankton), act as the food resource for predators such as the cnidarians, predatory polychaetes, e.g., scale worms, syllids, hesionids, phyllodocids and nereids, isopods and the large decapods such as lobster and crab.

Drift algae, including the different kelp species, are washed up on our shores mostly during the autumn and winter months but this event can occur at any time depending on when storms happen. Even before the drift weed is washed ashore, it acts as a floating refuge and dispersion method for crustaceans and juvenile fish (B. O' Connor, *pers. obs*.). The contribution kelps make to this drift weed is not known but Steneck *et al*. (2002) quote a figure of between 60–99% from Mann (2000) for eastern Nova Scotia. As the weed rots on the shore, it provides a valuable resource of organic matter for amphipods and hypoxic/anoxic-tolerant infaunal opportunistic polychaetes such as *Malacoceros* and *Capitella.* These in turn act as a food resource for bird species such as Curlew *Numenius arquata* (B. O' Connor, *pers. obs*.). Bustamente and Branch (1996) working on the west coast of South Africa, studied the most abundant intertidal grazers (*Patella* sp) and filter feeders (*Mytilus, Aulacomya* and *Gunnarea)* and investigated their connection with *in situ* local production and that generated from subtidal kelp forests. They found that the selected species used kelp-derived detritus as their main source of organic carbon and nitrogen. They also found that more generalised intertidal grazers relied mainly on the *in situ* epilithic algal species and that kelp-derived detritus represented more than 65% of particulate organic matter while phytoplankton contributed only 6%. They conclude that subtidal macrophyte production greatly influences the structure of intertidal rocky shore communities on the west coast of South Africa.

Soares *et al.* (1996), who also worked off the South African coast around Cape Agulhas found that the infaunal surf clam *Donax serra* was significantly negatively impacted by stranded kelp. They examined 12 beaches and found that densities of adult clams were significantly higher on beaches that had low stranded kelp cover but did note that this did not apply to juveniles. They postulate that kelp strandings interfere with *Donax* feeding and burrowing activities, dislodging animals of increasing size gradually downshore to the saturation and surf zones, where adult populations are eventually established. They go on to note that kelp gulls predate upon the dislodged clams.

Lavery *et al.* (1999) and Dugan *et al.* (2003) studied the activity of clearing drift weed from sandy beaches as a beach management practice in Australia and Southern California, respectively. Lavery *et al.* (*op. cit.*) reported that this activity caused an immediate decrease in the biomass of macrophyte detritus and densities of epifauna and fish. They found that values for these variables had returned to values similar to areas that had not been cleared within two months. They reported that there was no effect on sediment organic matter nor on density or richness values for benthic infauna; nevertheless they do state that a beach that had been cleaned for several years had a similar macroinvertebrtae assemblage to that of a non-cleaned beach at which macroalgae did not accumulate. Both of these beaches had a different assemblage than a beach on which drift algae did occur and that was never cleaned. They comment that at regularly cleaned beaches, the disturbance is temporary (in the order of days to weeks) and that the cleaning activity may mimic natural flushing of beaches and prevent the detrimental effects of algal accumulations on infaunal assemblages. Dugan *et al.* (*op. cit.*) came up with somewhat different findings to those of Lavery *et al.* (*op. cit.*); they record significant differences in community statistics such as depressed species richness, abundance and biomass between beaches that had been cleaned and those that had not been cleaned. They note that the addition of wrack strongly influences community structure on exposed sandy beaches.

Steneck *et al.* (2002), commenting on western Atlantic and Pacific ecosystems, note that detritus can make its way into nearby intertidal food webs through either the capture of fine kelp particles by polychaete and molluscan filter feeders or by browsers (limpets and urchins) feeding on larger pieces of drift kelp. In Ireland, some of the opportunistic species, e.g., the spionid *Malacoceros*, go through rapid density increases following the arrival of drift weed on the shore. However, these increases are quickly followed by total collapses when the resource is used up (B. O' Connor, *pers. obs.*).

B. Fish

The kelp *Laminaria hyperborea* is host to a rich fauna of mobile invertebrates and several studies have recognised the importance of these fauna in the diet of fish species (Nelson, 1979; Kennelly, 1983; 1991; Holmlund *et al.*, 1990; Nordeide and Fossa, 1992; Hoeisaeter and Fossa, 1993; Fossa, 1995; Fjosne and Gjosaeter, 1996;

Jorgensen and Christie, 2003; Christie *et al*., 2003). Mobile macrofauna (particularly crustaceans and molluscs) are important in the diet of many fishes and their abundance in the kelp forest makes this habitat a rich source of prey for many top down predatory consumers (Jorgensen and Christie, 2003; Christie *et al*., 2003). Christie *et al*. (*op. cit.*) estimated that an average density exceeding 100,000 mobile macrofauna individuals per m^2 could be expected in a Norwegian *L. hyperborea* kelp forest.

Variation in abundance of prey taxa and faunal groups may be reflected in the diet of some kelp fish species. For example, amphipods and gastropods were found to be the dominant faunal groups in studies of recovering and natural kelp forests in Norway (Moore, 1972; 1973; Schultze *et al*., 1990; Christie *et al*., 1998; 2003; Norderhaug *et al*., 2002). Correspondingly, these groups have been found to be dominant in the diet of various fish species associated with kelp habitat (Gordon, 1983; Fossa, 1995; Fossa *et al*., 1998; Fredriksen, 2003). Other studies have noted opportunistic tendencies in wrasse species with respect to variation in prey availability, with seasonal and temporal changes in the abundance of prey species reflected in the diet (Deady, 1995; Deady and Fives, 1995ab; Varian, 1998; Zemke-White and Clements, 2004).

There may also be some interspecific variation between kelp species in the foraging opportunities available to fishes. According to Schultze *et al*. (1990), the diversity and abundance of macroinvertebrates is higher in *Laminaria hyperborea* beds than in *L. digitata* stands. Invertebrate abundance has also been related to the age and size of the plant within kelp species. For example, Rinde *et al*. (1992) found that the number of individuals and species of kelp-associated flora and fauna increased significantly with increasing age of kelp plants. Thus, the availability of macroinvertebrates as food items for kelp fishes may depend to an extent on the species and age of kelp plants distributed within the kelp habitat.

Some Norwegian studies have considered the importance of fish in the trophic structure of the kelp forest ecosystem, i.e., as prey for seabirds and other fish (Røv *et al*., 1990; Lorentsen *et al*., 2004) and as top down predators and consumers of invertebrate fauna (Nelson, 1979; Kennelly, 1983, 1991; Holmlund *et al*., 1990; Nordeide and Fossa, 1992; Fosne and Gjosaeter, 1996; Fredriksen, 2003). Røv *et al*.

(*op. cit.*) and Lorentsen *et al*. (*op. cit.*) demonstrated the relationship between kelp forest, fish and seabird numbers through a close overlap between feeding areas of breeding Great Cormorants and kelp forests within their feeding range. Fredriksen (2003) investigated the trophic status and food web dynamics of a range of fauna, including some fish species, using stable isotope analysis for a *Laminaria hyperborea* ecosystem in Norway. Gut contents analysis carried out by Fossa *et al*. (1998) were used to verify results. The study found that the trophic positions of the different species of fish varied according to the composition of kelp invertebrate fauna in the diet.

C. Birds

In terms of foraging habitats, kelp forests provide three distinct habitats for birds (Foster & Schiel, 1985):

- Living attached plants associated with rocky substrata (kelp forests).
- Drift kelp floating in the open sea.
- Wrack – detached kelp washed up on the shoreline.

In addition to the kelp forest food chain, birds benefit indirectly from kelp via the influence of kelp detritus upon coastal food chains. By providing organic matter inputs to shore areas such as relatively nutrient-poor sandy shores, kelp detritus provides nutrient enrichment that sustains intertidal macroinvertebrate communities (secondary production) (Duggins *et al.*, 1989) and hence provide prey items for birds.

i. Kelp Forest

Kelp forests provide a foraging habitat for birds due to the associated and diverse invertebrate and fish communities present. In addition, a kelp forest also acts as a natural barrier from the surge effects of waves, particularly in the case of storms, and therefore provides a more sheltered foraging environment for birds.

Foster & Schiel (1985) describe three sub-habitats for birds within kelp forests:

- Surface Canopy
- Mid and Bottom Waters within Kelp Forests

- Fringe Areas

Surface Canopy

A dense and well-developed kelp forest may provide a buoyant mat upon which birds may perch. This is particularly noted in California USA where forests of the Giant Kelp *Macrocystis* spp. provide roost sites for various gull species and also a foraging platform from which they forage for fish and other prey in the kelp surface canopy (Foster & Schiel, 1985).

No Irish records of birds resting within kelp canopies were found during the current review but there is the potential for some bird species (e.g., gulls Family Laridae) to rest within this habitat by either perching or swimming. Indeed many seemingly unstable offshore structures provide perching platforms as they are relatively safe from shore predators and human disturbance. Roycroft *et al.* (2004) found that floating mussel long-line suspension buoys were used as perching platforms for a number of bird species such as Laridae (gulls), Oystercatcher *Haematopus ostralegus*, Ringed Plover *Charadrius hiaticula*, Hooded Crow *Corvus corone cornix*, Phalacrocoracidae (Shags and Cormorants), and Black Guillemots *Cepphus grylle*. Oystercatchers were also observed foraging along lengths of rope of mussel long-line (D. Roycroft, *pers.comm.*) which might be considered a particularly small and unstable foraging habitat.

Mid and Bottom Waters

Little published information exists as to specific interactions between foraging seabirds and kelp forests (e.g., Wilkinson, 1995).

Families of birds that may potentially forage within infralittoral reef kelp forests include those commonly using inshore waters:

Gaviidae (Divers)	e.g., Great Northern Diver *Gavia immer.*
Podicipedidae (Grebes)	e.g., Great Crested Grebe *Podiceps cristatus*
Phalacrocoracidae	e.g., Cormorant *Phalacrocorax carbo*, Shags *Phalacrocorax aristotelis.*
Anatidae (Ducks)	e.g., Eider *Somateria mollissima*

Laridae (Gulls)	e.g., Herring Gull *Larus argentatus*.
Sternidae (Terns)	e.g., Common Tern *Sterna hirundo*.
Alcidae (Auks)	e.g., Common Guillemot *Uria aalge*.

Members of the Gaviidae family that occur within inshore waters include the scarce Red Throated Diver *Gavia stellata* and Black Throated Diver *Gavia arctica*. The Great Northern Diver *Gavia immer* is the most numerous diver species off the Irish coast during winter (Colhoun, 2001). There are no substantiated links between any of these diver species and rocky reef and kelp habitats. Principal prey items include Cod *Gadus morhua*, Herring *Clupea harengus* and Sprats *Sprattus sprattus* and sandy bays appear to be the most preferred winter habitat in Ireland (e.g., Lack, 1986) although Ferns (1992) suggests that Great Northern Divers in Britain are more strongly associated with rocky coastlines.

Great Crested Grebes *Podiceps cristatus* occur in a variety of inland and coastal aquatic habitats and there appears to be no significant link between their distribution or foraging behaviour and kelp forests.

Members of the Phalacrocoracidae family include two piscivorous seabirds: Cormorant *Phalacrocorax carbo* and Shag *Phalacrocorax aristotelis.* Cormorants and Shags occur in Ireland during the breeding and non-breeding season and nest within colonies on cliffs, stacks and other rocky areas. Coastal breeding populations of Cormorants within Ireland are currently considered to be stable. In contrast, the number of Shags in Ireland has declined by 27% since the Seabird Colony Register census of 1985-1988 (Sellers, 2004). Both species are widely distributed in varying sized breeding colonies around the Irish coastline where suitable habitat exists.

Cormorants forage within shallow inshore marine waters (e.g., Lack, 1986; Johansen *et al.,* 2001). Previous studies have identified a connection between kelp forests, fish and Cormorants. For example, a relationship was found between the feeding areas of breeding Cormorants (*Phalacrocorax carbo*) and kelp forests within their feeding range (Røv *et al.*, 1990). In Norway, Cormorants and Shags (*P. aristotelis*) prey upon large numbers of gadoid fish (Barrett *et al.*, 1990) and kelp forests of *Laminaria hyperborea* are important habitats for juvenile gadoids (Sjøtun & Lorentsen, 2003).

The reported decrease of Cod *Gadus morhua* in the diet of Cormorants probably reflects the decrease in the Norwegian Cod population (Lorentsen *et al*., 2004) that in turn is linked to kelp harvesting and its negative effects on juvenile recruitment (Sjøtun & Lorentsen, 2003). However, there is no current evidence that Cormorant populations are in decline due to kelp harvesting, although longer-term population studies will be useful to monitor the effects of kelp harvesting (Lorentsen *et al*., 2004)

No clear relationship between Shags and kelp forests have been previously described. Sandeels *Ammodytes marinus* are a favoured prey item and these are thought to occur predominantly on sandy or gravel substrata (Wanless *et al.*, 1997), also the nursery grounds of this fish species. While Shags feed in deeper waters than Cormorants (21-40m: Wanless *et al.*, 1991) they also occur in areas of shallow rocky coast and prey upon fish and crustaceans (Cramp & Simmons, 1977; Ferns, 1992). Further, Sandeels have been recorded within Norwegian kelp forests (Hoeiaseter & Fossaa, 1993). Interactions between Shags and kelp forests are therefore likely.

Members of Anatidae family that may feed within kelp forests along Irish coasts are seaducks such as the Common Eider *Somateria mollissima*, Common Scoters *Melanitta nigra* and Red Breasted Merganser *Mergus serrator*, all of which feed in inshore waters particularly at low tide when the bottom is easier to reach (Ferns, 1992). Sea ducks are thought to prefer rocky substratum communities that are often dominated by vegetation such as kelp (Bustnes & Systad, 2001a). In particular, the rare Steller's Eider *Polysticta stelleri* (not found in Ireland) is noted to prefer foraging within kelp forests (*Laminaria hyperborea*) of northern Norway although kelp distribution alone, cannot explain the distribution of this wintering seaduck (Bustnes & Systad, 2001b).

The Irish breeding distribution of Common Eider extends westwards around the coastline from the Copeland Islands, Co. Down to Inishmurray in Co. Sligo with some additional nest locations recorded e.g., Inishkeeragh, Co. Mayo (Murray & Cabot, 2002). Common Eiders feed predominantly on molluscs and crustaceans but will also prey upon crabs and starfish (Lack, 1986; Ferns, 1992). Common Scoters will feed upon crustaceans and gobies and similar to the Red Breasted Merganser, are not solely restricted to rocky reef areas.

Interesting studies of the interactions between eiders and kelp forests have been conducted in Norway. A study that investigated the preferred substratum types used by foraging Common Eiders found that they clearly selected kelp forests throughout the winter months. Common Eiders and King Eiders *Somateria spectabilis* spent 50% and 17% of their feeding time respectively, within kelp forest (Bustnes & Lønne, 1997). A favoured prey item of the eider is the sea urchin *Strongylocentrotus droebachiensis* and consequently eiders may exert control at a local level by removing these voracious grazers from kelp forests (Bustnes & Lønne, 1995).

Gulls (Family Laridae) that are most likely to feed within shallow rocky infralittoral habitats include the Great Black-Backed Gull *Larus marinus*, Herring Gull *Larus argentatus,* and Lesser Black-Backed Gull *Larus fuscus* (Cramp & Simmons, 1985a). All would be considered to be omnivorous, predators and scavengers. Feeding methods include dipping to the surface to take prey items, surface or shallow plunging, surface seizing or shallow surface diving (Cramp & Simmons, 1985). Foraging within shallow sublittoral zones is likely to follow tidal cycles (Cramp & Simmons, 1985). Prey items include a wide range of fish and invertebrate species. The widespread distribution and opportunistic nature of gull foraging behaviour suggests it is unlikely that they are reliant on infralittoral reef habitats with kelp. However, time of year and proximity to breeding colony may lead to Herring Gulls and Great Black-Backed Gulls at times being predominantly shallow sublittoral feeders (Cramp & Simmons, 1985a). Seabird 2000 results show that Great Black-Backed and Herring Gull populations in Ireland have declined since the Seabird Colony Register of 1985-88. Lesser Black-backed Gull populations have increased, with increasing numbers nesting in inland sites.

Breeding terns in Ireland (Sternidae) comprise the Sandwich Tern *Sterna sandvicensis,* Roseate Tern *Sterna dougallii,* Common Tern *Sterna hirundo,* Arctic Terns *Sterna paradisaea* and Little Tern *Sterna albifrons*.

