

INFRALITTORAL REEF BIOTOPES WITH KELP SPECIES

**An overview of dynamic and sensitivity characteristics for
conservation management of marine SACs**

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PREFACE

The 1990s are witnessing a “call to action” for marine biodiversity conservation through wide ranging legislative fora, such as the global Convention on Biodiversity, the European Union’s “Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora” (the Habitats Directive) and more recently in developments to the Oslo and Paris Convention (OSPAR). These landmark legal instruments have in turn provided sufficient scientific rationale, legal mandate and social synergy to rally governments, NGOs, private industry and local communities into a new era of unprecedented conservation action.

Each of these initiatives identifies marine protected areas as having a key role in sustaining marine biodiversity. To manage specific habitats and species effectively there needs to be a relatively clear understanding of their present known distribution, the underpinning biology and ecology and their sensitivity to natural and anthropogenic change. From such a foundation, realistic guidance on management and monitoring can be derived and applied.

The Habitats Directive requires the maintenance and/or restoration of natural habitats and species of European interest at favourable conservation status across their biogeographical range. The designation and management of a network of Special Areas of Conservation (SACs) have a key role to play in this. The specific 'marine' habitats defined in Annex I of the Habitats Directive include:

- Sandbanks which are slightly covered by sea water all the time,
- Estuaries
- Mudflats and sandflats not covered by seawater at low-tide,
- Large shallow inlets and bays
- Lagoons
- Reefs
- Submerged or partly submerged sea caves

These habitats are vast in scope and challenging to quantify in terms of favourable conservation status, so there has been increased attention to 'sub-features' of these habitats which are in effect constituent components and/or key elements of the habitats from a range of biodiversity perspectives.

One initiative now underway to help implement the Habitats Directive is the UK Marine SACs LIFE Project, involving a four year partnership (1996-2001) between English Nature (EN), Scottish Natural Heritage (SNH), the Countryside Council for Wales (CCW), Environment and Heritage Service of the Department of the Environment for Northern Ireland (DOENI), the Joint Nature Conservation Committee (JNCC), and the Scottish Association of Marine Science (SAMS). While the overall project goal is to facilitate the establishment of management schemes for 12 of the candidate SAC sites, a key component of the project assesses the sensitivity characteristics and related conservation requirements of selected sub-features of the Annex I habitats noted above. This understanding will contribute to more effective management of these habitats by guiding the detailed definition of the conservation objectives and monitoring programmes and by identifying those activities that may lead to deterioration or disturbance.

A diverse series of sub-features of the Annex I marine habitats were identified as requiring a scientific review, based on the following criteria:

- key constituent of several candidate SACs;

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- important components of Annex I habitats in defining their quality and extent;
 - extensive information exists requiring collating and targeting, or there is minimal knowledge needing verification and extended study.

This resulted in the compilation a nine-volume review series, each providing an "Overview of Dynamics and Sensitivity Characteristics for Conservation Management of Marine SACs" for the following sub-features:

Vol. I	Zostera Biotopes
Vol II	Intertidal Sand and Mudflats & Subtidal Mobile Sandbanks
Vol III	Sea Pens and Burrowing Megafauna
Vol. IV	Subtidal Brittlestar Beds
Vol. V	Maerl
Vol. VI	Intertidal Reef Biotopes
Vol. VII	Infralittoral Reef Biotopes with Kelp Species
Vol. VIII	Cirralittoral Faunal Turfs
Vol. IX	Biogenic Reefs.

Each report was produced initially by appropriate specialists from the wider scientific community in the respective subject. These reports have been reviewed through an extensive process involving experts from academic and research institutions and the statutory nature conservation bodies.

The results of these reviews are aimed primarily at staff in the statutory nature conservation bodies who are engaged in providing conservation objectives and monitoring advice to the marine SAC management schemes. However these reports will be a valuable resource to other relevant authorities and those involved in the broader network of coastal-marine protected areas. In order to reach out to a wider audience in the UK and Europe, a succinct 'synthesis' document will be prepared as a complement to the detailed 9-volume series. This document will summarise the main points from the individual reviews and expand on linkages between biotopes, habitats and sites and related conservation initiatives.

These reports provide a sound basis on which to make management decisions on marine SACs and also on other related initiatives through the Biodiversity Action Plans and Oslo and Paris Convention and, as a result, they will make a substantial contribution to the conservation of our important marine wildlife. Marine conservation is still in its infancy but, through the practical application of this knowledge in the management and monitoring of features, this understanding will be refined and deepened.

We commend these reports to all concerned with the sustainable use and conservation of our marine and coastal heritage.

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Marine Science

EXECUTIVE SUMMARY

Introduction

What is kelp and why is it important?

Kelp is the common name given to the large, brown seaweeds found in the shallow coastal waters of temperate parts of the world. Kelp plants are large, from several metres (as in Europe) to several tens of metres tall (as in the NW Pacific), and when they are present in dense stands - known as "kelp forests" - they form an important habitat for thousands of species of other plants and animals. The kelp forests are possibly the most ecologically dynamic and biologically diverse habitats on the planet. These marine forests are the underwater equivalent of the terrestrial rain forests, with a wide variety of different species assemblages and ecological linkages. However, the kelp beds do not accumulate biomass as the rain forests do, they export their production to surrounding habitats. In north-west Europe the major kelp species is *Laminaria hyperborea* although others may be locally dominant e.g. *Laminaria saccharina*, *Laminaria digitata*, *Alaria esculenta* and *Saccorhiza polyschides*.

In the same way that terrestrial forests are under threat because they supply timber and valuable food species for humanity kelp forests are threatened by over-exploitation. The kelp species themselves are harvested for food, fertiliser and for the chemical industries, and the demand for the chemicals is increasing. Many of the animal species found in kelp forests are also commercially exploited. Lobsters, crabs, crayfish, abalone and many fish species are all harvested from kelp beds in different parts of the world. However, the kelp forests differ from the terrestrial forests in that kelp forests, with their very high productivity, provide the food source for most of the animals in the areas surrounding the kelp forests as well as within them. The material that is continually being lost from the kelp plants feeds into a complex recycling system of herbivores, detritivores, and bacteria, all of which form part of an immense web of interacting species of plants and animals that extend the influence of kelp forests far beyond the habitat of the kelp plants themselves.

Kelp distribution and kelp biotopes

There are at present 13 species of kelp found in European waters, of which 7 are found around the UK. One of the 7 is an alien species that escaped from cultivation and is extending its habitat on the Channel coasts and another is a southern species that is slowly extending its range to the north as sea temperatures rise.

There are at present 51 different descriptions of kelp habitat used in the Marine Nature Conservation Review system of classifying marine habitats. There are advantages and disadvantages of this classification system, but it is a standardised descriptive method which can be used for mapping areas of habitat. The MNCR database highlights the number of different types of kelp bed that are present in UK waters and with only 12 demonstration SAC sites scattered around the coasts, it is probable that some of the less common biotopes will be inadequately represented in the proposed areas.

Environmental requirements and physical attributes

Within the scope of this report it is not possible to consider the specific requirements for any of the many hundreds of species of animals and plants which are characteristic of the kelp biotopes. For the majority, the specific environmental requirements and the physical attributes of the individual species are not known.

Environmental requirements of UK species of kelp

As a consequence of commercial interests in the potential for harvesting kelp, a considerable amount of research has been conducted on the most valuable species. Kelps generally grow below mean low water of spring tides and attached to hard substrata, usually bedrock but boulders, cobbles and even small pebbles may serve as an attachment site depending on the local wave conditions. The type of substratum and the depth at which the plant is attached play a role in the appearance and lifespan of the kelp plants.

The major environmental factor affecting kelp plants is the irradiance available to them. Light and water clarity interact to determine the depth to which kelps can grow. In clear water, light can penetrate deeper than in silt laden water and at depth the colour of the light may also influence the depth to which kelps can grow. Kelp beds extend below 35 m in clear waters but, in some parts of the UK, the coastal water is so turbid that the deepest kelp plants are found at only 2 m. The action of waves also plays a part in determining the depth at which kelp plants can grow. Some species, such as *Alaria esculenta*, are able to survive under very rough conditions where *Laminaria hyperborea* plants are snapped in the shallows and only survive deeper down. Kelps do not tolerate wide fluctuations in temperature or salinity. Temperature in particular is thought to be the major environmental factor that limits the geographical range of each species. Kelp species all grow rapidly at certain (different) times of the year and have a high demand for nitrate and phosphate, but the long-term effects on coastal kelp bed communities of the increasing nutrient load in UK coastal waters are not known.

Physical attributes of UK species of kelp

Water currents as well as wave action affect the growth form of kelp plants. Where plants are sheltered from waves but subject to strong tidal currents, they may become long and luxuriant, whereas in relatively still waters the plants become silt covered, broader and may have a completely different appearance. Water movement influences the age structure of the population (which in turn plays a role in the biodiversity of the habitat). In shallow waters and where plants are subjected to rough waves, the average age of the kelps is lower than for populations in deeper or more sheltered areas.

Biology and ecological functioning

The biological and ecological role of kelp species and the interactions between the kelp beds and the surrounding ecosystems are not well known, either in Europe or in the world as a whole. Long-term research programmes have been undertaken in areas where the health of the kelp based communities has major economic importance (e.g. for the crayfish, lobster and abalone fisheries of the NE Pacific, South Africa and W. Australia). There have also been

research programmes where kelp is harvested on a large scale, but these have concentrated on the kelp plants themselves rather than on the ecosystem in which they grow.

Our current knowledge of the biology and ecology of the majority of species in the UK kelp beds is so limited that we have little detailed understanding of their functional and ecological interactions. Even the basic biological characteristics of many of the species are unknown and the species that are of key importance to the maintenance of kelp biotopes can not be firmly identified.

Biological characteristics of kelp

The life span of individual plants varies with species and local conditions between 1 and 20 years. As a general rule, mature plants do not increase in size very much from year to year, but the blade tissue grows from the base and tissue is continually lost from the distal end. This decaying tissue forms a major part of the POM (particulate organic matter) in coastal waters. Kelp beds contribute 2-3 times their standing biomass each year and provide the energy supply for filter feeders and detritivores beyond the boundaries of the kelp bed itself. If the growth area of the blade (just above the stipe) is damaged or removed, the whole plant dies - regrowth cannot occur. Rates of growth and photosynthesis vary between individual plants, between different species, with the time of year and with local conditions. The large, obvious plants are only one part of the life cycle of kelps, the sporophyte generation. The sporophyte plants produce large numbers of microscopic zoospores which settle and grow into the microscopic male and female gametophyte plants. These in turn produce the gametes and, after fertilisation, a new sporophyte plant starts to develop.

Ecological roles in kelp biotopes

Kelp plants are the major primary producers in the coastal waters of the UK but their role in coastal ecology is not well understood. The ecological interactions of most of the several thousand different species that may be found in kelp biotopes are largely unknown. One of the characteristics of kelp beds throughout the world is the patchwork of different species and groups of species that occur. These patches are not stable, but are constantly changing, usually slowly, sometimes rapidly, and the factors influencing this dynamic pattern are unknown. One of the most obvious and relatively well studied interactions is that between sea urchin species and kelps (although little research has been undertaken with UK species). Kelp beds are the habitat for several commercially harvested species in the UK, notably lobsters and crabs but, even for these common species, we have only a limited idea of their ecological roles.