Sandwich Terns are coastal breeders in Ireland and require sheltered, shallow waters that are within the foraging range from suitable nesting habitat such as low-lying islands or remote beaches (Cramp & Simmons, 1985b). Sandwich Tern distribution in Ireland is predominantly north-east and therefore does not reflect the abundance of rocky reef habitats off the western Atlantic coast of Ireland. However, foraging over offshore reefs has been previously recorded; foraging success being greatest during periods of low tide when fish are more accessible (Cramp & Simmons, 1985b).

Roseate Terns are restricted to a few breeding colonies in Ireland and no interactions with kelp forests are known. Little Terns nest exclusively within coastal habitats, predominantly sand and shingle beaches. They forage within sheltered and shallow coastal waters. The Irish breeding population has declined and is restricted to sites within Counties Wicklow, Wexford, Kerry, Galway, Mayo and Donegal (Pickerell, 2004).

Although there appears to be no specific information available with regard to tern and kelp interactions, a common link between all tern species is that they breed predominantly at coastal sites and forage within shallow inshore waters for prey items including marine fish and invertebrates. They are therefore sensitive to local changes in food availability (Dunnet *et al.*, 1990). Reef habitats with kelp are likely to form part of the foraging range of these birds (Cramp & Simmons, 1985b).

Members of the Auk family (Alcidae) that forage within inshore waters of Ireland include the Common Guillemot *Uria aalge*, Razorbill *Alca torda* and Black Guillemot *Cepphus grylle*. All require coastal rocky cliff areas for breeding habitats. Principal breeding sites of Common Guillemots in Ireland include Lambay Island, Rathlin Island, Great Saltee, Cliffs of Moher and Horn Head (Harris & Wanless, 2004). Principal breeding sites for Razorbill include Cliffs of Moher, Horn Head and Great Saltee. Common Guillemots feed mainly just offshore and the diet of an adult consists of marine fish, molluscs, crustaceans and polychaete worms. Although Guillemots and Razorbills forage in shallow waters close to shore, a large proportion of foraging trips from the breeding colony also extend further offshore (Bradstreet & Brown, 1985). No direct interactions with kelp forests have been described for Common Guillemots or Razorbills.

In contrast, Black Guillemots feed closer to the shore than other alcids and previous accounts highlight foraging within shallow sublittoral zones (Bradstreet & Brown, 1985). These birds prey upon e.g. butterfish (Family Stromateidae), blennies (Family Blenniidae) and pipefish (Family Syngnathidae) together with a wide range of reef invertebrates (Bradstreet & Brown, 1985; Ferns, 1992). Reef habitats with kelp are therefore likely to be important for this species.

Fringe Areas

Foster and Schiel (1995) suggest that the seaward fringe of kelp forests (the interface between kelp and open waters) may support the greatest diversity of birds that exploit aggregations of fishes and invertebrates along the forest edge. No specific information was found with regard to this interaction although the bird species involved will be the same as discussed above. The shoreward edge of a kelp forest (sublittoral fringe) is also an important foraging habitat, particularly at low tide when kelp and associated fauna are partially exposed. Birds that exploit this habitat include Oystercatchers, Turnstones *Arenaria interpres*, Curlew *Numenius arquata* and various gull species (Family Laridae). Oystercatchers for example, particularly forage upon Mussels *Mytilus edulis* but will also take crabs (e.g. *Carcinus maenas*) and amphipods. Prey items such as sea cucumbers (Holothuroidea) and sea anemones (*Actinia* spp) have also been recorded (Cramp & Simmons, 1983). Turnstone and Curlew are equally well adapted to foraging within this ephemeral habitat. Curlew probe beneath overturned kelp fronds with their long bill while Turnstones use their head to move aside the kelp to locate prey within. Gulls and crows (e.g. Hooded Crow *Corvus corone cornix*) are both opportunistic foragers. Hooded Crows will take mussels, small fish and any opportunistic prey species. Great Black-Backed Gulls will prey upon fish, sea urchins (Echinoidea), sea cucumbers (Holothuroidea), starfish (Asteroidea) and crustaceans amongst others within this habitat (Cramp & Simmons, 1985a). Herring Gulls have been observed preying upon large quantities of the sea urchin *Echinus esculentus* near Millport, Scotland (J. Davenport, *pers. comm.*).

The Grey Heron *Ardea cinerea* is a member of the Ciconiiformes family and is a widespread bird of streams, rivers, lakes and coastlines. The Grey Heron was the third most widespread species recorded during the non-estuarine coastal waterfowl survey of 1997/98 (Colhoun & Newton, 2000). Grey Herons feed upon rocky shores throughout the year (Ferns, 1992) and are a major predator of intertidal fishes (Carss

& Elston, 2003). Being restricted to foraging in shallow water (<50 cm deep) (Cramp & Simmons, 1977) herons are therefore constrained by the tidal cycle.

Large numbers of Grey Herons forage on rocky intertidal shores of Scottish sea-lochs and abundance is positively associated with the total area of algal coverage of the shore (*Fucus* spp. and *Ascophyllum nodosum*) (Carss & Elston, 2003). The structural complexity, shelter and food afforded by vegetated shores leads to a greater abundance of fish and ultimately a greater abundance of higher avian predators (Carss & Elston, 2003).

ii. Drift Kelp

Accumulations of drift kelp in pelagic waters may provide a roosting site for seabirds (Foster & Schiel, 1985). Drifting kelp mats may also transport amphipods and sessile benthic invertebrates within their mass (Cherel *et al.,* 2002) and are therefore attractive to foraging seabirds. Off the California coast, shorebirds have been recorded foraging within floating mats of the kelp *Macrocystis pyrifera* (Bradley & Bradley, 1993). Drifting accumulations of Laminarian kelp species also provide this habitat within Irish waters. Observations of up to ten gulls resting and foraging within these drift mats are known (M. Mackey, *pers. comm*.).

iii. Wrack

A considerable biomass of kelp is washed up onto rocky and sandy shores as a consequence of natural loss from the frond as the plant grows, the annual casting of the frond of *Laminaria hyperborea* (Wilkinson, 1995) and biomass removed in the event of storm surges. The washed up kelp on shores is called wrack, and together with deposits of other algae (e.g., fucoids) constitutes an important habitat for foraging birds (Foster & Schiel, 1985).

Kelp wrack on both sandy and rocky shores provides an important habitat for a diversity of shore and terrestrial bird species that forage for invertebrate prey within and beneath the wrack. Examples of birds that forage within the kelp wrack zone include Oystercatchers, Turnstones, Curlew, Bar-Tailed Godwit *Limosa lapponica*, Sanderling, *Calidris alba* (L. Lewis, *pers. obs*.) and various gull species. Turnstones in particular are well adapted to turn the wrack over to reveal invertebrate prey such as amphipods and crabs beneath. Purple Sandpipers *Calidris maritima* show a strong degree of preference for rocky shores (Summers *et al*., 2002) and kelp wrack is considered their most profitable foraging habitat due to the abundance of kelp fly (Family Coelopidae) larvae (Dierschke, 1993). Similarly, the foraging success (in terms of energetic profitability) of Turnstone foraging amongst wrack is greater than for those feeding within shore areas with no wrack deposits (Fuller, 2003).

Coelopid larvae are the most abundant stage of the kelp fly within wrack deposits (coelopid larve 413 l^{-1} (range 0 –2600), pupae 29.3 l^{-1} (range 0 – 400) and adults 0.6 l^{-1} (range 0 – 6) (Fuller, 2003). The profitability of kelp fly larvae is also utilised by Dunlin *Calidris alpina*. During autumn migration, juvenile Dunlin forage on kelp wrack on Helgoland (S E North Sea) and achieve a high intake rate through eating kelp fly larvae (17.8 min^{-1}). This consequently leads to a rapid fattening rate prior to onward migration (Dierschke, 1998). Within Ireland, staging Whimbrel *Numenius phaeopus* have also been observed to utilise this prey resource while members of the family Hirundinidae (e.g. Barn Swallow *Hirundo rustica*) take emerging kelp flies whilst on the wing (O. Merne, *pers. comm.*).

Further studies from across the world highlight shorebird use of kelp and macrophyte wrack habitats:

- Studies in Australia have found that the Pied Oystercatcher *Haematopus longirostris* and the Hooded Plover *Charadrius rubricollis* obtain a significant proportion of their energy intake from prey found in decomposing kelp on sandy shores (Dr I. Taylor, *pers. comm.*).
- In the 1970's, kelp *Macrocystis pyrifera* recovery on the Californian coast was followed by an increase in shorebirds along a stretch of rocky coastline. In particular two species, Black Turnstone *Arenaria melanocephala* and Ruddy Turnstone *Arenaria interpres* showed dramatic increases (Bradley & Bradley, 1993).
- On sandy California shores the abundance of two shorebird species Black-Bellied Plover *Pluvialis squatorola* and Western Snowy Plover *Charadrius alexandrinus nivosus* were positively correlated with the biomass of

macrophyte wrack and the abundance of wrack-associated invertebrate fauna (Dugan *et al.*, 2003).

Observations in Ireland and studies across the world therefore suggest that many shorebird species are dependent on kelp wrack habitats. However, wrack deposits are rarely monospecific and other macrophyte wrack (e.g., *Fucus* spp., *Ascophyllum nodosum*) may be equally as important (e.g., Carss & Elston, 2003) in providing this important foraging habitat.

In addition to shorebirds, kelp wrack is used as a foraging habitat by many terrestrial birds including crows, pipits, wagtails and starlings (Ferns, 1992; A. Walsh & O. Merne, *pers.comm*).

Kelp wrack also benefits birds via its role in providing organic matter to coastal marine ecosystems. Research into trophic relationships between subtidal and intertidal ecosystems have demonstrated strong links between subtidal primary producers (including kelp and other macrophytes) and intertidal consumers such as invertebrates. Kelp detritus contributes a large proportion of the particulate organic matter inputs to both rocky and sandy shores and previous research has highlighted its importance for higher trophic levels such as invertebrate consumers (secondary production) (e.g., Mann, 1973; Duggins *et al.*, 1989). Previous studies have shown that growth rates of benthic suspension feeders (e.g., Mussels *Mytilus edulis*) are higher in areas with extensive kelp forests (Duggins *et al.,* 1989) although Soares *et al.* (1996) found a negative relationship between the amount of intertidal stranded kelp and the abundance of the Wedge Clam *Donax serra*. Bustamanate & Branch (1996) suggested that benthic intertidal consumers (invertebrates) relied heavily on inputs from kelp forests and that kelp-derived detritus may regulate invertebrate populations and community structure. As birds are higher consumers within this trophic pathway, they will therefore benefit indirectly from the inputs of kelp detritus maintaining populations of invertebrate prey. The beneficial effects for birds will therefore be longer lasting than that of the physical presence of the kelp wrack habitat itself.

An interesting and indirect interaction between kelp and birds is found in Scotland (e.g., South Uist) where, traditionally, kelp has been hand harvested and used as a natural fertiliser on machair. The kelp detritus adds nutrients to the soil thereby enriching the habitat for invertebrates. Consequently, the abundant food supply has led to machair being an extremely important breeding habitat for many wading bird species such as Dunlin, Ringed Plover *Charadrius hiaticula*, Lapwing *Vanellus vanellus* and Redshank *Tringa totanus* (J. Love, *pers. comm*.).

4. Reproduction

A. Invertebrates

As there are no invertebrates that are exclusively found on kelp or within kelp forests, they do not explicitly require the presence of kelp for reproduction purposes. However, some molluscs, e.g., gastropods and nudibranchs, do attach egg strings to either the holdfast or stipe.

B. Fish

A number of studies have indicated the importance of kelp forests as habitat for spawning and reproduction in fish species (Gordon, 1983; Schultze *et al*., 1990). The vegetative habitat attracts a number of fish species that exhibit nest-building where the fish makes a nest from algae in which it lays its eggs (Appendix 3). Other species have sticky eggs that adhere to the weed or substratum of the habitat. In Scotland, Gordon (*op. cit.*) noted that the bulbous holdfasts of *Saccorhiza polyschides* are particularly suitable as a nesting site for Small Headed Clingfish, *Apletodon microcephalus,* and Two-Spotted Gobies, *Gobiusculus flavescens*. Schultze *et al*. (*op. cit.*) also reported Pogge, *Agonus cataphractus*, eggs in the rhizoid of *Laminaria* around Helgoland. Kelp habitat fish species that have pelagic eggs are listed in Appendix 3.

The importance of kelp habitat as a nursery area for the development of juvenile fishes has been widely recognized (Carr, 1983; Shaffer, 2003; Lorentsen *et al*., 2004). In Norway, several studies have identified kelp forests as being important nursery habitat for juvenile gadoids (Saithe and Pollack, *Pollachius* spp.) (Fossa, 1995; Sjøtun and Lorentsen, 2003) and in Sweden, Borg *et al*. (1997) conducted experiments to show that juvenile Cod, *Gadus morhua*, prefer vegetative habitats over sandy bottoms. Schultze *et al*. (1990) recorded juveniles of the Lumpsucker, *Cyclopterus lumpus,* and the Striped Sea Snail, *Liparis liparis,* in *Laminaria hyperborea* beds in Helgoland, whilst Gordon (1983) observed juveniles of Montagu's Sea Snail *Liparis montagui,* Shore Rockling *Gaidropsaurus mediterraneus* and Goldsinny Wrasse *Ctenolabrus rupestris* in the bulbous holdfasts of *Saccorhiza polyschides* in Scotland. In Ireland, juvenile fishes can be seen in the benthopelagic zone of kelp habitat in the summer (S. Varian, *pers. obs*.).

In North America, Carr (1983) described the use of the *Macrocystis* canopy by large numbers of juvenile rockfish (*Sebastes* spp.) as a nursery and refuge area. Similarly, Murphy *et al*. (2000) found that *M. pyrifera* kelp beds provide important habitats for rockfish and other species. Recently, Shaffer (2003) reported the preferential use of kelp habitat by juvenile salmon (i.e., Chinook, *Oncoryhnchus tshawytscha*, Chum, *O. keta* and Coho, *O. kisutch*) and forage fish (i.e., Surf Smelt, *Hypomesus pretiosus*) along the shorelines of coastal Washington.

5. Shelter

A. Invertebrates

The under-storey habitats created by the kelp plants give rise to microniches that support a somewhat similar community of species. Notable additional species would be the large decapods such as lobster and cray fish. Although these two commercial species are not exclusively found in kelp forests, pot and trammel fishermen do set their gear on or close to kelp in order to catch them (B. O' Connor, *pers. obs*.). Eckman *et al.* (1989) studied the effects of kelp on water flow and particle transport near the seabed to investigate the effect that kelp forests have on local and under-storey current velocity. By using tracers, they reported that under-storey conditions in kelp habitats were exposed to weak fluid transport and were characterised by greater rates of deposition relative to rocky substrata at similar depth but without kelp. They showed that by using tracers, kelps inhibited transport of suspended particles from the overlying water column to the sea floor. Mork (1996) and Andersen *et al.* (1996) studied over- and under-storey current velocities and, contrary to Eckman *et al.* (1989), reported that the differences were slight with under-storey velocities being *ca*.

5–8% lower than velocities above the canopy. However, they did record that the differences between outer and inner parts of the kelp bed *ca*. 258 metres apart were 70–85% with the highest value being at low tide.

B. Fish

The complexity of kelp habitat structure provided by both biotic and abiotic elements has been recognised as one of the factors contributing to diversity and abundance in fish communities (Bodkin, 1988). Within the temperate nearshore marine environment, macroalgae may provide physical orientation and add considerably to the structural complexity of rocky substratum, effectively extending the substratum up into the water column (Quast, 1968a; Wheeler, 1980; Bodkin, 1988). Increased structural complexity increases shelter, or refugia, available to fishes while also providing habitat for the prey species used as a forage base by reef fishes.

A number of studies have reported greater fish diversity in kelp habitat than in non-vegetative areas. In southern San Luis Obispo County, Laur *et al*. (1988) monitored fish assemblages from 1976 to 1980 following changes from urchin-dominated to kelp-dominated reefs and found that numbers of fishes were greater in the kelp forests. Similarly, Ebeling and Laur (1988) compared fish assemblages on two reefs near Santa Barbara, California, during periods of urchin dominance and kelp dominance. They concluded that a net increase in fish abundance and diversity could be expected following the change from urchin barrens to kelp forest although the presence of kelp seemed to be of little consequence to some species, e.g., *Chromis punctipinnis* (Cooper). More recently, a study of vegetative sites in Alaska found that kelp and seagrass beds supported a higher species richness than those sites with only filamentous algae (Murphy *et al*., 2000).