The structure of the kelp bed is complex and within kelp beds there are many different habitats, i.e. bedrock, crevices, sediment pockets, the kelp plants themselves. The diversity of niches within the biotopes and the productivity of the kelps are two reasons for the diversity of species that can be found in a small area. A single kelp holdfast may be "home" to several thousand small animals from as many as 80 different species. There are pelagic and benthic components of the habitat, with groups of species that are planktonic, nektonic, mobile, encrusting, or sedentary. The kelp bed can be divided into forest and parkland areas, each with a range of species of flora and fauna. The kelps in a forest area are so close together that the blades form an almost complete canopy, trapping almost all of the available light. Below the canopy are understorey plants and animals attached to the bedrock or to the kelp plants. Parkland areas occur at the lower fringes of forests and contain more scattered kelp plants and a wide diversity of animal and plant species.

Keystone species and biotic interactions in kelp beds

Although many species have been described from kelp biotopes, the species that are of greatest importance to the structure and function of the ecosystem (keystone species) have not been identified. With the diversity of habitats within them, kelp beds are likely to play a significant role as nursery areas for a wide variety of species, but this topic has not been studied in any detail within Europe. Kelps are the major primary producers in the biotopes, but the complex web of interactions depending on them remains largely unknown. In some instances, the trophic level and the dietary habits of even the most common and obvious animals in the kelp biotopes are not known. Sea urchins are known to graze in kelp beds (sometimes their activities result in large areas being denuded of kelps) and the blue-rayed limpet is a destructive grazer of kelp holdfasts, but information on the population biology of these grazers and their interactions with the kelps or other species is incomplete. Within the kelp forest there is competition between algal species for light and space, and within all the kelp biotopes there is competition for space on substrata, leading to the dynamic patchiness mentioned previously.

Biodiversity within kelp biotopes

The numbers of species that are found in the kelp beds of the world place these submarine coastal forests on a par with coral reefs and tropical rain forests in terms of the biological variety present in them. Although the MNCR database provides a good starting point, no complete lists exist for the species that are found in any of the kelp biotopes in UK waters. To date, biological surveys have had to be restricted to readily observable and identifiable species, so that biota which are microscopic, cryptic, nocturnal, hidden, ephemeral or heteromorphic have been largely overlooked. The taxonomic skills needed to recognise and identify biological samples are getting rarer within the scientific community, making it difficult to produce consistent evaluations of biodiversity. The high levels of expertise needed, and the time consuming nature of the work, make accurate identification costly. However, the biota within kelp beds change on both spatial and temporal scales and shifts in the population structures or distribution patterns of closely related species would be excellent monitoring tools for detecting ecological changes within SACs.

Sensitivity to natural events

Kelp plants themselves are not particularly sensitive to short term fluctuations in the natural environment, but this does not necessarily apply to other species, whose sensitivity's are largely unknown. The effects of storm damage, fluctuations in sea urchin numbers and the potential effects of climate change on kelp species have been studied elsewhere in the world but long term studies have not been undertaken in the UK.

Sensitivity to human activities

Kelp has for centuries been traditionally collected for use as a fertiliser in coastal districts, but modern methods of kelp harvesting have a more significant direct influence on kelp biotopes. The chemicals extracted from kelps are commercially valuable and harvesting methods destroy the whole plant. In Europe the most commonly harvested species are *Laminaria digitata* and *L. hyperborea*. Because of these commercial interests, research has been conducted on the effects of harvesting on the kelp species themselves but almost nothing is known of the effects of kelp biomass removal on the other biotic components of kelp

biotopes. This paucity of ecological information applies world-wide. Harvesting methods developed in Europe permit the kelp biomass to recover to harvestable levels within 3-4 years, but preliminary studies of the associated flora and fauna in Norwegian kelp beds indicate that full recovery has still not occurred even 10 years after harvesting of mature kelp plants.

Marine aquaculture can affect kelp biotopes in several ways. Stock species or feed material may be collected from kelp biotopes, waste materials may cause local nutrient enrichment or detrital deposition, and chemicals used to control disease, sea-lice or micro-organisms may have unforeseen effects on the ecological balance within a biotope. The effects of increasing levels of nutrients in UK coastal waters on kelp biotopes have not been monitored. There may be direct effects on the physiology of the kelp species and increased turbidity from phytoplankton blooms may alter or have altered the depth distribution of the kelps. Major chemical pollution events, such as oil spills, are usually sporadic but can be low level, persistent and pernicious, as with antifouling chemicals and pesticides. Toxic compounds are known to be concentrated with progression along food chains (mercury, DDT) with unpredictable long-term results (Minnimata disease; near extinction of birds of prey). Only recently has it been recognised that toxic compounds may have subtle but very long-term effects on reproductive success, immune systems or developmental processes. Coastal alterations and channel dredging that result in increased turbidity and sedimentation may wipe out local kelp beds by reducing the available light to levels below that at which the kelps can develop. Increased levels of sediment may also smother other components of the kelp biotope. The effects of predator removal or the introduction of alien species within kelp biotopes have not been studied.

Although the effects of climatic events such as the El Niño on Pacific kelp beds have been investigated, little is known of short term climatic effects in the European kelp biotopes. Global warming may result in the distribution patterns (presently unknown) of kelp biotopes shifting in response to changes in water temperatures. Depletion of the northern ozone layer may result in depth distribution changes and reduced productivity of the kelp species, with uncertain consequences for the kelp biotopes.

Monitoring and surveillance options

Methods for the monitoring or surveillance of marine conservation areas are at a relatively early stage of development. The natural, background patterns of change within kelp biotopes are not known and much basic biological information about the components of kelp biotopes is lacking. The identification and taxonomic status of a significant proportion of the biota is uncertain and there are high levels of spatial and temporal variability within kelp biotopes. Unfortunately, long term environmental projects are expensive and require a level of continuity of personnel and funding which has been unavailable. Factors at present known to influence kelp ecosystems should be incorporated into monitoring and surveillance plans, with additions and refinements to the plans made as data becomes available. Prior to the adoption of methodological options, decisions need to be made on precisely *what* is to be monitored and *why*.

Gaps and requirements for further research

The availability of diving equipment has changed our appreciation of the complexity of kelp biotopes. Unfortunately, investigations of ecological interrelationships in marine habitats became deeply unfashionable in the early 1970s with regard to research funding and this has left considerable gaps in our basic understanding of the ecology of coastal habitats. The topics which require further research in order to facilitate the commitment to conservation of

coastal marine ecosystems start with very basic questions such as “where are all the kelp biotopes”? Key species within kelp biotopes need to be identified and the ecological interactions of these species need to be understood. The role of kelps as major primary producers in coastal ecosystems requires investigation, as do the biological factors which affect the growth and population structure of the kelp population. The effects of long-term (decades) changes in the environment on the stability and health of kelp biotopes are largely unknown.

Concluding comments on the application of information for conservation management relevant to marine SACs

The time scale over which a management plan for a kelp forest is to operate has to be decided. Unfortunately, political and biological time spans are often quite distinct. With the exception of direct harvesting of kelp, little is presently known about the long term effects of many present day human activities on kelp biotopes. Much of the net production of kelp plants is exported from the kelp forest to coastal ecosystems as a whole, and is generally thought to sustain many inshore fisheries. Each kelp forest, and possibly each area within a kelp forest, may have a different biological composition, and our knowledge about the associated flora and fauna is too sketchy to permit broad generalisations to be drawn. Kelp biotopes are renowned for their species richness and diversity and, as such, present a challenge with regard to monitoring their status.

Any management scheme will be dependent on the quality of the monitoring programmes to provide adequate scientifically robust data. International experience demonstrates that local co-operation and voluntary systems alone are, in practice, inadequate to protect habitats and the biota that they sustain. Therefore, a coherent system of conservation legislation and policing is required in the UK. Kelp biotopes require more research into management-related aspects in order to permit efficient management plans and monitoring programmes to be developed. The level of long term commitment (decades), by Government, to marine conservation should be reassessed with regard to fulfilling the requirements of the Habitat Directive.

I INTRODUCTION

A. STUDY AIMS

This report has been prepared as a summary of the biological and ecological information available to date (1998) on the kelp beds in European, and more specifically in UK, coastal waters. It is one of a series of nine reviews on coastal marine habitats that have been identified as being of significance in terms of the EU Habitats Directive and which are included in the UK Marine SAC's Project.

The "kelp forests" have been selected as biotope complexes to be scientifically reviewed for the UK Marine SACs Project for the following reasons:

- Kelp forests occur in 8 of the proposed demonstration marine SACs within the UK (see Table 1)
- Kelp forests have considerable conservation value because they harbour a very high diversity of organisms, confined to a very narrow fringe along the coastline.
- The kelp forests throughout Europe are threatened by the effects of several forms of human activity, including harvesting and eutrophication
- *Laminaria hyperborea* and *Laminaria digitata* are regarded as commercially valuable species and demand for exploitation is increasing; this should be counterbalanced by the provision of reserve areas.

B. WHAT IS KELP AND WHY IS IT IMPORTANT?

Kelp is the colloquial name given to the large, brown seaweeds of the order Laminariales which dominate much of the shallow sublittoral in temperate parts of the world. Kelp plants are physically large, from several metres to several tens of metres tall, and when they are present in dense stands known as "kelp forests" they form an important habitat for other organisms. The kelp forests that are found fringing the temperate sea shores of the world are possibly the most ecologically dynamic and biologically diverse habitats on the planet. These marine forests are the underwater equivalent of the terrestrial rain forests and, just as there are African, Asian and American tropical and temperate rain forests, so in the various oceans of the world are there different species assemblages and ecological linkages in the kelp forests. In north-west Europe the major kelp species is *Laminaria hyperborea* although others may be locally dominant in particular ecological situations e.g. *Laminaria saccharina*, *Laminaria digitata*, *Alaria esculenta* and *Saccorhiza polyschides*.

There are many thousands of animal species that live within the kelp forests of the world, either on the rock substratum or on the kelp plants. There are also thousands of different species of seaweeds in these forests, forming layers of plant life in the same way that terrestrial forests have layers of plants (canopy, epiphytes, sub-canopy, understorey, etc.). However, the kelp forests differ from the terrestrial forests in that kelp forests, with their very high productivity, provide the food source for most of the animals in the areas surrounding the kelp forests as well as within them. The material that is continually being lost from the kelp plants feeds into a complex recycling system of herbivores, detritivores, and bacteria, all

of which form part of an immense web of interacting species of plants and animals that extend the influence of kelp forests far beyond the habitat of the kelp plants themselves.

In the same way that terrestrial forests supply timber and valuable food species for humanity - and so are threatened to destruction by over exploitation - kelp forests are also under threat. Kelp species themselves are harvested as feedstock for fertiliser and chemical industries and for food, at a present rate (world-wide) of about 2.5 million tons per year. Kelp extracts have a multitude of applications as homogenising and gelling agents (toothpaste, non-drip paint, etc.) and demand for these chemicals is increasing. Other species of algae in kelp beds also have commercial value as human foodstuffs or as a fodder crop in aquaculture (e.g. *Dulse*, *Palmaria palmata* in Ireland). Many of the animal species found in kelp forests are also commercially exploited, lobsters, crabs, crayfish, abalone and many fish species are all harvested from kelp beds in different parts of the world.