The kelp forest habitat comprises two distinct components: the substratum or reef on which the kelp grows and the kelp that makes up the forest. The substratum component may range from nearly flat with little 3-dimensional structure to large rocky outcrops with high vertical relief and complex structure (Bodkin, 1988). The influence of these separate structural components needs to be considered when exploring ecological preferences in fishes relative to kelp habitats. A number of studies in North America have investigated the abundance and diversity of fishes associated with kelp forests over rocky reefs with various degrees of bottom relief (Quast, 1968b; Miller and Geibel, 1973; Russel, 1977; Ebeling *et al*., 1980; Larson and DeMartini, 1984; Stephens *et al*., 1984). Larson and DeMartini (*op. cit.*) examined two areas with similar low relief substratum; one with kelp and the other depauperate of kelp. They concluded that in areas of low relief, kelp forests could enhance the standing stock of fishes. However, Stephens *et al*. (*op. cit.*) compared fish assemblages in an area of high bottom relief before and after the development of a kelp forest and concluded that the presence of kelp has little effect on the abundance of most fish species in a high relief environment. Thus, the substratum component appears to play a key role in the relationship between fish species diversity and kelp habitat.

Impact Review

Methods of Kelp Harvesting

In France, to effectively harvest large amounts of *Laminaria digitata*, a mechanical kelp harvester was developed called “Scoubidou”. This piece of machinery is operated from an 8–12 meter long boat manned by one or two harvesters. The larger boats can carry two Scoubidou's. The Scoubidou twists and wraps around the kelp after which it is pulled out by an hydraulic arm; it can pull up about 10 kg of *L. digitata* per extraction, which takes about 30 seconds.

Laminaria hyperborea harvesting is a well-established industry in Norway. FMC BioPolymer AS harvests yearly 140,000–180,000 tonnes of *L. hyperborea* for the alginate industry. It is harvested by specially designed seaweed trawlers that use a dredge developed by the company. The 15 boats that operate along the Norwegian coast today can carry between 30 and 150 tonnes each. The harvesting dredge has worked well in Norway; however, if the coastline is too rocky the harvesting machinery cannot be deployed.

Production

Repeated cutting of kelp forest is experienced by the plants as a type of environmental disturbance or pressure. Different harvesting regimes will have different effects on both the target species and the containing ecosystem. For this reason we discuss in some detail the most likely harvesting methods and their associated impacts, under the following headings:

The impact of harvesting on species composition of kelp beds

Hawkins and Harkin (1985) and Smith (1985) have studied the effects of removing the algal canopy in kelp beds. Hawkins and Harkin (*op. cit.)* simultaneously removed *Laminaria digitata* and *L. hyperborea* at sites in the Isle of Man where they co-existed; subsequently *L. digitata* exclusively re-occupied the substratum. Thus, the exploitation of mixed areas may promote a relative increase in *L. digitata* beds at the expense of *L. hyperborea*. In 1997, the productivity of *L. digitata* began to decrease on many sites in Brittany while *Sacchoriza polyschides* was recorded in greater numbers at the same sites (Arzel, 2000). As competition between *L. digitata* and *S. polyschides* is known to occur, the question to be answered is whether *L. digitata* is in decline, thus offering more space for *Sacchoriza* colonization or whether *L. digitata* is being actively displaced by *S. polyschides* competition.

Several explanations are under investigation (Arzel, 2000):

- the exploitation method : successive modification of the harvesting tool have resulted in more stipes being left on the substrate than previously.
- the *Sacchoriza* life cycle is shorter than that of *L. digitata*, thus favouring the former, on a substratum already open to recruitment by intensive cutting, much as *L. digitata* displaced *L. hyperborea* in the case already discussed.
- 10% of the boulders are turned upside down during harvesting, resulting in fast colonization of the blank face by opportunistic fast-growing Chlorophyceae, then by *S. polyschides.*
- the abrasive effect of sand is an indirect effect of substrate loss. Abrasion is lethal to Laminariales gametophytes and young sporophytes.
- climatic events: the frequency of major storms has increased over the last decade with direct effect on kelp beds : plants are torn away and more sand abrasion occurs.
- water temperature : an increase in temperature has been documented in Brittany which is at the southern limit for *L. digitata*. The upper temperature for *L. digitata* is 20°C and in Brittany this can be reached in summer. *Sacchoriza* is more temperature tolerant and is distributed down to northwest coasts of Africa.
- photo-inhibition from U.V radiation is often lethal to sporophytes and especially on gametophytes. This factor may harm *L. digitata* during summer especially on the younger individuals after harvesting of most of the protective canopy.
- pollution.

It is clear that unforeseen changes in species composition are associated with intensive harvesting of the kelp resource. There appears to be a tendency for short lived species to replace long lived species. This tendency must result in the reduction of populations of *L. hyperborea,* when intensively harvested.

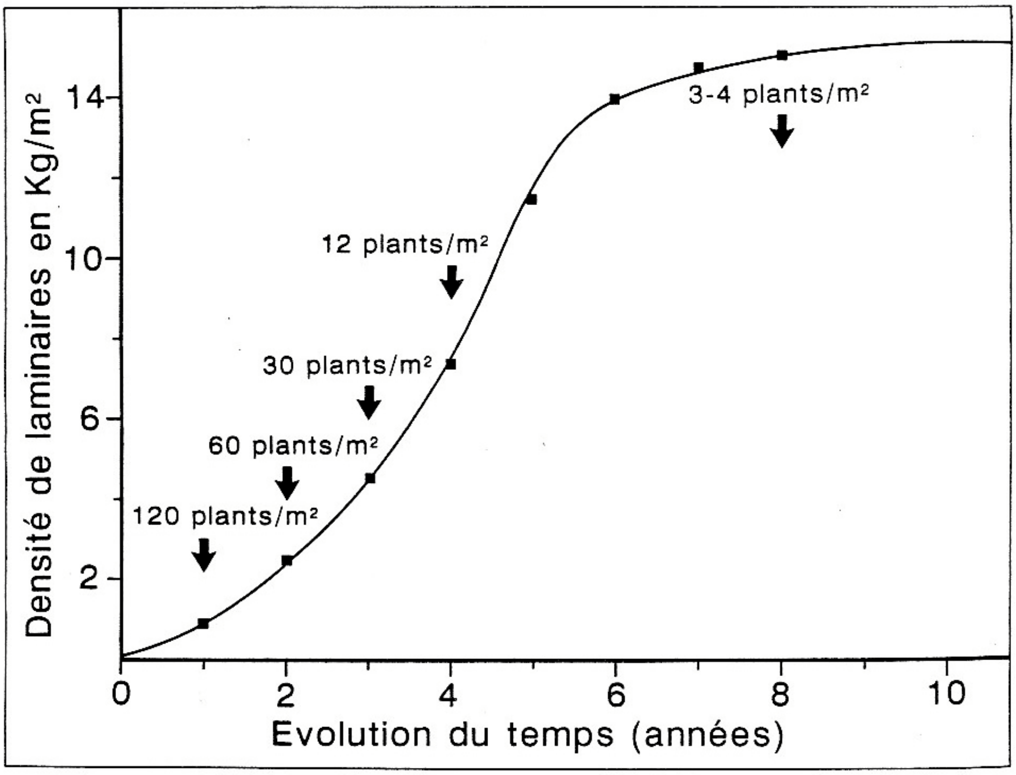
Scale of kelp removal

It is self evident that the impact of kelp harvesting is proportional to the percentage of kelp removed from a given area. Kelp removal results not only in loss of biomass but also of an active provider of very substantial amounts of POM and DOM into the ecosystem. Complete removal of the kelp forest will reduce food availability very severely in shallow enclosed bays. On open steeply shelving coasts the effect will be less.

Time and frequency of cutting

Given the seasonal cycle of growth and nutrient absorption, the time of harvesting will also have an effect on the ecosystem. On land, repeated harvesting often results in nutrient depletion. This problem seems far less likely at sea. The sea itself is the nutrient reservoir and only in bays almost entirely cut off from the sea, does nutrient exhaustion seem a possibility. However, it is possible that regrowth in nutrient rich upwelling areas such as the south west coast may be faster than in semi-isolated nutrient poor areas such as Kilkieran Bay. In any event removal of kelp in early summer will remove part of the ecosystem's reserve of inorganic nutrients, which may not be replenished until Autumn. Because *Laminaria* plants are perennial and take several years to reach maximum size, complete removal of the kelp forest must result in a decline in primary production for several subsequent seasons until maximum carrying capacity is again reached.

Figure 5 shows that a French population of *Laminaria digitata* took four years to reach maximum standing crop after a complete clearance of a kelp bed. Frequent cutting would serve to maintain the population at a lower standing crop, made up of smaller but more numerous plants, than would be found in an unaffected population. For optimum management of the resource (from the harvester's



Reconstitution des populations de laminaires après une récolte totale.

Figure 5 Re-establishment of a *Laminaria* population after a complete clearance, y axis shows biomass and x axis shows time in years

viewpoint), Pérez (1971) recommended harvesting in year three, to allow sufficient sporulation to allow population renewal. Chapman (1984) estimated the number of microscopic plants of *L. digitata* to be *ca.* 900,000 per square meter, i.e., approximately one individual per square mm. It is commonly accepted that several millions of spores are produced per square cm of sorus. Considering that sori may cover between 50% to 80 % of thalli at maturity, it is easy to appreciate the huge potential of *Laminaria* for regrowth, once plants are old enough (3 years for *L. digitata*) to produce abundant spores. After 3 years, thallus growth *of L. digitata* will start to decline and most plants die after 5 years. These considerations suggest that a management regime for kelp beds designed to maximize harvestable yield will result in a 3 year rotataion, the elimination of all plants older than this age and a consequent reduction in the supply of detrital carbon to the surrounding ecosystem.

Blade cutting vs. complete plant removal.

Harvesting and population restoration has been studied in France since 1970 and in the years following a change from hand harvesting to mechanical harvesting using the “scoubidou tool” in Brittany. Both methods were compared, i.e., tearing off the whole plant vs. leaving the stipe in place after cutting. In both cases, population regrowth followed the same pattern with restoration of a *Laminaria digitata* population taking 18-20 months. It was observed that leaving the stipe in place after cutting allowed young kelp plantlets to grow on or close to the adults’ holfasts. But in turn the stipe vestiges slowly decayed while secreting toxic compounds sometimes over a period of 6 months, thus hindering spore germination or plantlet growth. On the other hand tearing off the whole plant avoided this problem. Another effect of removing the holdfasts was to eliminate part of the calcareous film on the surface of the substrate. This film often offers an “aléatoire” fixation substratum. When kelp plants have grown into adults this layer is no longer strong enough to maintain the large plants that are then torn away by currents.

In the case of hand cutting, a part of the stipe remained attached to the substratum while mechanical harvesting removed the whole plant (allowing 10% extra weight yield). Removing stipes opened more surface for settlement thus allowing more recruitment (Fig. 6). Chapman (1984) found that the red seaweed film that developed on the substratum allowed a tenfold increase in kelp species recruitment. In terms of maximizing yield, there is an obvious advantage in mechanical harvesting and removal of the entire plant. Moreover the scoubidou tool used is selective and only removed plants greater than 80 cm. Taking off the larger plants increased light availability for young sporophyte recruitment and growth. The effect of the tool on the substratum itself was also observed. Arzel (1998) reviewed data accumulated over the total 30 year period of mechanical harvesting in France. He found that the stones removed during harvesting would have provided holdfasts for 600 tonnes wet weight of plants, accounting for only 0.2% of the total estimated biomass harvested. These findings show that an efficient mechanical harvesting regime would remove entire plants rather than cutting the blade. This practice would result in repeated disturbance of the bottom and the selective removal of all older plants.

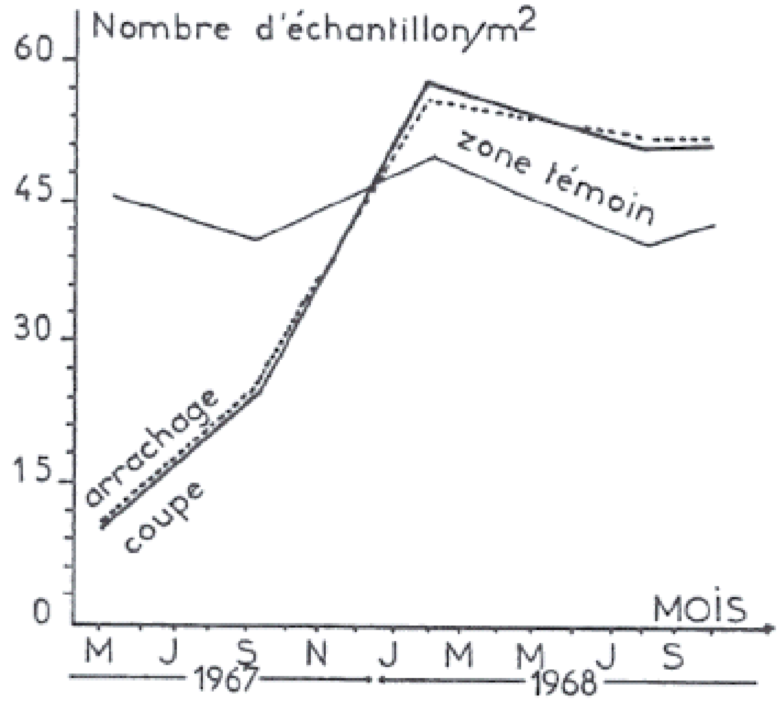


FIG. 28. — *Evolution de la densité* (nombre de thalles au m²) *dans la zone A soumise à une récolte par coupe, dans la zone B soumise à une récolte par arrachage, dans la zone C témoin.*

Figure 6 Progression of populations in areas cleared by cutting-solid line and complete thallus removal-dotted line. Y axis is thalli per m^2, x axis is time in months

Optimum management of resource exploitation - implications for kelp bed structure and productivity

Recently, Arzel (2000) recommended some actions be undertaken for better resource management of French *Laminaria digitata* populations. An inspection of his recommendations provides an indication of the structure of intensively managed kelp beds. His suggestions include:

- algal bed restoration and substrate preservation: replace the stones taken away with the kelp, bring in artificial substrata to increase the settlement surface.
- increase algal bed productivity: the harvesting campaign should take into account the progressive increase in weight of kelp in May and June. Starting harvest after this period would allow over 25% increase in yield.

- fallow years, as successfully practiced in Norway in the case of *Laminaria hyperborea*: this practice allowed yearly landings over 250,000 tons wt wg with capture efficiency of 17-25%.
- improve harvesting tools: dredges of the type used in Norway are relatively efficient yielding 2.5-4 tonnes per ha. This is equivalent to 15% in terms of individuals captured and 30% in terms of biomass. But many stipes are damaged, with 2 stipes broken for every 1 captured. Dredges could be improved to yield a 1:1 ratio.
- regulation of seaweed harvesting: quotas determination, harvesting season based on the biological cycle of kelp species.

Pérez (1971) suggested that hand cutting resulted in populations of old plants while mechanical harvesting opened dense populations to light and space and favoured recruitment and plantlet growth. In addition, younger populations contain a higher percentage of alginic acid and are of a better quality than older kelps. These suggestions, while logical from the point of view of maximizing harvestable yield, will result in uniform populations of young plants growing on a frequently disturbed or even artificial substratum. A large proportion of the plants' production will not be released into the ecosystem but removed. Repeated harvesting will probably result in monospecific stands of faster growing species and the elimination of the longer living *L. hyperborea.* Such a regime will result in a simplified ecosystem with a diminished level of primary production available for consumption by other trophic levels.

This short review of likely harvesting practices strongly suggest that the impact of kelp harvesting is not confined to removal of biomass but also affects species dominance, substratum composition and population structure.

Tegner and Dayton (2000) suggest that as kelp beds are adapted to some disturbance, limited harvesting is possible and appears not to cause problems on the US west coast and Norway. French research summarised above allows one to envisage the characteristics of a kelp bed managed for harvesting. Repeated removal of the mixed population of L. *digitata* and L. *hyperborea* will eventually result in the dominance of the former species, probably because it has a shorter life expectancy and is better adapted to constant population renewal. The effect of a three-year harvesting cycle will be to eliminate older plants, which play a larger part in POC and DOC production as well as acting as refugia for a more varied epiphytic flora and fauna. Pulling off entire plants will have a severe impact on associated bottom flora and fauna, which will also be exposed to direct light from the surface, destruction of habitat and possibly predation.

These changes in population structure and habitat appear similar to the changes that occur when “old forest” is converted to managed woodland. Old trees are removed, the ground flora is homogenized, and population structure is altered to produce younger trees of uniform size. Such changes are usually associated with a reduction in biodiversity and the disappearance of specialized detritus (rotting wood) based food chains. In both kelp and terrestrial forests the regime is designed to optimize conversion of the sun’s energy into harvestable biomass and minimize the production of non-usable material such as spores, seeds, rotting wood, detritus eroded from the kelp blade etc. These are the very products which are used by other species in the ecosystem and it is not unexpected that biodiversity declines in these circumstances.