C. DEFINITIONS

At this point, it is necessary to provide some definitions of the terms that will be used in this review.

Kelp is the term at one time used for the ash obtained from burning seaweeds (400,000 t yr⁻¹ fresh weight in Northern Europe around the year 1800, Jensen 1979), the ash was used as a source of soda and potash for the glass and soap industries and later as a source of iodine. Folk memory (Northern Ireland) suggests that the stipes were the main component burned, the *Laminaria* blades together with the other species collected (*Ascophyllum nodosum* and *Fucus vesiculosus* for the main part) being valuable as a soil conditioner and fertiliser. In time the name “kelp” was transferred to the main constituents that were burned - *Laminaria* spp. - and since then, kelp has become a common colloquial term applied to the large brown seaweeds of the taxonomic order Laminariales, throughout the world.

Kelp plants are composed of distinct parts; the **blade** or **lamina** is the very obvious, largely thin, flat, flag-like portion of the plant. This is supported by the **stipe**, the stalk of the plant which may vary in length and thickness between different plants. The plant is attached to the substratum by the **holdfast**, which resembles a collection of roots but serves only as an anchor, having no nutrient gathering role. The root-like structures are known as **haptera**. Some kelp species produce **sporophylls** which are additional structures above the holdfast and below the blade which may resemble small, thicker blades or may be flattened outgrowths from the stipe. The large kelp plants in coastal waters are the **sporophytes**, they are all diploid (“2N”, they have two sets of chromosomes and produce male or female spores by meiosis). The **gametophyte** plants are microscopic and are haploid (“N”, have one set of chromosomes and produce eggs and sperm by mitosis).

Kelp forest is the term generally used to describe the nature of the kelp biotope in the upper infralittoral, where the plants are densely distributed and the large laminae overlap each other to form a canopy that excludes light. The upper limit of the forest is determined by the effects of storm waves, the tidal cycle (desiccation stress) and competition with other macroalgal species for space and light.

Kelp parkland is the term used to describe the kelp biotope in the lower infralittoral, where the kelp plants are more widely spaced and the laminae do not form a canopy cover. The lower limit of the parkland may be determined by the available light, the available substratum or by grazing pressure from sea urchins.

A *biotope* is defined as the *habitat* (i.e. the environment's physical and chemical characteristics) together with its recurring associated *community* of species, operating together at a particular scale. The habitat is taken to encompass the substratum and the particular conditions of wave exposure, salinity, tidal streams and other factors which contribute to the overall nature of the location. The term *community* is here used to signify a similar degree of association of species which regularly recurs in widely-separated geographical locations; the degree of similarity will vary, depending on the scale considered" (Connor *et al*, 1997).

- It should be noted that in the EC Habitats Directive, the term habitat is used in a much wider sense, to include the species or community living in the habitat; the common usage of this term is therefore synonymous with the term "biotope".

Bioindicators are plant or animal species which can be used to deduce environmental characteristics without the need to measure those characteristics continually. For example, rhododendrons are terrestrial plants that are indicators of acidic soils

D. CONSERVATION SIGNIFICANCE OF KELP FORESTS

Kelp beds are a characterising feature of the UK coastal ecosystem and, although similar biotopes are also found in Norway, Ireland and the Brittany coasts of France, the kelp beds of the UK are more diverse and extensive than elsewhere in the EU. Within a narrow fringe around the coast a fabulous diversity of species may be found. Kelp beds have considerable conservation value for the following reasons:

- Kelp plants are the major primary producers in the UK marine coastal habitat. Within the coastal euphotic zone (from high water mark to the depth of light penetration) kelps produce nearly 75% of the net carbon fixed annually on a shoreline with approximately 40% suitable substratum for macroalgal attachment (Birkett, Dring & Savidge, unpublished).
- Each year, the kelp plants in the kelp beds produce about 2.7 times more biomass than the standing biomass of the kelp plants (Birkett, Dring & Savidge, unpublished).
- Kelp detritus (particulate organic matter; POM) and dissolved organic matter (DOM) are exported from kelp beds and support ecosystems on soft bottoms (Thrush, 1986).
- Kelp plants structurally support a diverse epiflora.
- Kelp plants structurally support a diverse epifauna.
- The holdfasts of kelp plants form a sheltered habitat for a diverse assemblage of animals.
- Many of the organisms that live in kelp habitats are rare, unusual or poorly known
- Kelp beds are dynamic ecosystems, where competition for light, space and food result in the species-rich, but patchy, distribution patterns of flora and fauna on the infralittoral reefs.
- Although kelp population structure can recover from physical damage in the course of 5 -7 years, the re-establishment rates of the fauna and flora associated with the kelps appears to take a much longer as yet unknown period to return to pre-disturbance status.

In consideration of the points outlined in the above paragraphs, the candidate SACs were selected so as to include areas with extensive and varied kelp biotopes. Project demonstration sites selected which contain kelp biotopes are listed in Table 1.