Flora

No peer reviewed published reports or papers are known of kelp harvesting and impact on associated marine flora in Ireland. Studies from other countries are used for a comparison and to determine possible impact and risk of mechanical harvesting on associated flora. Most studies elsewhere only take fauna into account. Nevertheless survey work on the impact of harvesting on associated marine flora has been carried out in Norway and the Irish Seaweed Centre and the Martin Ryan Institute carried out some survey work from 2001-2003. Results from these studies are presented also.

California

The Giant Kelp *Macrocystis pyrifera* sustains one of the most diverse, productive, and dynamic ecosystems on the planet (Dayton 1985). Many species of algae, invertebrates, fishes, and mammals are commonly observed within Giant Kelp forests (North 1971; Foster and Schiel 1985). The distributions of many of these organisms are known to be linked tightly to the presence of *M. pyrifer*a, due to a variety of trophic and habitat associations (North, 1971; Foster and Schiel, 1985). *M. pyrifera* forests provide vast amounts of energy (Jackson, 1987), highly structured three-dimensional habitats (Coyer 1985, 1987) and large amounts of fixed carbon (Graham *et al.*, 2003). Kelp loss due to deforestation can occur by a variety of abiotic and biotic processes, such as episodic storms, El Ninõ–Southern Oscillation events, herbivore overgrazing or mechanical harvesting (Graham *et al.*, 1997). Such deforestation events can wipe out entire *M. pyrifera* populations with concomitant decreases in the abundance of various associated algae (Graham, 2002) although the community consequences of localised kelp deforestation have not been quantified. As such, data is lacking on the impact of deforestation at the community and species level (Graham, 2004). Nineteen years of species presence–absence data for both forested and deforested areas in the Channel Islands National Park, California were analysed and represents the first quantification of the effects of deforestation on an entire kelp forest community (Graham 2004). The main effect of deforestation on the structure of the producer level was a reduction of kelp and macroalgal assemblages in forested areas into a few low-lying macroalgae and the shut down of the production of kelp and macroalgal derived phytodetritus. This effectively shifted feeding of many primary consumers from attached and phytodetrital kelp and macroalgae to phytoplankton phytodetritus although little is known about the trophic importance of live or detrital phytoplankton, benthic microalgae, bacteria, or fungi in this system (Graham, 2004).

Numerous studies dating back to 1915 have investigated the potential effects of harvesting Giant Kelp in California including the effects of harvesting on frond growth and regeneration, holdfast development, individual plant survival, survival of populations of plants, and effects on plants associated with Giant Kelp (Donnellan and Foster, 1999; CDFG E.I.R., 2001). Most of this research addressed the effects of large-scale mechanical kelp harvesting. The editors of the California Department of Fish and Game Final Environmental Document (CDFG E.I.R., *op. cit.*) concluded from these studies that no significant effects are apparent from routine mechanical and hand-harvesting practices as long as individual plants are harvested no more than three times per year. Research in southern and central California has suggested that overharvesting (i.e. cutting the fronds of the same plant four or more times within 12 months) results in decreased yield and reduced plant survival, and increases in associated understory plants (Miller and Geibel, 1973).

Kelp harvesting clearly has short-term effects; the abundance of kelp canopy and associated invertebrates decreases when kelp is cut and removed from the nearshore environment by harvesting. Kelp fronds grow very little after being severed, and uncut fronds growing up from four feet below the surface (the maximum harvested depth by law) or lower must replace the surface canopy (Brandt, 1923). North (1968) reported that the initial growth rate of kelp plants was retarded after being harvested, but no significant difference was detectable between harvested plants and uncut control plants within a month after harvesting. The rate of surface canopy regeneration following harvesting is variable, depending on conditions such as the proximity of the growing subsurface kelp fronds to the surface plant growth rate, nutrient availability and irradiance levels (CDFG E.I.R., 2001).

Studies of the effects of harvesting on *Nereocystis* (Bull Kelp) have been conducted in California and in British Columbia (Nicholson, 1970; Leaman, 1980; Foreman, 1984; Roland, 1984). However, the most intensive studies on the effects of harvesting on *Nereocystis* were done in Barkley Sound, British Columbia. In these studies, a variety of harvest methods were evaluated including hand–harvesting, strip harvesting, patch harvesting (Foreman, *op. cit.*) and lamina harvesting (Roland, *op. cit.*). Bull Kelp, unlike Giant Kelp, has only one pnuematocyst per plant and reproductive sori are produced on the blades. Therefore, any activity that removes the pnuematocyst and blades results in the death of that plant as well as loss of regenerative and reproductive material. In the study conducted by Foreman (*op. cit.*), 100 m^2 plots were harvested over a three-year period (1978 to 1980). The canopy within the harvested plots was removed using a mechanical harvester, which cut to a depth of 1 m below the surface. All harvesting occurred in late August or early September. The results of this investigation revealed that there were no detectable harvesting impacts on plant density between the control and harvest plots. In addition, comparisons of mean plant biomass for harvested and control plots also failed to show significant differences. The main conclusion from this study was that natural year–to–year variability in high density *Nereocystis* beds is greater than harvesting–induced variability, conditioned on controlling the areal extent and timing of the harvest.

Foreman (1984) noted that if sustained harvesting were to be achieved, consideration must be given to harvesting after spore production has occurred or in a manner that leaves sufficient plants to ensure adequate recruitment in the following year. One way to harvest bull kelp throughout the year and still sustain recruitment potential in the next would be to hand–harvest or to use the strip method. Harvesting *Nereocystis* by hand allows for selective removal of post–sori released plants. The second method recommended by Foreman (*op. cit.*) was strip harvesting. This method involves removing the entire canopy in a given width, perpendicular to the prevalent water current and down current from a strip of equal or greater width. He also suggested that harvest be limited to 20% of the bed or that about 4 times the harvest width be left undisturbed. By using this harvest technique, large quantities could by harvested at one time while upcurrent plants would be available to release sori into the cleared area. However, the second method should only be used on high to moderately dense stands.

Roland (1984) examined the effect of partial blade removal as a harvest method of Bull Kelp. In this study, all but 30 cm of the blades were removed to allow continued blade and plant growth. Plants were either treated to single or multiple harvests. Overall survival of plants was not affected by the two treatments when compared to control plants. However, the lamina growth rates and production of sori for the single and multiple cut plants were significantly reduced. Total plant biomass (wet kg per plant) of the single and multiple cuts was 50% lower than the control. Work conducted by Nicholson (1970) in California supports these findings. Roland (*op. cit.*) concluded that use of this method would not affect the overall recruitment and sustained yield of *Nereocystis* beds, particularly if the harvest method was staggered between different plants. However, the multiple harvest of lamina was inefficient in view of the low yield relative to initial crops.

Currently, targeted Bull Kelp harvesting takes place in Crescent City for use in an abalone mariculture operation. To date, there has been no evidence that harvesting causes significant effects on the *Nereocystis* populations in this state. In the waters off British Columbia, the kelp forests are composed of 80% *Nereocystis luetkeana* and 20% *Macrocystis integrifoli*a (DFG, 2000). The Ministry of Agriculture, Fisheries and Food for British Columbia allows harvest of only 20% of the standing stock of Bull Kelp per year with the following constraints: 1) only the frond may be cut and the cut must be at least 4 inches from the bulb, allowing the blade to continue to grow; 2) harvest time is limited by the time of herring spawn within an area; in most cases the harvest season is between June and October; 3) all licenses are issued annually. The restrictions placed on Bull Kelp harvest are not based on concern that harvesting will adversely impact the kelp forests of the province, but based on the concerns of commercial herring fishermen that harvesting will affect their fishery because the herring lay their eggs on the blades of Bull and Giant Kelp. The Ministry considers the Pacific herring fishery, which exists in provincial waters, to be more economically valuable than any potential kelp harvesting industry could be.

South Africa

Two species of kelp are harvested in South Africa, *Ecklonia maxima* and *Laminaria pallida*. Close to 0.7 million tonnes wet weight was harvested in 1995. These species are harvested for the alginate and liquid fertilizer industry and to a lesser extent for macroherbivore farmers (Chritchley *et al*., 1996). The effects of harvesting of the kelp *Ecklonia maxima* at Danger Point, Gans Bay, South Africa showed that plants taller than 0.5 m had no effect on the species diversity or biomass of other benthic flora and fauna not attached to *Ecklonia*. However, kelp recruitment from sporelings settling after harvesting was slow and sporadic during the following two years but improved in the years thereafter. The main factor preventing good kelp recruitment appeared to be large numbers of grazing invertebrates. Due to such a slow recovery, large-scale harvesting of whole plants is not recommended but current research is investigating the effect of harvesting the fronds only. Results show that cutting the fronds 30 cm from their origin on the primary blade has the least effect on the kelp plants and maximises regrowth (Matthews, 1997). Kelp harvesting experiments in Jacobs Bay, South Africa examined the impact of removing all kelps with stipes longer than 50 cm in a 20 m x 20 m area. The area has few benthic grazers and kelp recruitment and re-growth has been satisfactory (Matthews, 1997).

A destructive practice of inshore habitats is shallow-water diamond mining on the west coasts of South Africa and Namibia. In that process, kelp is cut and sucked up with gravel that is sorted on the shore and then deposited intertidally. High natural variability in benthic community structure made it difficult to distinguish mining impacts even a short time after mining had ceased. Nevertheless, mining reduced the species diversity and abundance of both intertidal and subtidal communities. Recovery did, however, occur within 2 years. During, or immediately after mining, the intertidal community became characterized by the near disappearance of grazers, proliferation of fast-growing, opportunistic foliose algae and decreased cover of filter-feeders. Subsequently, grazers increased, curtailing the algae. In contrast, mining reduced subtidal algal cover. Kelp was cut to facilitate mining, foliose algae were removed and smothered as rocks were overturned, and reef-building filter-feeders diminished (Pulfrich *et al*., 2002).

Chile

Kelp forests of the Chilean coast consist of large brown macroalgae that have been widely studied. Research has focused primarily on reproductive, ecological and community aspects of associations dominated by *Macrocystis* spp. (Dayton, 1985), *Ecklonia* spp. (Bold and Wynne, 1985) and *Lessonia* spp. (Villouta and Santelices, 1986; Vásquez, 1992). Many of these species are used as raw material for the alginate industry (Sharp and Pringle, 1990; Vásquez and Santelices, 1990). The intensity of harvesting *Lessonia* along the Chilean coast could increase as this species is used as a food source for abalone (*Haliotis discus hannoi*) farming, an industrial activity that recently started in Chile (Ortiz, 2003). Increasing harvesting pressure can impact the kelp forests and associated species. High harvesting pressure may change stable flora and fauna communities into a different communities (Ortiz, 2003). Vásquez (1995) described the ecological effects of harvesting brown seaweed species inhabiting the Chilean coastal ecosystems such as *Durvillea antarctica* (Chamisso), *M. pyrifera* (L. C.Agardh), *L. nigrescens* Bory and *L. trabeculata* Villouta et Santelices. Kelp harvesting alters the habitat structure and can be considered as a strong disturbance for flora and fauna (Vásquez and Santelices, 1984). The effects of macroalgae harvesting on the entire ecosystem depends on many factors, amongst them biological factors, such as the presence/absence of grazers, seasonality and reproduction of the algae. Santelices (1982) carried out removal experiments with *L. nigrescens* in the absence of grazers and demonstrated a changing community depending on the season. When this species is harvested in summer, the community shifts to an *Ulva* dominated community, followed, in some cases, by replacement by *Gelidium chilensis*

(Montagne, Santelices et Montalva). *G. chilensis* prevents the settlement of *Lessonia* spp. (Santelices and Ojeda, 1984). Experimental removal of *L. trabeculata* showed a positive effect on settlement of its recruits (Vásquez, *op. cit.*).

Canada

The fishery for the green sea urchin (*Strongylocentrotus droebachiensis*) commenced in New Brunswick in the late 1980's in response to increasing demands from Asian markets. Members of the scallop industry initiated fishing and the harvesting practices were based on familiar fishing gear (scallop drags or dredges) with similar operations occurring simultaneously in Maine. Because of the potential impact of scallop gear on the shallow water populations in areas not traditionally fished, a study was initiated in 1993 to document (1) the proportion of sea urchins damaged during the harvesting operation, (2) the impact on and subsequent recovery time of the associated benthic flora and epifauna, and (3) the impacts on the bottom substratum. The results showed that the dragging operation increased the breakage rate of the kelp, *Laminaria longicruris*. No differences were observed between the experimental and control plots after three months. Robinson *et al.*, (2001) concluded that there were short-term impacts from dragging, but the observable effects on the bottom from the single dragging event were gone in less than 3 months. Longer-term effects of dragging were unknown.

Isle of Man

Kain (1975) examined recolonization by algae of artificially cleared areas in a *Laminaria hyperborea* forest in Port Erin, Isle of Man. Cleared concrete blocks were colonized by *Saccorhiza polyschides*, *Alaria esculenta*, *Desmarestia* spp., *L. hyperborea*, *L. digitata*, *L. saccharina* and un-specified red algae at 0.8 m depth. *S. polyschides* dominated within 8 months but had virtually disappeared after 77 weeks to be replaced by laminarians, including *A. esculenta*. After about 2 $^1/_2$ years, *L. hyperborea* standing crop, together with an understorey of red algae, was similar to that of virgin forest. Red algae were present throughout the succession increasing from 0.04 to 1.5% of the biomass within the first 4 years. Colonizing species varied with time of year, for example blocks cleared in August 1969 were colonized by primarily *L. saccharina* and subsequent colonization by *L. hyperborea* and other laminarians was faster than blocks colonized by *S. polyschides*; within 1 year the block was occupied by laminarians and Rhodophyceae only. Succession was similar at 4.4 m, and *L. hyperborea* dominated within about 3 years. Blocks cleared in August 1969 at 4.4 m were not colonized by *S. polyschides* but were dominated by red algae after 41 weeks, e.g., *Delesseria sanguinea* and *Cryptopleura ramosa*. Kain (1975) cleared one group of blocks at two monthly intervals and noted that Phaeophyceae were dominant colonists in spring, Chlorophyceae (solely *Ulva lactuca*) in summer and Rhodophyceae were most important in autumn and winter.

France

Traditionally *Laminaria digitata* was harvested by hand and dragged up the coast by horses; however, due to increased demand for this seaweed mechanical harvesting was developed. Frequently harvested *L. digitata* beds are showing a shift towards homogeneity with respect to plant age. Mechanical harvesting removes plants longer than 60 cm existing of plants aged 2-5 years. The one-year old plants are left to grow for the following years harvest together with the remaining older plants. On average, 30% of the population of a kelp forest is harvested. Frequently harvested beds consist of a lower percentage of 3-5 year old plants, and consequently the age structure within kelp populations shifts towards 1-2 year old plants. The change in population structure also affects recruitment (*L. digitata* becomes fertile in the second year) and the overall biomass of the stocks with highest biomass per plant found in 3-4 year old plants (Arzel, 1998). Recruits derived from spores released in autumn showed a significantly faster growth rate in comparison to those derived from spores released in spring (Pérez 1971). Obviously, the growth of the latter is suppressed by shading from older plants because the density of plants and the biomass of stocks are highest during summer to autumn. By contrast, recruits from the spore dispersal event in autumn are developing at a time of the year when the overall biomass of the kelp beds is decreasing. Narrowing the age class distribution to 1-2 year old plants will reduce the overall output of spores and consequently the success of recruitment (Werner & Kraan, 2004). Even under unexploited conditions, the overall annual mortality of kelps in beds can reach up to 50% (Arzel 1989). The decline of standing stocks of *L. digitata* over the last 5 years may be the result of over-exploitation. In most areas off the coast of Brittany, kelp beds are harvested without allowing the standing stock to recover over a longer period than the time between the harvesting seasons. Potential factors leading to an exhaustion of stocks may be the removal of more than 30% of the standing stock during a harvesting period due to over-harvesting together with natural losses of plants, which can affect up to 50% of the populations (Arzel 1998).

In certain areas off the coast of Brittany, the homogeneity of *Laminaria digitata* beds after harvesting is increasingly disturbed due to the development of *Saccorhiza polyschides*. Reasons for the increasing abundance of *Saccorhiza polyschides* are not clear. This kelp is an opportunistic fast-growing annual species and can reach a size of up to 3 metres in length in a period of 8 months (Norton & Burrows 1969b). It competes with *L. digitata* and *L. hyperborea* for space and grows on disturbed substrata such as unstable boulders and smaller rocks (Lüning 1990). It rapidly colonises free space created after harvesting. Due to their rapid growth, young *Saccorhiza* plants quickly shade developing *L. digitata* sporelings, which are consequently arrested in their growth or displaced (Arzel 1998). In autumn/winter *Saccorhiza* plants decay and are removed from the substratum due to storms and heavy water motion. With the reduction of shading, young *Laminaria* sporophytes can resume development although decreasing light levels in winter result in low growth rates. Fast growth and competition with other *Laminaria* species do not sufficiently explain the increased occurrence of *S. polyschides* in recent years. Slight changes in water temperature may play an important role (Werner & Kraan, 2004).