Table 1. UK project demonstration sites (candidate SACs) containing infralittoral reefs with kelp (kelp beds)		
	EU habitats listed	
Papa Stour	Reefs; seacaves	
Loch Maddy	Shallow inlets & bays; lagoons	
Sound of Arisaig	Sandbanks	
Berwickshire, Northumberland coast	Mud-sandflats; reefs; seacaves	
Strangford Lough	Shallow inlets & bays	
Lleyn peninsula & the Sarnau	Estuaries; reefs	
Cardigan Bay	Reefs	
Plymouth Sound & Estuaries	Sandbanks; estuaries; shallow inlets & bays	

E. KELP DISTRIBUTION IN EUROPEAN AND UK WATERS

In almost any coastal area of Europe where there is a suitable substratum (rock, boulder, cobble, artificial substrata) and adequate water quality, one or more species of kelp may be found. On the western coasts of the UK, the geological conditions result in a complexity of bays and headlands, rocky shores and cliffs, offshore islands and islets, intertidal and submerged reefs which are ideal for the development of kelp forests. With the exception of heavily silt-loaded estuarine areas, all subtidal, stable rock substrata within the photic zone of northern Europe are likely to be colonised by kelp. On the Eastern coasts of the UK, in particular from the Thames estuary to the Ouse estuary, and in the southern parts of the North Sea, the coasts are mostly either depositional shores or are formed of friable rock, unsuitable for kelp attachment and so distribution is sporadic at best. Further north, as rocky shores become more prevalent once again, kelp beds reappear along the coasts. In the north west of Scotland, particularly around the Hebrides where the habitat is especially suitable with gently shelving rocky basins between many of the islands, the kelp forests cover an enormous area of the subtidal seabed with *L. hyperborea* being the dominant kelp. Kelp beds of a similar extent are found on the coasts of Brittany, where the dominant species is *L. digitata*.

1. *Kelp species*

a. In European waters

There are at present 13 species (confirmed) of kelp found in European waters of which two are introduced aliens which have escaped from cultivation. Of the remaining species, 4 have a northern (boreal) distribution and 4 have a southern distribution, while the other 3 species are found in both northern and southern waters (see Table 2). There is some debate as to the validity of the species of *Laminaria* in the simplices group (*L. saccharina*). In northern waters (Scotland and the Faeroes) there are kelp plants that have been identified as *L. longicuris* and *L. faroensis*. However, other authors regard these as local growth forms of *L. saccharina*. For the purposes of this review, the debatable species will be considered as forms of *L. saccharina*.

An excellent review of the history of the evolution of the marine benthic flora and its distribution patterns can be found in Lüning (1990, chapter 2). The relatively large numbers of different kelp species found in European waters are the result of the pattern of tectonic activities and the development of oceanic circulation patterns over the last 15 million years. As a result, we now have, within European waters, kelp species representative of both North Atlantic and North Pacific genera, of warm water origin, of cool water origin and of Arctic water origin.

Table 2. Kelp species found in European waters		
Species name and authority	distribution	habitat depth
<i>Alaria esculenta</i> (Linnaeus) Greville	Spitzbergen; Murmansk to southern Brittany	+1 - 35 m
<i>Laminaria digitata</i> (Linnaeus) Lamouroux	Spitzbergen; Novaya Zemlya to mid- Bay of Biscay	+1 - 3 (40)m northern 0-10 m southern
<i>Laminaria hyperborea</i> (Gunnerus) Foslie	Spitzbergen; Murmansk to mid-Portugal	1 - 47 m *
<i>Laminaria japonica</i> Areschoug	Mediterranean, introduced alien	no data
<i>Laminaria ochroleuca</i> de la Pylaie	Cornwall - Morocco; Mediterranean	0 - 30 (75) m
<i>Laminaria rodriguezii</i> Bornet	Mediterranean	50 - 120 m
<i>Laminaria saccharina</i> (Linnaeus) Lamouroux	Spitzbergen; Murmansk to Portugal	0 - 20 m
<i>Laminaria solidungula</i> J. Agardh	Spitzbergen, Novaya Zemlya	1.5 - 20 m
<i>Phyllariopsis brevipes</i> (C. Agardh) Henry et South	southern Bay of Biscay to Morocco; Mediterranean	0 - 30 m
<i>Phyllariopsis purpurascens</i> (C. Agardh) Henry et South	northern Spain to Morocco; Mediterranean	no data
<i>Saccorhiza dermatodea</i> (de la Pylaie) J. Agardh	Spitzbergen; Novaya Zemlya to mid- Norway	0 - 20 m
<i>Saccorhiza polyschides</i> (Lightfoot) Batters	mid-Norway to Ghana; parts of Mediterranean	0 - 30 m
<i>Undaria pinnatifida</i> (Harvey) Suringar	Channel coasts; Mediterranean, introduced alien	+1.5 - 15 m
Information abstracted from Lüning (1990) and references * MNCR survey of St. Kilda, 1997		

b. In UK waters

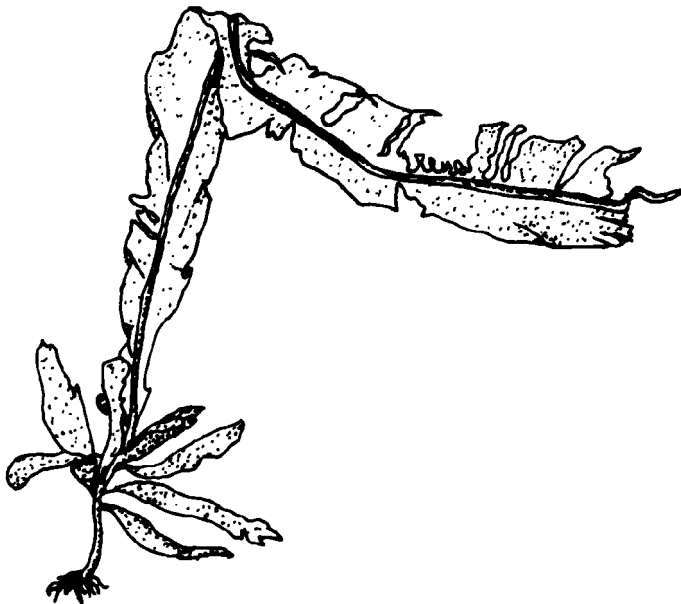
There are 7 species (confirmed) of kelps found in UK waters, one of which is a recently introduced alien (*Undaria pinnatifida*) and one of which is a southern species the range of which is extending northward (*L. ochroleuca*). The most common species in kelp beds are *L. digitata* and *L. hyperborea*, the latter often out-competing the former in shallow water in the northern parts of the UK.