The introduction of fallow periods of one to two years may improve the recovery of *Laminaria* beds significantly by increasing the average age within the populations and as a consequence recruitment. It is also seen as a method to allow *L. digitata* to replace *Saccorhiza polyschides* because the latter is an annual species that dies off in winter. Due to its slower growth compared to *S. polyschides*, it is assumed that it may take 2-3 years for *L. digitata* to successfully re-colonise areas that were previously dominated by *S. polyschides* (Kain, 1976).

Norway

Norway is the only European country where *Laminaria hyperborea* is currently harvested in large quantities. The raw material is used for alginate extraction by the domestic hydrocolloid industry. Norway has developed special harvesting machinery, which meets the specific requirements with respect to kelp species and coastal conditions. Kelps form large forests along the north-eastern Atlantic coastline, where

Laminaria hyperborea (Gunn.) Foslie is the dominant species. Kelp forests are estimated to extend between 5,000 and 10,000 km^2 along the Norwegian coast and are affected by both biological and physical disturbances. Grazing by sea urchins clears large areas (Waage-Nielsen *et al.*, 2003) whereas storms and harvesting (kelp trawling) often clear smaller areas due to variations in topography and depth, leaving a fragmented kelp forest landscape rather than large cleared areas (Rinde *et al.*, 1992; Christie *et al.*, 1994).

Kelp harvesting takes place in all seasons on the Norwegian west coast, and approximately 170,000 tonnes of kelp are harvested every year. Generally, a kelp trawl removes all canopy-forming kelp plants in a 4 m wide track. Depending on the composition of vegetation in the understory, the track is either barren or vegetated by small understory algae, including kelp sporelings. All that remains of the canopy plants is a few holdfasts (Waage-Nielsen *et al.*, 2003). Due to improved light conditions, these recruits grow out in dense stands forming the next generation of canopy forming algae. Within 2 - 4 years they reach a plant height of 1-1$^1/_2$ metres (Rinde *et al.* 1992; Christie *et al.* 1994). The age composition of canopy-forming kelp plants in different trawled areas indicate that recruits develop during several years before trawling, showing that regrowth does not solely depend on the recruitment success in the year of trawling (Christie *et al.*, 1998). Intraspecific competition leads to a reduction of canopy plant density. After a fallow period of 5 years, plant density is still higher and age of canopy forming plants is still lower than in untrawled areas (Christie *et al.*, 1994). Differences in plant growth (length) and growth of the holdfast were found at different study sites along the Norwegian coast as well as differences in age distribution of kelp populations. With increasing latitude, growth is slower and average plant age in undisturbed kelp beds is higher (Sjoetun *et al.*, 1993; Christie *et al.*, 1998). The authors concluded that the restoration of the flora and fauna community associated with kelp forests depends significantly on the recovery of kelp demography and structure. The latter may vary depending on environmental factors specific to a particular site. Therefore, harvesting times might be adjusted accordingly. Full recovery of the biotope is likely to take in excess of 5 years. The quality of the habitat changes as a plant becomes older; its size increases and structural changes take place in the stipe, especially with the establishment of an increasing number of epiphytic red algae (Christie *et al.*, 1998). Even the epiphytes change as they undergo seasonal fluctuations in both size and composition (Whittick, 1983). In a study of the regrowth of kelps and the accompanying recovery of kelp fauna and epiphytic algae in trawled tracks of different ages, Christie *et al.* (1998) found that kelp plants reached the normal canopy height within 3–5 years. Within the same period, large numbers of organisms colonized the recovering kelp plants but the diversity of the holdfast fauna and stipe epiphytes did not reach the same level as in the natural kelp forest. An explanation may be that the habitat had not fully recovered. Christie *et al.* (1998) found that the regrowing kelp forest was more homogenous in structure than natural kelp forests and contained fewer and less voluminous stipe epiphytes (mainly red algae).

Sustainable harvest is vital for the alginate industry and depends on the time necessary for regeneration of *L. hyperborea* plants. Decisions regarding the time interval of trawling are generally based on unpublished data of kelp regrowth provided by the industry itself (Christie *et al.* 1998). However, independent investigations in the late 1980s and 1990s have contributed to the prolonging of the harvesting cycle from 4 to 5 years (Sivertsen 1991; Rinde *et al.* 1992). Regrowth of kelp plants is also crucial for the recovery of the whole kelp forest ecosystem.

Ireland

A small-scale study by the Irish Seaweed Centre as part of a EU CRAFT proposal examined the effect of mimicing mechanical harvesting on associated flora and fauna, biodiversity and re-colonisation.

Re-colonisation

Due to the short duration of the project, only one removal experiment was conducted. An area of 20 m^2 was strip-harvested in March 2002 for biomass assessment and was monitored for species change and re-colonisation. For this report only associated flora are described. One of the most obvious changes was the appearance of small kelp plants of *Saccorhiza polyschides* and many *Dilsea carnosa* plants, compared with the unaffected kelp forest. During October 2002, the following percentages of covering species were noted: 40% *S. polyschides;* 20% *Dilsea carnosa; 10 % Oudionella sp, Ahnfeltia plicata*, *Polyides rotundus*, and *Plocamium cartilagineum*; 10 % *Corralina officinalis* and *Osmundia pinnatifida;* 5% *Chondrus crispus;* 5%

Pylophora crispa, 1% *Ceramium nodulosum*, *Ceramium rubrum* and *Plumaria elegans* and 4% crustose *corallina* algae. Incidental specimens of *Lomentaria clavelosa, Acrosorium* and *Dictyota dichitoma* were also found.

In March 2003, the first small kelp species were detected. Due to the size of the plants it was not possible to identify them to species level, however, these young kelp plants at that depth were most probably *Laminaria hyperborea*. A few small intact *Saccorhiza polyschides* (20%) were also found. *Dilsea carnosa* (5%) was present but at lower levels than the year before. Furthermore, the species composition was similar to that of the year before, however, percentage cover was lower. This might be a seasonal effect (e.g., while *Delesseria* occurs all year around it particularly dominates during summer). The remarkable finding of this experiment was the appearance of *S. polyschides* during the summer, disappearance in winter and re-appearance in spring. This was not observed within the undisturbed kelp forest in the vicinity. Due to time constraints and project duration recolonisation was followed for only one year. Therefore, a full restoration of the harvested area was not observed although regrowth followed a similar pattern recorded in other studies (Kain 1976b; Sivertsen 1991). The replacement of *S. polyschides* by *L. digitata* and/or *L. hyperborea* is reported to take 2-3 years (Kain, 1976).

Biodiversity

During the course of the study a total of 50 *Laminaria digitata* and 50 *L. hyperborea* plants were examined and a total of 17 floral epiphytes were identified attached to the blade, stipe or holdfast. A lower number was found for *L. digitata* with 9 floral epiphytes (see Table 5). Most species were encountered on the stipe and holdfast. The blade contained fewer species and often only a few dominant species. The number of different species is strongly correlated with the age of the kelp with more species and genera occurring on older kelp. Also, the progressive development of the epiphyte community with increasing age of the host is seen (Rinde *et al.*, 1992). The age of the *L. hyperborea* plants at the sample site followed a normal distribution with most plants in the 3 year old category and the oldest plants being 7 years old (Evertsen, 2003). Seventeen species of flora were found which agrees with Christie *et al.* (1998) who found 13 species of epiphytic flora on stipes of *L. hyperborea* from

Norway. The numbers of algal epiphytes on L. digitata were lower due to a smooth stipe. Moreover, the outer layer is shed every year to remove epiphytes.

Table 5. Total of floral epiphytes encountered on 50 *Laminaria digitata* and 50 *L. hyperborea* stipes.

Flora on *Laminaria hyperborea*	**Flora on *Laminaria digitata***
Chlorphyceae	**Rhodophyceae**
Cladophora rupestris	*Polisiphonia macrocarpa.*
Ulva sp.	*Plocamium cartilageneum*
	Ptilota gunneri
Rhodophyceae	Crutose *corallines*
Pterosiphonia pennata	*Palmaria palmata*
Lithophylum	*Brogniatella bysoides*
Lithothamnion	*Lithosiphon sp.*
Phylophora sicula	*Ptilota pulmosa*
Polisiphonia sp.	
Corallina officinalis	**Phaeophyceae**
Palmaria palmata	*Fucus* sp
Lomentaria articulata	
Ptilota plumosa	
Delesseria sanguinea	
Cryptopleura ramosa	
Polysiphonia lanosa	
Membranoptera alata	
Phycodrus rubens	
Phaeophyceae	
Laminaria digitata	
Sacchariza polyschides	

Most species on *L. digitata* were encountered in/on the holdfast and on the lamina with 9 floral epiphytes. No data on numbers of species on *L. digitata* was found in the literature. When areas are harvested by mechanical harvesting all sessile organisms on the kelp will be removed with most species on the stipe and holdfast. Recruitment strongly depends on how kelp is harvested. Harvesting in patchy patterns in different zones allows for easy recruitment from the surrounding kelp forest (Norderhaug *et al*., 2002; Waage-Nielsen *et al*., 2003). Recovery and recruitment is more difficult in large strip harvested areas over several 100 meters, although Frederiksen *et al*. (1995) have shown that spores of *L. hyperborea* can disperse over 200 m.

Invertebrates

Kelp forests are affected by both biological and physical disturbance; grazing by sea urchins can clear extensive areas (Mann, 1977; Chapman, 1981; Hagen, 1995) and the Blue Rayed Limpet is also known to feed on kelp fronds (Birkett *et al.*, 1998), physical disturbance due to storms and harvesting can clear smaller areas (Waage-Nielsen *et al.*, 2003). The impact of urchin grazing on Irish kelp beds has not been recorded to date. Disturbance to kelp forests occurs on different time scales: grazers and storms (hours/days), intra-annual cycles of epiphytes (months), longevity of kelp (years) and trophic level dysfunction (decades and more). Steneck *et al.* (2002) comment that kelp forests can be surprisingly ephemeral and that they can be entirely wiped out by thermal events, storms or outbreaks of herbivores and disappear within a year but that they can return almost as quickly (see also Pearse and Hines, 1979).

Velimirov (1983), working off southern Africa, noted that wave-induced sweeping of kelp fronds resulted in relatively barren areas around the stipes thereby restricting grazers from having access to the plants. In some clearance experiments, he found that the exposed new space had been totally re-settled by macroinvertebrates within 50 days.

The bulk of work that deals with the recovery rates of flora and fauna following removal of kelp has been carried out in Norwegian waters. A recovery experiment was carried out on the west coast of Ireland, near Spiddal, Co. Galway but the experiment lasted only 1 year (S. Kraan, *pers. comm*.). Christie *et al.* (1998) studied the effects of kelp harvesting on epifaunal communities off the coast of Norway. They state that recolonisation of areas where harvesting has taken place depends not only on the recovery time of the kelp itself but also on how successfully the invertebrates are able to re-establish themselves in the system. They report that a mature kelp forest normally contains an understory vegetation of recruits that can re-colonise the area once the adults are removed and note that *Laminaria hyperborea* was abundant after 4 years in an area that had suffered from over-grazing by sea urchins. Some variation on growth rates was demonstrated for the two locations they studied and a recovery period of 4 years for one location against 6 years for the other was recorded for the kelp to return to its pre-harvest height. In the same paper, the authors state that the age of kelp is important for epiphytic/faunal cover and note that the proportion of stipes settled by epiphytes was significantly lower in trawled tracks three years after trawling. This reduction in epiphyte cover would have a direct effect on the numbers of epifaunal species present. Variation in holdfast macrofaunal species and numbers of individuals was high within replicates. While numbers of individuals were higher one year after harvesting compared to epiphyte numbers, average numbers of species increased slowly with increased age of the kelp. They reported that it took six years for faunal abundances to stabilise. Christie *et al.* (*op. cit.*) also examined species groups (polychaetes, isopods, gastropods and amphipods) to quantify changes in abundance during the post-trawling period and found for the most part that all groups showed significant increases in numbers per holdfast over time.

Waage-Nielson *et al.* (2003) investigated the dispersal ability of kelp fauna to a cleared (harvested) area by studying their colonisation of artificial substrata (kelp mimics) exposed for a short 3 day period and a longer 35 day period at different sites in existing kelp forests and at harvested sites. Lengths of untwisted hemp rope were used to mimic kelp habitats. Of a total of 128 mobile species, most of the kelp fauna (111 species, *ca*. 87%) showed a rapid colonisation of the artificial substrata within the cleared area. Amphipods and gastropods dominated in terms of numbers of species and numbers of individuals.

In the short term experiment, the artificial substrata were rapidly colonized by high numbers of species and individuals; 106 species and 9,801 specimens were identified after 3 days exposure in September and 52 species and 5,047 individuals in November. Seven species accounted for 48% of the total number of species. The amphipod, *Apherusa* sp, comprised 80% of the total number of amphipods in September and 79% in November and the gastropod *Rissoa parva* was the dominant species accounting for 83% and 90% of the total gastropod numbers. Mussels (primarily *Turtonia*, *Musculus* and juvenile *Mytilus*), isopods and decapods were also abundant in the artificial substrata. Only small numbers of polychaetes and tanaids colonized the 3 day mimics. These authors recorded no reduction in the rate of colonization, either as numbers of species or numbers of individuals, from the mimics within the existing forest and those placed at increasing distances from the harvested areas.

With regard to the longer term experiment, the numbers of individuals and numbers of species increased with the length of exposure time. A total of 21,933 individuals represented by 128 species were recorded after 35 days and there were no significant differences between sites in numbers of species or total abundance. Thirteen species accounted for 50% of the total number of species (14 species made up 49% in natural holdfasts). This longer experiment developed a closer resemblance to the fauna found on natural kelp plants than the shorter time scale of 3 days and also led to a higher diversity of species. They found no significant differences between sites in the numbers of gastropods or amphipods and that there were no significant differences between the sites for the four most abundant gastropod species. *Rissoa parva* accounted for 90% of the total number of gastropods in this longer term study while for amphipods, *Apherusa* and the Family Sthenothoidae accounted for 31% and 28% of the total number, respectively. Caprellids and aroids decreased in numbers from the site within the kelp forest out to the cleared area. The amphipod *Jassa falcata* which accounted for *ca*. 10% of all amphipods within the untrawled site, was only recorded at less than 1% in the artificial substrata after 35 days. The same results were recorded for the bivalves. Wagge-Nielsen *et al.* (2003) also noted that, in general, gastropods and amphipods colonised the artificial substrates faster than mussels, polychaetes, isopods and tanaids. Decapods had a more variable colonisation rate.

The results presented by Wagge-Nielsen *et al.* (2003) show that the fauna of laminarian forests is highly mobile and exhibits high dispersal rates. This was shown by the high numbers of species and numbers of individuals in the artificial substrata after only 3 days and the fact that the kelp mimics placed in cleared areas were settled as fast as those placed within the kelp forest. Notwithstanding this fast dispersal rate, the ability varies from one faunal group to another. This was illustrated by (1) significant increases in numbers of both species and individuals after an increase in time from 3 – 35 days, (2) differences in mobility as noted above and (3) the fact that species groupings in the artificial holdfasts became more similar to those in the natural holdfasts over time. The study shows that amphipods and gastropods are well capable of re-colonising kelp plants within a short period whereas polychaetes, bivalves, isopods and tanaids are slower. Some species that were recorded on the natural kelp plants, albeit in low numbers, were not recorded on the kelp mimics after 35 days. Wagge-Nielsen *et al.* (*op. cit.*) comment that their absence might be explained by a lack of particular habitat properties of the kelp mimic material, low dispersal ability or because their inherently low densities, may present less opportunities for encountering a mimic.

The study showed that both juvenile and adult amphipods and gastropods actively move into available substrata throughout the year. Wagge-Nielsen *et al.* (2003) go on to postulate that the observed differences in mobility may be more important for species with direct development than for those species with pelagic larvae. Species with planktonic larvae have the advantage of being able to colonise new or cleared areas throughout the larval period and they can also be dispersed over extensive areas of the coast by tidal currents. Species with direct development have neither of these advantages and depend on the juveniles or adults to disperse the species. They also state that the kelp fauna has several alternative habitats or refugia other than the kelp itself and they comment that the importance of these areas will depend on factors such as topography and exposure to wave/surge action.