The species listed in Table 3 are the most commonly found kelps which form the foundation of the kelp biotopes found in European waters. In the Mediterranean and on the south-western Atlantic coasts of the EU, kelp plants are often found in deeper waters and growing in more mixed communities, the kelp species therefore forming a less dominant component within the coastal ecosystems.

name	common and local names
<i>Alaria esculenta</i>	dabberlocks (British Isles)
<i>Laminaria digitata</i>	horsetail kelp, sea girdle, sea wand, red ware (British Isles); anguiller, tali (Brittany, France); fingertare, silketare (Norway); fingertang (Sweden, Germany); kelp, horsetail kelp (USA).
<i>Laminaria hyperborea</i>	tangle, redware, cuvie, cuvy (British Isles); trolltare, stortare, stokktare, palmetare, skrame, hestatare, havetare, kurvtare, stolpetare (Norway); Palmetang (Germany); tali-penn, tali-ebrel (Brittany, France).
<i>Laminaria ochroleuca</i>	none - species recent in UK waters
<i>Laminaria saccharina</i>	oar weed, sea-belt (sugar-kelp, D. Connor pers.comm.)
<i>Saccorhiza polyschides</i>	bulbous <i>Laminaria</i> , bulbous rooted tangle, furbelows, sea furbelows, great furled <i>Laminaria</i> , furbelowed hangers (British Isles); sekktare (Norway); carocha, caixeira, cintas, golfe, limo-correira, limo-corriola (Portugal).
<i>Undaria pinnatifida</i>	Wakame

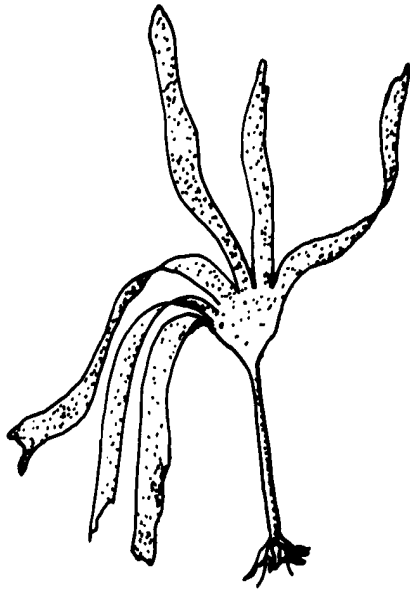
c. Illustrations and descriptions of the kelp species found in UK waters

Alaria esculenta



The holdfast is compact and haptera are usually short; the stipe is flexible and usually short; older plants may have flat, leaf-like sporophylls growing from the stipe at the base of the blade; the blade is a rich brown colour, simple (ribbon-like) in form and with a well defined conspicuous midrib; the blade tissue is remarkably supple to the touch and the entire blade is very flexible; the blade length varies both seasonally and with the location, but is commonly 30-90 cm; the blade becomes tattered distally during the summer due to abrasion of the tissue at the tip.

Laminaria digitata



The holdfast is formed of conspicuous root-like haptera, gripping the substratum, the holdfast of older plants may become conical; the stipe is cylindrical or may be slightly flattened and is flexible, smooth, and variable in length depending on location; the stipes are relatively rarely colonised by epiflora but this may depend on the age of the plant and its location; the blade is dark brown, large, tough, flat and usually split into 5-12 fingers or straps (digitate); the blade length varies with season, age of plant and location, reaching over 1 m under suitable conditions; the shape of the blade-stipe junction varies seasonally from cuneate (pen nib shaped) in autumn & winter, to cordate (heart shaped) in early spring through the summer (Gayral & Cosson, 1973). ***This species is often difficult to distinguish from L. hyperborea, particularly when plants are young.*** The two species can be separated by the absence of mucilage ducts in the stipe (they are present in the stipes of *L. hyperborea*) and the benzidine test (Jensen & Haug, 1952) which slowly turns freshly cut tissue of *L. digitata* to a yellow-brown colour.

Laminaria hyperborea

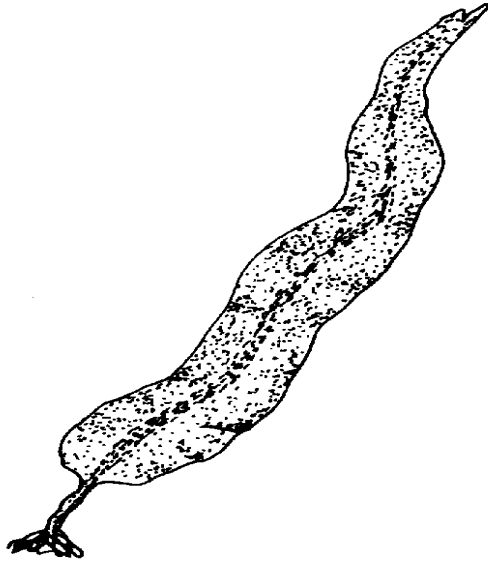


The holdfast is formed of conspicuous haptera forming a conical attachment in mature plants; the stipe is cylindrical but thicker at the base of the plant, it is rough textured (except in very young plants) and is stiff rather than flexible; the length of the stipe varies depending on the depth and location; stipes are often heavily colonised by epiflora and epifauna; the blade is very dark brown, large, tough, flat and usually split into 5-20 fingers or straps (digitate); the blade length varies with season, age of plant and location, reaching over 2 m. under suitable conditions; each year the new blade grows below the old one (starting in November), leaving a distinct collar between the two and the old blade tissue is shed in the spring and early summer. ***This species is often difficult to distinguish from L. digitata, particularly when plants are young.*** However, mucilage ducts are present throughout the plant and the benzidine test (Jensen & Haug, 1952) immediately turns freshly cut tissue to a bright red colour.