Wagge-Nielsen *et al.* (2003) comment at the end of their discussion that, after disturbances such as kelp trawling, the kelp forest community shows a certain ability to recover quickly and that the fauna shows little vulnerability to such disturbances. They go on to say that in addition to the high level of mobility within some groups, many species have planktonic larvae that colonise new habitats efficiently. They do note that incomplete recovery of the community is related to an incomplete recovery of the habitat: Christie *et al*. (1998) found that kelp plants less than four years old had smaller holdfasts and that the stipe epiphytes were not fully developed.

Jørgensen and Christie (2003) studied the dispersion of kelp-associated fauna in more detail and the aim of the work was to characterise medium-scale dispersion patterns of the mobile fauna with a focus on the horizontal, vertical, diurnal and nocturnal activity. As for the study by Wagge-Nielsen *at al.* (2003), Jørgensen and Christie (*op. cit.*) also used kelp mimics for their experiments. For the diurnal studies, the kelp mimics were placed in the kelp forest for 10 hours either at night or during the day. They found that there was a higher rate of colonization during the hours of darkness than in daylight hours that may reduce exposure to predators. The amphipods *Apherusa bispinosa*, *Corophium* spp and *Jassa falcata* showed particularly high activity at night and the authors noted that the amphipods were 11 times more common in night time samples than day light samples. Gastropods were only twice as common in night time samples compared to day light ones.

For the horizontal and vertical studies, the mimics were placed in the forest for four days. Jørgensen and Christie (2003) note that amphipods and isopods are active swimmers whilst gastropods spin out mucous threads and are then picked up by currents and drift within and above the kelp forest. The colonisation rates on kelp mimics were similar to those recorded by Wagge-Nielsen *et al.* (2003). The results also showed that large numbers of animals dispersed both horizontally along a benthic gradient and vertically along a pelagic gradient. They comment that food or space may be the limiting resource in kelp forests.

From the above findings, it appears that at least some elements of the kelp community can re-establish themselves over a very short time scale compared to other marine communities; experiments with plates to follow succession on rocky subtidal habitats typically take *ca*. 2 years to manifest an assemblage that resembles the resident community (J. Costelloe, *pers. comm*.). Recovery of a *Serpula vermicularis* reef in Salt Lake, Clifden, Co. Galway following deoxygenation due to oxygen-sediment demand took somewhat less at 1 year (B. O’ Connor, *pers. obs*.). The collapse and recovery of a similar assemblage has been recorded in the Ordovician by Steele-Petrovich and Bolton (1998). The speed with which those elements within the kelp community disperse and re-colonise relates to their naturally high levels of mobility and apparent lack of fidelity to an area.

The role that kelp forests play in regulating current flow through the canopy and into the understorey has been examined by a number of workers, i.e., Eckman *et al.* (1989), Mork (1996) and Andersen *et al.* (1996) (see invertebrate section in Gap Analysis section below). Given the size and density of kelps, it might be presumed that their biomass may have a measurable impact on dampening the velocities and altering current flows. One might also hypothesise that removal of the forests may not only affect local oceanographic conditions but also increase exposure levels on adjacent intertidal areas.

Fish

There have been few studies on the effects of mechanical kelp harvesting on fish species diversity and associations. Some preliminary research by Sjøtun and Lorentsen (2003) in Norway has suggested that harvesting of *Laminaria hyperborea* beds might negatively affect fish recruitment. They found that juvenile gadoids (Saithe and Pollack, *Pollachius virens* and *P. pollachius*) disappeared from newly harvested areas. However, there have been no long term studies carried out on the response of fish populations to kelp harvesting.

Considering the role of kelp habitat in relation to shelter, diet and reproduction of fish species (discussed above), it is likely that the removal of kelp forest would have some knock-on effects, depending on the nature of the kelp habitat association for each species. For example, the removal of structural complexity and vegetation may reduce suitability of a harvested area as a nursery or spawning site for some fish species, thus impacting on reproductive ecology. In addition, any variation in abundance of mobile invertebrates and forage fish associated with kelp forest removal (particularly small crustaceans such as amphipods, gastropods, isopods), is likely to affect the diet of top down consumers such as fish (Jorgensen and Christie, 2003; Christie *et al*., 2003). In North America, a study by (Bodkin, 1988) showed that a decline in juvenile rockfishe, i.e., *Sebastes* sp, (an important prey item for larger piscivorous fishes) associated with kelp forest removal may have had a subsequent impact on the forage base of the larger kelp forest fishes, demonstrating a trophic cascading effect in fishes.

Apart from the obvious direct impacts, there may be indirect effects of removing kelp from the marine environment for fishes occupying habitats that are adjacent to the impacted kelp habitat. For example, recent research in Norway has shown that kelp is important for stabilising wave movement (Mork, 1995; Nilsen and Mork, 1995; Andersen *et al*., 1996). The removal of this stabilising effect through clearance of large areas of kelp forest may have consequences for associated inshore habitats. This, in turn, may have implications for fish species that have not been considered as ‘kelp habitat fish species’ in the present study, as they may be dependant on the shelter or feeding opportunities afforded by habitat indirectly associated with kelp. Other species may be indirectly associated with kelp habitat through use of inshore areas as migratory corridors to reach freshwater spawning sites, e.g., the Atlantic Salmon *Salmo salar* (Tesch, 1977; Page and Burr, 1991).

In order to assess the potential threat of kelp removal on the fish species identified in Appendix 1, a number of life history traits were reviewed for each species and provided in Appendix 3. It was anticipated that information on these traits would provide greater clarity as to the likely nature of a particular species’ relationship with kelp habitat, thus providing greater insight into the potential vulnerability of that species to kelp habitat removal. The relative occurrence or conservation status of the species was also reviewed and this information was drawn from a combination of assessments available in the literature (i.e., Went, 1957; Went and Kennedy, 1976; Anon, 1994; Quigley, 1996; Froese and Pauly, 2004). The information presented in Appendix 3 facilitated a purely descriptive analysis. More information on the biology and ecology of fish species in relation to kelp habitat in Ireland would obviously be required for a more comprehensive analysis.

A number of criteria were considered to indicate sensitivity of a fish species to removal of kelp species, i.e.,

(a) Uncommon occurrence (i.e., occasional, local, scarce or rare) or vulnerable conservation status in Ireland.
(b) Dependence on algae for nest building, egg laying, reproduction and/or nurseries.
(c) Dependence on forage fishes associated with kelp as a food source.
(d) Dependence on shallow (< 30 m) inshore kelp dominated areas for habitat, i.e., the species is unlikely to exploit deeper areas as habitat.

Ranking of these criteria was not considered due to the difficulty in quantifying the risk associated with each criterion relative to each fish species. There was also a degree of overlap between criteria due to the broad scope of the descriptions used in the analysis. However, a species was considered to be at increasing risk relative to the number of criteria related to its ecology.

Of the 37 species of fish considered in the analysis, 16 species were found to be related to criterion (a) (3 were occasional, 3 were local, 7 were scarce, 3 were rare and 2 were vulnerable), 10 were related to criterion (b), 8 were related to criterion (c) and 23 were related to criterion (d). A relatively high proportion of species were related to criterion (a). However, this may be a reflection of the fact that the species list included data collected from surveys carried out in other European countries. For example, some species that may be common in Norway (such as the Norway Bullhead *Taurulus lilljeborgi*) may be regarded as uncommon in Ireland (Quigley, 1996).

Species that appear to be most dependent on the kelp habitat are those species that occupy territories in an area of kelp habitat all year round whilst also relying on algae for nest building, e.g., Corkwing Wrasse *Crenilabrus melops* (Deady, 1995). Other wrasse species may be commonly associated with kelp but do not rely on algae for reproduction like the nest builders, e.g., Goldsinny Wrasse *Ctenolabrus rupestris* do not build nests and are more dependent on rocky substrate than on algae for habitat (Varian, 1998). However, the conservation status of these fish species is not classed as uncommon or vulnerable. Uncommon species that inhabit shallow inshore areas and rely on algae for reproduction (i.e., criteria (a), (b) and (d)), e.g., Montagu's Sea Snail *Liparis montagui,* would appear to be more sensitive to the effects of kelp removal.

Species classified as threatened or vulnerable by the IUCN (Anon, 1994), such as *Gadus morhua* Cod, *Anguilla anguilla* European Eel and *Salmo salar* Atlantic Salmon, warrant particular attention as populations may already be under pressure from threats such as fishing. The Atlantic Salmon is also an Annex II species under the EU Habitats Directive 1992 and the European Communities (Natural Habitats) Regulations 1997. Thus, it is important that the sensitivity of these species is considered a priority in the conservation management of any potential kelp harvesting industry. However, it should be noted that the current paucity of information on the relationship and association of these species with kelp habitat in Ireland makes it difficult to determine potential impacts.

Birds

In general, there is little scientific information with regard to direct interactions between seabirds and kelp forests. Birds occupy an important but little studied trophic level within the kelp forest food chain yet the complexity of the kelp forest food chain is evident from previous research (e.g., Estes *et al.*, 2003; Fredriksen, 2003). Relatively more information is available regarding shorebirds and kelp wrack. However, the majority of published scientific information comes from research conducted in other geographical regions and often examines species of kelp or birds that do not occur within Ireland.

Despite the paucity of scientific data however, there appears to be very important ecological interactions between kelp forests and birds. These are summarised below:

- Kelp forests provide a foraging habitat due to the abundance and diversity of associated fauna that makes this ecosystem one of the most productive on earth (Mann, 1973). In addition to invertebrates directly associated with infralittoral reef habitats with kelp, kelp forests serve an important role in the reproductive ecology of mobile and pelagic fish and invertebrates that ultimately end up as potential prey items for birds.

- Kelp forests contribute significantly to coastal secondary production, supporting complex food webs in intertidal zones (Duggins *et al.*, 1989). This production ultimately supports coastal bird populations.

- Kelp wrack provides a breeding habitat for kelp flies (Coelopidae) that provide an important prey source for many coastal and terrestrial bird species. Current research (from published studies outside of Ireland) suggests that kelp wrack may be a very important foraging habitat for many species of birds, especially during periods of migration.

Impacts will be greater for birds that are considered to be of conservation concern. The conservation importance of bird species largely relates to the population status of each particular bird species, within its breeding and/or wintering range. Bird species of conservation importance may be listed on either or both of the following:

Council Directive of 2 April 1979 on the Conservation of Wild Birds (79/409/EEC) ('Birds Directive').

This directive relates to the conservation of all species of naturally occurring birds in the wild. The directive lays down protection, management and control of these species and lays down rules for their exploitation. The directive applies to the birds, their eggs, nests and habitats. Species of conservation importance are listed under Annex I of the directive. This legislation is the basis for designation of Special Protection Areas (SPAs).

Birds of Conservation Concern in Ireland (Newton *et al.*, 1999).

This document set out by BirdWatch Ireland and RSPB Northern Ireland, presents a priority list of bird species within Ireland. The list is divided into Red List Species of high conservation concern, e.g., species that have undergone significant population declines (> 50%) since 1900. Amber List Species are defined as having medium conservation concern, e.g., species whose breeding population has declined by 25% - 50% in the past 25 years. Green List Species are species whose conservation status is presently considered as favourable.

The conservation status of bird species listed in this current report (and that occur within Ireland) are provided in Appendix 4.

Mechanical kelp harvesting is currently conducted in Norway and France on a regulated basis and in Norway occurs on a five-year cycle to allow kelp regeneration. Kelp forests are generally considered to have a good capacity for regeneration (Wilkinson, 1995). Previous studies have shown that if small understorey kelp plants are left undisturbed (as in the Norwegian method of mechanical kelp harvesting) they will grow and form a new canopy within 2-3 years (Christie *et al.*, 1998). However, recolonisation of the kelp forests by flora and fauna is a slow process and a review of previous studies found that the biodiversity of a kelp forest is not regained even 6 years after trawling (Wilkinson, 1995).

Mechanical kelp harvesting therefore amounts to a significant ecological disturbance to the entire kelp ecosystem. The effects of this disturbance on birds are difficult to assess without being able to accurately quantify the relationships between birds and kelp, for example, to ascertain to what extent birds are reliant on the kelp ecosystem. Currently the effects of mechanical kelp harvesting on birds are largely unknown (Jan Bustnes, *pers. comm*.). One previous Norwegian review suggests that many of the effects of kelp trawling will be localised and provided that trawling does not occur near sites of specific bird interest, negative effects will be minimised (Bustnes *et al.*, 1997).

Following the current review, the following generalisations can be made:

1. Relatively few bird species in Ireland appear to be directly reliant on kelp forests for feeding habitats. Many seabirds forage in a wide variety of habitats, e.g., both rocky and sandy substrata and forage both inshore and further offshore. However, certain species of seabird appear to be associated with kelp forests to a greater extent. These include the Cormorant, Shag, Black Guillemot and sea ducks such as the Common Eider. Many other bird species described in the current review will forage within kelp habitats but this will constitute only a portion of their foraging habitat.

2. Potential impacts of kelp harvesting upon birds will be greater for breeding birds that forage closer to their coastal colonies during the breeding season.

3. If kelp harvesting results in significantly lower organic matter input (in the form of kelp wrack) to intertidal shore ecosystems (both sandy and rocky shores) there is a potential for ecological impacts upon invertebrate community structure and dynamics. This includes both intertidal invertebrates and strandline dipteran coelopid flies. The knock-on effects could be significant for foraging shorebirds, particularly during migration. Further studies are needed to ascertain the abundance and importance of kelp wrack relative to the occurrence and importance of wrack of other seaweed species.

4. An impact upon the kelp ecosystem could lead to imbalance within trophic pathways. For example, if kelp harvesting results in a reduction of predators (e.g., birds, lobsters and crayfish) within the ecosystem then important top-down control processes may be impaired. For example, populations of grazing sea urchins may flourish if unchecked by predators, with deleterious effects for existing and regenerating kelp beds (Steneck *et al.*, 2002).

Future Research

Production

Nearly all the data in this review derive from work conducted outside Ireland. While it is reasonable to expect that findings from nearby countries will apply to Ireland, it is probable that some differences in production will occur. In general terms, the Atlantic coast of Ireland has a warmer temperature regime than Norway, Eastern Canada or even Scotland. Van den Hoek (1975) in a study of seaweed biogeography placed Ireland and Brittany, but not Scotland, Norway or eastern Canada in the warm temperate eastern Atlantic region. This region has a different and more diverse flora and fauna. Kelp harvesting may have different impacts in Ireland than in more northern countries. The experience of harvesting in Brittany compared to Norway must be studied very carefully before decisions are made on mechanical harvesting in this country. Necessary future research includes:

- Work on species replacement as a response to intensive harvesting. Will the French experience of spreading *Sacchoriza polyschides* dominance occur in Ireland?
- Research on coastal food chains in Irish waters. What species rely on kelp productivity? Will they be harmed if intensive harvesting occurs? Are they of commercial importance, (e.g., lobsters, crabs)?
- How dependent is kelp production on nutrient supply? Will known nutrient poor areas such as the inlets of south Connemara support intensive harvesting or is nutrient upwelling or other nutrient inputs necessary for commercial success (it is notable that successful mussel farming which depends on planktonic and macroalgal productivity is concentrated in the more nutrient rich inlets along the Irish coast)?
- Basic primary production measurements such as those of Mohammed and Fredriksen (2004) must be repeated in Irish Atlantic waters before large scale mechanical harvesting takes place.

Flora

A large portion of research on the effects of kelp harvesting show little in the way of negative effects on the near-shore environment (Santelices and Ojeda, 1984; Sharp and Pringle, 1990; Malloch, 2000) although some studies have found that kelp harvest has significant impacts on the kelp forest communities (Vasquez and Santelices, 1990; Chambers *et. al*., 1999). However, all of these studies are based on kelp forests in California, Chile, Canada and Tasmania and could only act as an example for Irish kelp forests as species and environmental conditions are different in Ireland. Nevertheless, a large amount of work has been done on kelp species and forests in France and Norway that are similar to the Irish species and kelp forests and results from these studies may be applied to an Irish situation.

Few investigations on *Laminaria digitata* and *L. hyperborea* are known from Irish waters and these are mainly on kelp ecology (Edwards, 1980). Recent research conducted by the Irish Seaweed Centre provides some information about associated flora, kelp growth, biodiversity and regeneration of kelp forests after experimental harvesting (Werner & Kraan, 2004). However, it must be noticed that the trials were conducted only over a one-year period, which is too short to monitor complete restoration of the kelp beds in experimentally harvested areas. Moreover, the small-scale trials cannot substitute for investigations on the impact of commercially used harvesting gear (e.g., scoubidou and seaweed dredge) and do not take geographical distribution into account and therefore a lack of knowledge remains.

Estimates of total kelp resources (i.e., *Laminaria. digitata* and *L. hyperborea*) for Ireland is unknown. Some estimates and extrapolation are known and provide an approximation of kelp biomass (Hession *et al*., 1998). Despite wide-ranging estimates, accurate quantification of the size of the Irish kelp resource is necessary before any discussion on sustainable exploitation and mechanical harvesting can take place. To make kelp resources accessible for exploitation, however, biomass estimates for both *L. digitata* and *L. hyperborea* are necessary due to the different biological characteristics of these two species requiring different management strategies. The species also have different desirability in terms of exploitation.

In order to increase the knowledge on specific characteristics of kelp species, its associated flora and the kelp ecosystem in Irish waters further research programmes should be developed. The following priority research areas have been identified:

- Biomass and standing stock surveys of *Laminaria digitata* and *L. hyperborea* on the west coast of Ireland from Counties Donegal to Wexford.
- Investigation of the associated floral epiphytes on kelp, seasonally and geographically.
- If experimental harvesting is pursued, the establishment of a monitoring programme on the regeneration of kelp beds after such harvesting has been conducted will be essential. Harvested areas should be surveyed and monitored until full restoration has taken place.
- Comparative investigations of growth rates of *L. digitata* and *L. hyperborea*, age class distribution and biomass in different parts of the Irish coast, which differ in exposure, water temperature and nutrient availability.
- Investigation of reproduction times, recruitment and effective spore dispersal distance of the kelp species of interest.
- Interdisciplinary studies on kelp forest ecology in Irish coastal waters consisting of biodiversity, productivity of kelp forests and food webs.

Invertebrates

It is clear that licensing of mechanical harvesting on an area of seafloor will effectively sacrifice resident biological communities from reaching their natural equilibrium. In terms of cataloguing the extent of this loss, the results of research on the effects of removal of kelp on the macroinvertebrate communities carried out in other parts of the world vary and, for this reason, a project to determine the effects of this activity in Irish waters is justified.

No work has been done in Irish waters to evaluate the role of drift weed in intertidal macroinvertebrate ecology and there are no data on the volumes of drift weed that are washed up. Furthermore, the percentage that kelps make up as part of the total volume is unknown.

The results of studies undertaken on the dampening effects of kelp to date are also from sites outside Ireland. If similar studies in Ireland report significant differences to the findings of Eckman *et al.* (1989), then removal of kelp may have potential negative effects on larval supply to the seabed. If, however, the findings of Andersen *et al.* (1996) and Mork (1996) are demonstrated for Irish waters, then this is not an issue.

It is recommended that the following studies be undertaken:

- Investigate the seasonal deposition of drift weed on Irish shores, the contribution of kelp species to that deposition and the response of intertidal macrofaunal communities;
- Explore the influence of kelp beds on localised hydrographic regimes.

Fish

There are considerable gaps in the literature in relation to fish species associated with kelp habitat in Ireland. Although review of the BIOMAR database was useful in providing some published records (Picton and Costello, 1998), much of the information on fish species that may be associated with kelp habitat in Ireland was drawn from the wider European literature with many of the records for fish species obtained from coincidental observations reported in surveys designed for investigation of benthic invertebrate communities (e.g., Moore, 1973, Gordon, 1983; Schultze *et al.*, 1990, Abbott and Perkins, 1977; Christie *et al.*, 2003; and Waage-Nielsen *et al.*, 2003). There has been some research conducted on fish species associations in Norwegian kelp forests but there are problems when using these associations in the identification of species that may be sensitive to development of mechanical kelp harvesting in Ireland due to biogeographical variation in fish communities. A quantitative survey of fish species associated with kelp habitats at different locations around Ireland would provide the most comprehensive and quantitative information.

The lack of information associated with fish habitat diversity in Ireland is part of a wider information deficit on the biology, ecology and conservation status of non-commercial inshore fish species. Some gaps in the literature may be partially attributed to the scarcity of a particular species, or difficulties associated with obtaining samples for study by fish biologists (Quigley, 1996). However, the lack of commercial importance and significance of some species as a natural resource has resulted in a lack of prioritisation in terms of research funding historically. Increasing emphasis on fish habitat diversity in relation to marine biodiversity and related legislative obligations in relation to the marine environment should provide an impetus for pursuit of such information.

In the light of the current information deficit and information requirements, it is recommended that future research should include the following:

- A comprehensive survey of fish species and top down predators associated with kelp habitat in Ireland giving due consideration to the influence of seafloor relief.

- Investigation of the biology and ecology of fish species sensitive to kelp habitat removal, with consideration of associated impacts on fish population dynamics, including research on reproductive ecology.

- Independent review of the conservation status of fishes in Ireland, with identification and prioritisation of fish species requiring attention, taking into account Ireland's responsibilities to legislation relating to marine biodiversity.

- Investigation of fish species diversity and resource partitioning associated with habitats and subfeatures, with comparisons between fish species associations and trophic connections relative to biotopes and marine benthic communities identified through marine biodiversity research.

Birds

If mechanical kelp harvesting is introduced into Ireland further studies are essential and should include:

- Seabird research designed specifically to assess distribution, foraging behaviour and diet within inshore waters and in relation to the location of known kelp forests. These would be particularly useful in areas close to breeding colonies (when seabirds may forage closer to shore) to ascertain the proportion of foraging time birds spend within kelp areas.

- Birds tend to aggregate in areas of high prey density and availability (Prater, 1981) and seabirds are sensitive to changes in their food supply. Given sufficient detailed knowledge as to how species respond to changes in food supply there is the potential for seabirds to be used as bio-indicators (Furness & Camphuysen, 1997) as to the ecosystem effects of kelp harvesting.

- Studies to determine the importance of kelp wrack for shorebirds and terrestrial birds in relation to the occurrence and importance of other macrophyte wrack. These studies should also target the potential use of this habitat by migrating birds, for which, kelp wrack may be particularly important.

- A Before-After-Control-Impact (BACI) study (Underwood, 1994) to determine numbers and diversity of bird species using kelp areas both before and after mechanical kelp harvesting.

- There is a general lack of knowledge with regard to foraging behaviour of seabirds in inshore and particularly near-shore environments. Increased scientific knowledge in this area would enable the impacts of a range of coastal developments to be assessed more readily.

Conclusions

Even well managed kelp harvesting puts substantial ecological pressure on natural kelp beds by increasing disturbance levels and removing resources from the ecosystem. Such activities are not compatible with the conservation objectives of, and should not be permitted in, NATURA 2000 sites.

In non-designated areas, well managed and controlled kelp harvesting could be envisaged but experience to date in the Irish inshore zone gives no grounds for optimism that “owned in common” resources can be managed rather than over exploited and then abandoned. Any kelp harvesting project must be carefully monitored throughout its lifetime. Possible unwanted side effects include the replacement of *Laminaria hyperborea* first by *L. digitata* and then *Sacchoriza polyschides*, removal of biomass necessary for other trophic levels and the elimination of older plants of all species. Despite economic limitations there is a reasonable case for encouraging research on the cultivation of kelp for harvesting rather than relying on wild populations. This case relies on the fact that kelp absorbs large quantities of nitrogen and phosphorus (1000 kg wet weight contains 15kg of nitrogen) and may be of use in removing excess nutrients. It is probable that the economic benefits of managing excess production of nitrogen in coastal waters will eventually far outweigh those of the limited commodity market for alginates that is possible using Irish wild kelp beds.

Several case studies conclude that no significant effects are apparent from routine mechanical and hand-harvesting practices in the long-term on the kelp standing stock and its associated flora (California and *Macrocystis*, Canada and *Laminaria longricuris*, Norway and *L. hyperborea*). Nevertheless, all studies showed a short-term effect that disappeared over time ranging from weeks (*Macrocystis*) to 5 years (*L. hyperborea*). Norwegian scientists suggested that harvesting should occur at 6 - 7 year intervals to suit the growth/recruitment cycle and to allow total re-establishment of the epiphytic communities before the next trawling season. Other studies concluded that there were insufficient data or a lack of knowledge, i.e., California and Tasmania. One study in Chile showed a shift in community structure from a kelp dominated habitat to an *Ulva* dominated habitat, which was finally replaced by *Gracilaria*. However, this was a small-scale scientific handharvesting trial and performed in the absence of grazers and was dependent on season. Nevertheless, the same study demonstrated a positive effect on recruitment of the kelp *Lessonia trabeculata*. No case studies are known from Ireland except for a few investigations on *Laminaria digitata* and *L. hyperborea* conducted by the Irish Seaweed Centre. These studies provide some information about associated flora, kelp growth, biodiversity and regeneration of kelp forests after experimental harvesting. However, the trials were only conducted over a one-year period that was too short to monitor complete restoration of the kelp beds in experimentally harvested areas. Moreover, the small-scale trials cannot substitute for investigations on the impact of commercially used harvesting gear (e.g., scoubidou and seaweed dredge) and do not take geographical distribution into account and therefore a lack of knowledge remains.

It is self-evident that the harvesting of kelp has significant negative impacts on invertebrates even though recovery rates for some taxa are very short: removing the kelp by whatever means involves the removal of the epifaunal communities, more than likely some of the epibenthic species and obviously, the key stone species on which these communities depend. For this reason, introducing this sort of activity into areas that have been designated as conservation sites is regarded as inappropriate. The fact that a well-regulated and seemingly sustainable industry has developed in Norway using research data on re-colonization rates of both plants and invertebrates suggests that this sort of model may be appropriate for trial in other locations. It has to be noted, however, that these experiments were carried out to support an industry to harvest kelp. Constant removal of kelp will never allow the macrofaunal community to re-establish itself fully and it must be accepted that the licensing of such activities effectively sacrifices that area of seabed of ever becoming a natural community again, that is, until the activity stops permanently. This situation is somewhat analogous to farming practices on land whereby management practices do not allow the natural vegetation to re-colonise cleared ground. References to the ephemeral nature of kelp forests in locations outside Ireland and the role that sea urchins and top predators can have in regulating the kelp beds have not been observed in Irish waters to date. The longer cycles recorded for north west Atlantic waters need to be assessed for Irish waters and with the postulated rise in sea water temperatures due to climate change, the extent and character of the kelp forests may be affected.

Emphasis in fisheries research has been focused on the biology of commercial species due to the obvious need to manage these resources in a sustainable manner. The development of a mechanical kelp industry in Ireland would present a challenge for fisheries management in terms of marine biodiversity as it could impact on the habitat of species that have not previously received much attention scientifically. In addition, the knowledge required for determining the impacts of seaweed harvesting on fish populations is unlike the information that has been required for fisheries stock assessment, in that the *habitat* of the fish population is targeted rather than the individuals themselves. This undoubtedly presents a challenge as fish populations have generally been managed in the context of a reproductively active standing stock being able to sustain itself in a healthy habitat. The removal of healthy habitat may have much wider implications for the marine ecosystem, requiring a real consideration of the ecosystem approach to management and research. The current paucity of information in relation to fish habitat associations in Ireland and Europe needs to be addressed further so that well informed decisions can be made with regard to conservation management of sensitive fish species and essential fish habitat.

Birds occupy an important yet littled studied trophic level within the kelp forest food chain. What is clear however, is that any negative ecological impacts of mechanical kelp harvesting will have direct and in-direct knock-on effects for birds. Important areas for birds are protected through the designation of Special Protection Areas (SPAs) under the EU Directive 79/409/EEC on the Conservation of Wild Birds. In general, mechanical kelp harvesting should not be conducted near important breeding bird colonies, near important sites for wintering shorebirds and waterfowl or near important staging areas for migratory birds. The ecosystem effects of mechanical kelp harvesting are likely to depend on harvesting frequency, harvesting intensity and biomass removal rates. However, given an ecosystem approach (Ugarte & Sharpe, 2001) in terms of careful management and regulation for a sustainable kelp harvesting industry, there is great potential for impacts upon birds to be minimised.

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Appendix 1 Fish taxa recorded in kelp habitat in the temperate waters of Europe that may be associated with similar habitat in Ireland. (Juv, juvenile; ad, adult; remains, taxa recorded in gut contents of Great Cormorants, *Phalacrocorax carbo*, (birds fed in areas dominated by *Laminaria hyperborea*)). (Information sources from Moore (1973), Abbott and Perkins (1977), Dunne (1981), Gordon (1983), Miller (1986), Schultze et al. (1990), Høisæter and Fossa (1993), Picton and Costello (1998), Fredriksen, (2003), Christie et al. (2003), Waage-Nielsen et al. (2003), Lorentsen at al. (2004), *pers. comm*. Deady and *pers. obs*. (S. Varian)).

Genus and species	**Common name**	**Stage of life history observed**	**Kelp species association**	**Record location**
Cyclopterus lumpus (Linné, 1758)	Lumpsucker	Juv/ad/remains	*L. digitata/L. hyperborea*	Helgoland/Norway/Ireland
Liparis liparis (Linné, 1758)	Striped Sea Snail	Juv/ad	*L. digitata/L. hyperborea*	Helgoland/Norway
Liparis montagui (Donovan, 1804)	Montagu's Sea Snail	Ad	*S.polyschides/L. hyperborea*	Ireland/Scotland/Norway
Agonus cataphractus (Linné, 1758)	Pogge	Eggs	*L. hyperborea*	Helgoland
Pholis gunellus (Linnaeus, 1758)	Butterfish	Eggs/ad	*S.polyschides, L.hyperborea*	Ireland/Scotland/England/Norway
Gaidropsaurus mediterraneus (Linnaeus, 1758)	Shore Rockling	Juv	*S.polyschides*	Scotland
Ctenolabrus rupestris (Linnaeus, 1758)	Goldsinny Wrasse	Juv/ad/remains	*S.polyschides*, *Laminaria* beds	Ireland/NI/Scotland/Norway
Crenilabrus melops (Linnaeus, 1758)	Corkwing Wrasse	Ad	*Laminaria* beds	Ireland/Norway
Centrolabrus exoletus (Linnaeus, 1758)	Rock cook Wrasse	Ad	*Laminaria* beds	Ireland/Norway
Labrus bergylta (Ascanius, 1767)	Ballan Wrasse	Ad	*Laminaria* beds	Ireland/Norway
Labrus mixtus (Linnaeus, 1758)	Cuckoo Wrasse	Ad	*Laminaria* beds	Ireland
Sprattus sprattus (Linnaeus, 1758)	Sprat	Ad	*Laminaria* beds	Ireland/Norway
Hyperoplus lanceolatus (Le Savage, 1824)	Great Sandeel	Remains	*L. hyperborea*	Norway
Ammodytes sp.	Sandeels indet	Ad	*Laminaria* beds	Ireland/Norway
Pollachius virens (Linnaeus, 1758)	Saithe	Ad/remains	*L. hyperborea*	Ireland/Norway
Pollachius pollachius (Linnaeus, 1758)	Pollock	Ad	*L. hyperborea*	Ireland/Norway
Gadus morhua (Linnaeus, 1758)	Cod	Juv/ad/remains	*L. hyperborea*	Norway
Spinachia spinachia (Linnaeus, 1758)	Sea Stickleback	Ad/remains	*L. hyperborea*	Norway
Taurulus bubalis (Euphrasen, 1786)	Long Spined Bullhead	Ad	*L. hyperborea*	Ireland/Norway
Taurulus lilljeborgi (Collett, 1875)	Norway Bullhead	Ad	*L. hyperborea*	Norway
Myoxocephalus scorpius (Linnaeus, 1758)	Bull-rout/Short Horn Sculpin	Remains	*L. hyperborea*	Norway
Anguilla anguilla (Linnaeus, 1758)	European Eel	Remains	*L. hyperborea*	Norway
Trisopterus minutus (Linnaeus, 1758)	Poorcod	Remains	*Laminaria* beds	Ireland/Norway
Ciliata mustela (Linnaeus, 1758)	Five-bearded Rockling	Remains	*L. hyperborea*	Norway
Zoarces viviparus (Linnaeus, 1758)	Viviparous Blenny	Remains	*L. hyperborea*	Norway
Parablennius gattorugine (Linnaeus, 1758)	Tompot Blenny	Ad	*Laminaria* beds	Ireland
Gobiesocidae	Clingfishes	Eggs/juv/ad	*S. polyschides*	Scotland
Gobiusculus flavescens (Fabricius, 1779)	Two-spotted Goby	Eggs/ad/remains	*S.polyschides*/*Laminaria* beds	Ireland/Scotland/Norway
Gobiidae	Gobies indet.	Ad/remains	*Laminaria* beds	Ireland, Norway
Anarhichas lupus (Linnaeus, 1758)	Wolf-fish	Remains	*L. hyperborea*	Norway
Bothidae	Left Eye Flounders	Remains	*L. hyperborea*	Norway
Zeugopterus punctatus (Bloch, 1787)	Topknot	Remains	*L. hyperborea*	Norway
Phrynorhombus norvegicus(Gunther, 1862)	Norwegian Topknot	Remains	*L. hyperborea*	Norway
Microstomus kitt (Walbaum, 1792)	Lemon Sole	Ad/remains	*L. hyperborea*	Ireland/Norway
Hippoglossoides platessoides (Fabricius, 1780)	Long Rough Dab	Remains	*L. hyperborea*	Norway
Pleuronectes platessa, Linnaeus, 1758	Plaice	Ad	*L. hyperborea*	Ireland
Scyliorhinus canicula (Linnaeus, 1758)	Dogfish	Ad	*Laminaria* beds	Ireland
Conger conger (Linnaeus, 1758)	Conger Eel	Ad	*Laminaria* beds	Ireland
Scomber scombrus, Linnaeus, 1758	Mackerel	Ad	*Laminaria* beds	Ireland
Callionymus reticulatus, Valenciennes, 1837	Reticulated Dragonet	Ad	*L. hyperborea*	Ireland
C. lyra, Linnaeus, 1758	Dragonet	Ad	*L. hyperborea*	Ireland

Appendix 2 Macroinvertebrate species recorded from *Laminaria* holdfasts and within kelp forests in Irish waters.

Protozoa
Astorhiza limicola

Porifera
Scypha compressa
Clathrina coriacea
Leuconia barbata
Polymastia mamillaris
Cliona celata
Cliona vastifica
Hymeniacidon perleve
Hemimycale columella
Ulosa digitata
Mycale macilenta
Corybas ovulum
Amphilectus fucorum
Iophon hyndmani
Myxilla rosacea
Stylopus hibernica
Dysidea fragilis

Cnidaria
Abietinaria abietina
Actinia equina
Aglaophenia pluma
Aglaophenia tubulifera
Alcyonium digitatum
Campanularia raridentata
Caryophyllia smithii
Clytia johnstoni
Dynamena pumila
Gonothyrea gracilis
Halecium beanii
Halecium halecinum
Haliclystus auricula
Halicorniaria pennatula
Hydrallmania falcata
Kirchenpauria pinnata
Lafoea pocillum
Laomedea flexuosa
Nemertesia antennina
Obelia geniculata
Plumularia setacea
Sertularia cupressina
Sertularia operculata
Sertularella polyzonias
Telia felina

Polychaeta
Amblyosyllis formosa
Amphictene auricoma
Amphiglena mediterranea
Anaitides maculata
Arenicola marina
Arenicolides ecaudata
Bispira volutacornis
Branchiomma bombyx
Brania clavata
Brania pusilla
Cirratutulus cirratus
Caulleriella bioculata
Eulalia viridis
Eulalia sanguinea
Exogone gemmifera
Hydroides norvegica
Harmothoe impar
Hediste diversicolor
Kefersteinia cirrata
Lysidice minetta
Lagisca extenuata
Lepidonotus squamatus
Mysta picta

Mystides limbata
Nereis pelagica
Odontosyllis ctenostoma
Pholoe minuta
Pionosyllis divaricata
Polydora ciliata
Pomatoceros triqueter
Sabellaria spinulosa
Scolelepis foliosa
Sphaerodorum gracilis
Sphaerosyllis ovigera
Spirorbis rupestris
Spirorbis tridentatus
Trypanosyllis zebra
Typosyllis armillaris
Typosyllis krohni
Typosyllis prolifer
Websterinereis glauca

Sipunculida
Nephasoma minuta

Cumacea
Bodotria scorpioides

Isopoda
Dynamena bidentata
Idotea granulosa

Amphipoda
Amphithoe rubricata
Apherusa jurinei
Bathyporeia pilosa
Hyale nilsonni
Hyale pontica
Jassa falcata
Jassa ocia
Lembos websteri
Megaluropus agilis
Melita palmata
Orchomenella nana
Pariambus typicus
Podocerus variegatus
Sthenothoe monoculoides
Caprella acathifera

Decapoda
Cancer pagurus
Homarus gammarus
Hyas areneus
Inachus phallangium
Palinurus elephas
Pagurid sp
Pilumnus hirtellus
Porcellana longicornis

Pycnogonida
Ammothelia hispida
Ammothelia longipes
Anoplodactylus virescens

Cirripedia
Balanus crenatus
Balanus improvisus
Balanus balanoides
Chthalmus stellatus
Verruca stroemia

Polyplacophora
Acanthochitona sp.

Prosobranchia
Acmea testudinalis
Aplysia punctata
Bittium reticulatum
Diodora apertura
Gibbula cineria
Calliostoma zizyphinum

Gibbula umbilicalis
Helcion pellucidum
Littorina mariae
Nassarius incrassatus
Onoba semicostata
Patella vulgata
Rissoa parva
Tricolia pullus
Trivia monarcha

Opisthobranchia
Elysia viridis

Lamellibranchia
Hiatella arctica
Monia squama
Musculus discors
Mytilus edulis
Paphia rhomboides
Patina pelliucida
Trivia arctica
Turtonia minuta

Bryozoa
Aetea anguina
Aetea sica
Alcyonidium hirsutum
Alcynonidium mytili
Alcyonidium polyoum
Alderina solidula
Amphiblestrum flemingii
Bowerbankia gracilis
Bowerbankia citrina
Callopora lineata
Callopora aurita
Callopora dumerilii
Callopora rylandi
Cauloramphus spiniferum
Celleporina hassallii
Celleporella hyalina
Cellepora pumicosa
Chorizopora brongniartii
Cribrilina cryptoecium
Electra pilosa
Escharoides coccinea
Echarella immersa
Escherella variolosa
Escharella ventricosa
Fenestrulina malusii
Hippothoa divaticata
Hippothoa flagellum
Hippoporina pertusa
Membranipora membranacea
Membraniporella nitida
Microporella ciliata
Parasmittina trispinosa
Porella concinna
Pyripora catenularia
Reptadeonella violaccea
Rhynchozoon bispinosa
Scruparia ambigua
Scrupocellaria reptans
Smittina landsborovii
Smittoidea reticulata
Schizoporella unicornis
Schizomavella auriculata
Schizomavella linearis
Schizobrachiella sanguinea
Schizotheca fissa
Turbicellepora avicularis
Walkeria uva

Echinodermata
Amphipholis squamata
Ophiothrix fragilis
Asterina gibbosa
Asterias rubens
Henricia oculata
Pawsonia saxicola

Ocnus lacteus
Holothuria forskali
Psammechinus miliaris
Echinus esculentus
Antedon bifida

Tunicata
Aplidium proliferum
Botryllus schlosseri
Ciona intestinalis
Dendrodoa grossularia
Leptoclinides faeroens
Molgula complanata

Appendix 3 Description of habitat, diet, reproduction and occurrence of fish species directly associated with kelp in Ireland and Europe.
(Information sources: Rae, 1965; Muus and Dahlström, 1974; Russell, 1976; Tesch, 1977; Dunne, 1980, 1981; Compagno, 1984; Deelder, 1984; Andriashev, 1986; Banister, 1986; Barsukov, 1986; Federov, 1986; Fricke, 1986; Miller, 1986; Nielsen, 1986; Stein, 1986; Bauchot and Saldanha, 1986; Quignard and Pras, 1986; Flintegård, 1987; Erwin and Picton, 1990; Cohen et al., 1990; Smith, 1990; Wheeler, 1979, 1992; Deady and Fives, 1995a,b; Frimodt, 1995; Sobel, 1996; Cooper and Chapleau, 1998; Varian, 1998;Gibson, 1999; Muus and Nielsen, 1999; Froese and Pauly, 2004). (Records for conservation status and occurrence of fish species in Ireland were taken from Anon, 1994 (IUCN); Went, 1957 (W), Went and Kennedy, 1976 (W); Minchin, 1987 (M); Quigley, 1996 (Q); Froese and Pauly, 2004 (F)).

Genus and species	Habitat	Diet	Reproduction	Occurrence in Ireland
Cyclopterus lumpus	Migratory; moves from deep water to spawn inshore in summer Juvenile nurseries in kelp	Crustaceans, fish, polychaetes, jellyfish	Nest guarder, demersal eggs	Occasional (F/M)
Liparis liparis	Inshore, demersal	Crustaceans, fish, polychaetes	Demersal eggs	Uncommon; local (Q)
Liparis montagui	Inshore, demersal Spawns in winter	Crustaceans	Non guarder, eggs laid on algae	Scarce (F/M)
Agonus cataphractus	Inshore, demersal	Polychaetes, crustaceans	Non-guarder, eggs laid on algae	No info (F/Q)
Pholis gunnellus	Inshore, demersal May migrate to deeper water in winter, winter spawner	Polychaetes, crustaceans, molluscs, fish eggs	Clutch guarders, demersal eggs	Occasional (F/M)
Gaidropsaurus mediterraneus	Inshore, demersal	Fish, crustaceans, algae	Pelagic eggs	Scarce (F/M) Indeterminate (Q)
Ctenolabrus rupestris	Inshore, demersal, territorial	Crustaceans, molluscs, polychaetes	Pelagic eggs	Fairly common (F)
Crenilabrus melops	Inshore, demersal, territorial	Crustaceans, molluscs, bryozoans	Nests made of algae	Fairly common (F/M)

Appendix 3 continued

Centrolabrus exoletus	Inshore, demersal, shoaling	Crustaceans	Nest made of algae	Fairly common (F/M) Local (Q)
Labrus bergylta	Inshore, demersal, territorial	Crustaceans, molluscs	Nests made of algae	Fairly common (F/M)
Labrus mixtus	Inshore, demersal, territorial	Crustaceans, molluscs	Nests made of algae	Fairly common (F/M)
Sprattus sprattus	Inshore, migratory Migrates between winter feeding and summer spawning grounds	Zooplankton	Pelagic eggs	Common (F/W)
Hyperoplus lanceolatus	Inshore, demersal	Zooplankton, small fish	Demersal eggs	Scarce (F/M)
Pollachius virens	Inshore and offshore, demersal	Fish, crustaceans	Pelagic eggs	Scarce (F/M)
Pollachius pollachius	Inshore, benthopelagic	Fish, cephalopods, crustaceans	Pelagic eggs	Common (F/M)
Gadus morhua	Inshore and offshore, benthopelagic, schooling	Invertebrates and fish	Pelagic eggs. nurseries associated kelp	Vulnerable (IUCN)
Spinachia spinachia	Inshore, benthopelagic Prefers weedy coastal areas	Small invertebrates	Nests made of algae	Common (F/W)
Taurulus bubalis	Inshore, demersal, intertidal Prefers rocky bottoms and algae	Crustaceans, polychaetes, molluscs, ophiuroids, fish	Demersal eggs	Common (F/M)
Taurulus lilljeborgi	Inshore, demersal Prefers rocky seabed and algae	Small crustaceans, fish	Demersal eggs	Uncommon; rare (Q)
Myoxocephalus scorpius	Inshore, demersal Rocky seabed with sand, mud, or weed	Large crustaceans, fish, polychaetes	Demersal eggs	Common, occasional (F/M)

Appendix 3 continued

Anguilla anguilla	Demersal, catadramous, amphihaline May spend up to 3 years on Atlantic coasts before entering freshwater as elvers. Lives under rocks/crevices and in mud.	Consumes virtually the whole aquatic fauna occurring in its area.	Pelagic eggs, (spawns in Sargasso Sea)	Vulnerable (Q)
Trisopterus minutus	Benthopelagic, 15-200m on muddy sandy bottoms	Crustaceans, polychaetes, fish	Pelagic eggs	Fairly common (F/M)
Ciliata mustela	Inshore, demersal, resident intertidal Prefers rocky seabed	Crustaceans, polychaetes algae, gastropods, fish	Pelagic eggs	Fairly common (F/M)
Zoarces viviparous	Inshore, demersal Lives under stones and amongst algae down to 40m	Crustaceans, gastropods, chironomids, fish eggs	Internal fertilisation Gives birth to live young	Rare (Q)
Parablennius gattorugine	Inshore, demersal Prefers rocky seabed and algae	Invertebrates	Clutch guarder, demersal eggs	Fairly common (F/W)
Gobiusculus flavescens	Inshore, demersal	Planktonic crustacea, Chaetognaths	Eggs adhere to algae	Common/abundant (F/M)
Anarhichas lupus	Demersal. Solitary in habit. Prefers rocky seabed from 1-500m	Molluscs, crabs, lobster, sea urchins	Clutch guarders, demersal eggs	local (Q)
Zeugopterus punctatus	Inshore, demersal Inhabits stony/rocky ground in the algal zone	Crustaceans, fish	Pelagic eggs	Scarce (F/M)
Phrynorhombus norvegicus	Inshore, benthopelagic Occurs in rocky areas	Fish, invertebrates	No data	Scarce (M) Indeterminate (Q)
Microstomus kitt	Demersal, prefers stony seabed	Small invertebrates; mostly polychaetes	Pelagic eggs	Scarce (F/M)

Appendix 3 continued

Hippoglossoides platessoides	Demersal. Depth ranges from 10m, but most abundant between 90-250m on soft bottoms	Invertebrates, fishes	Pelagic eggs	No info (F)
Pleuronectes platessa	Demersal. Depth range 0-200m Prefers sand and gravel seabeds.	Mainly molluscs and polychaetes	Pelagic eggs	Common (M/W)
Scyliorhinus canicula	Inshore, demersal Occurs on sandy, gravel, coralline, algal or muddy seabeds	Crustaceans, molluscs, cephalopods, fishes	Oviporous, a single egg laid per oviduct	Common (F/W)
Conger conger	Demersal, Prefers rock and sandy seabeds Stays near the coast when young and moves to deeper waters upon reaching adulthood	Crustaceans, fish, cephalopods	Reproduces only once in its life;off coast of Portugal in Atlantic	Common (F/W)
Scomber scombrus	Pelagic, abundant in cold and temperate shelf areas up to 200m Overwinter in deeper waters, moving inshore in spring	Zooplankton, small fish	Pelagic eggs	Fairly common (F/W) (seasonal abundance)
Callionymus reticulatus	Demersal, inshore Prefers sandy and muddy seabeds.	Crustaceans	Pelagic eggs	Rare (Q)
C. lyra	Demersal, inshore. Prefers sandy and muddy seabeds	Mainly worms and crustaceans	Pelagic eggs	Fairly common (M/W)

Appendix 4 Conservation status of bird species cited in report

SPECIES	**Listed on Birds Of Conservation Concern (Newton *et al.*, 1999)**	**Listed on Annex I of EU Birds Directive (79/409/EEC)**
Red Throated Diver *Gavia stellata*	Amber List	*
Great Northern Diver *Gavia immer*		*
Great Crested Grebe *Podiceps cristatus*	Amber List	
Cormorant *Phalacrocorax carbo*	Amber List	
Shag *Phalacrocorax aristotelis*		
Grey Heron *Ardea cinerea*		
Eider *Somateria mollissima*	Amber List	
Common Scoter *Melanitta nigra*	Red List	
Red Breasted Merganser *Mergus serrator*	Amber List	
Oystercatcher *Haematopus ostralegus*		
Ringed Plover *Charadrius hiaticula*		
Lapwing *Vanellus vanellus*	Red List	
Sanderling *Calidris alba*		
Purple Sandpiper *Calidris maritima*		
Turnstone *Arenaria interpres*		
Dunlin *Calidris alpina*	Amber List	
Redshank *Tringa totanus*	Amber List	
Black-Tailed Godwit *Limosa limosa*	Amber List	
Bar-Tailed Godwit *Limosa lapponica*	Amber List	*
Curlew *Numenius arquata*	Red List	
Whimbrel *Numenius phaeopus*		
Common Gull *Larus canus*	Amber List	
Herring Gull *Larus argentatus*		
Lesser Black-Backed Gull *Larus fuscus*		
Great Black-Backed Gull *Larus marinus*		
Little Tern *Sterna albifrons*	Amber List	*
Sandwich Tern *Sterna sandvicensis*	Amber List	*
Common Tern *Sterna hirundo*	Amber List	*
Arctic Tern *Sterna paradisaea*	Amber List	*
Roseate Tern *Sterna dougallii*	Red List	*
Black Guillemot *Cepphus grylle*	Amber List	
Common Guillemot *Uria aalge*	Amber List	
Razorbill *Alca torda*	Amber List	
Swallow *Hirundo rustica*	Amber List	
Rock Pipit *Anthus petrosus*		
Meadow Pipit *Anthus pratensis*		
Pied Wagtail *Motacilla alba*		
Grey Wagtail *Motacilla cinerea*		
Hooded Crow *Corvus corone cornix*		
Starling *Sturnus vulgaris*		