Laminaria ochroleuca

In appearance this plant is very similar to *L. hyperborea*, but the stipe and the frond are a much lighter colour with a yellowish cast. The stipes are smooth and generally lack epiphytes and epifauna.

Laminaria saccharina



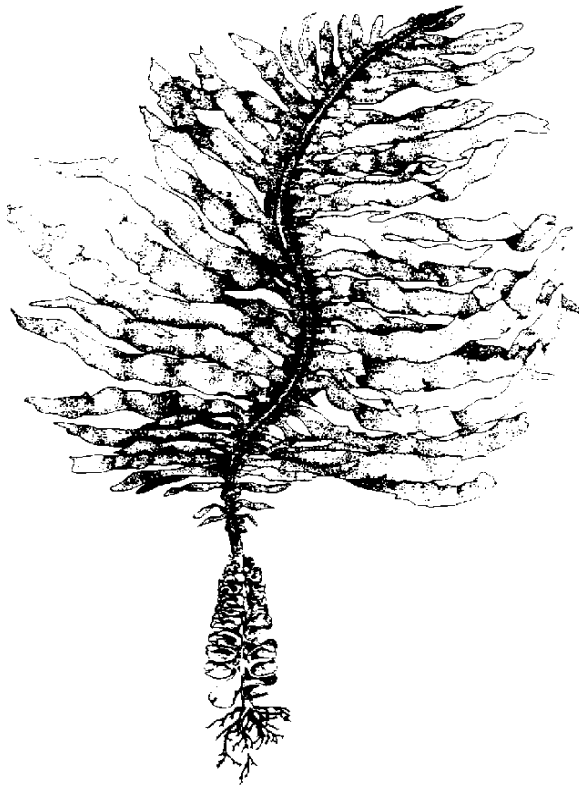
The holdfast is usually compact, the haptera usually short; the stipe is flexible and usually short; the blade is golden brown, a simple ribbon form, with a thicker ribbon of tissue forming a midrib; the blade tissue may be supple to the touch or feel substantial (depending on local wave conditions) but the entire blade is flexible; the blade may be 10-50 cm wide, smooth or bullate, and the wider plants from sheltered sites may develop luxuriant marginal undulations (not shown here); the plant length varies both seasonally and with location, commonly reaching 30 cm-1.5 m; blades become tattered distally especially during the late summer.

Saccorhiza polyschides



The holdfast is initially formed of haptera but these become obscured by the growth of a large bulbous hollow expansion of tissue, up to 30 cm. in diameter, covered by short protuberances and attached to the substratum by un-branched haptera; the stipe is flattened and is twisted towards the base and is very tough but not rigid; in older plants the base of the stipe bears tough, undulating lateral extensions or frills (sporophylls); the blade is dark brown, broad, flat, tough and divided into 3-30 fingers or straps (digitate); both blades and stipes are variable in length depending on depth, plant age and location, but plants can become more than 3 m in length; the distal portions of the blade become tattered late in the growing season.

Undaria pinnatifida



The holdfast is formed of haptera, and at present in the UK this species is most often found attached to some man-made structure rather than to the local substratum; the stipe is usually short (10-30 cm) and in mature plants bears convoluted outgrowths or frills (sporophylls); the blade is brown and is initially simple and broad with a distinct midrib; older plants have thicker blade tissue which splits horizontally down to the midrib to form fingers or straps; the distal portion of the blade and the straps are tattered; at the end of the season the blade may become covered by colonial animals.

2. Distribution of kelps in European coastal waters

Alaria esculenta



This is an Arctic-cold temperate amphioceanic seaweed, which is the only member of the genus *Alaria* found in the North Atlantic, although there are about 10 species in the North Pacific. The most southerly population of the species is on the coast of Brittany, but it is found on the south-western coasts of England and has been reported on the Channel coasts. It is also found around most of Ireland and northwards to Rockall and Iceland. The species is present around the coasts of Scotland and northwards along the Norwegian coast but is absent from the Baltic and most of the North Sea although it is found on the

English coast as far south as Flamborough Head. It has been reported from the Barents Sea and Svarlbard Archipelago and is found on the western coasts of Novaya Zemlya. It is also found outside European waters.

Laminaria digitata



This is a North Atlantic Arctic-cold-temperate species which does not occur in the North Pacific. The southernmost occurrence of this species in European waters is on the southern coasts of Brittany. It is found around south-western England, the coasts of Ireland and northward to Rockall, the Faeroes and Iceland. It is also found along both coasts of the English Channel, and the North Sea coasts of Scandinavia. It is absent from the east coasts of England and from the Baltic. It is apparently extending its range into the southern part of the North Sea, given suitable habitat. Its northerly range extends into the Barents Sea and the western

shores of Novaya Zemlya and it is reported from the Svarlbard Archipelago. It is also found in the North Atlantic outside European waters.

Laminaria hyperborea



This is a European North Atlantic cold-temperate species which does not extend into areas influenced by Arctic waters. Its southernmost habitat is Cape Mondego in mid-Portugal and the range then extends northward around the corner of the Iberian peninsula onto the northern coast of Spain. It is absent from the Bay of Biscay and then is found on the southern coasts of Brittany and along the channel coasts of France and England. It is found around Ireland, on Rockall, the Faeroes and around Iceland. It is found in the south-west of England, Wales and around the Scottish coasts and, in all these north-western areas, forms dense

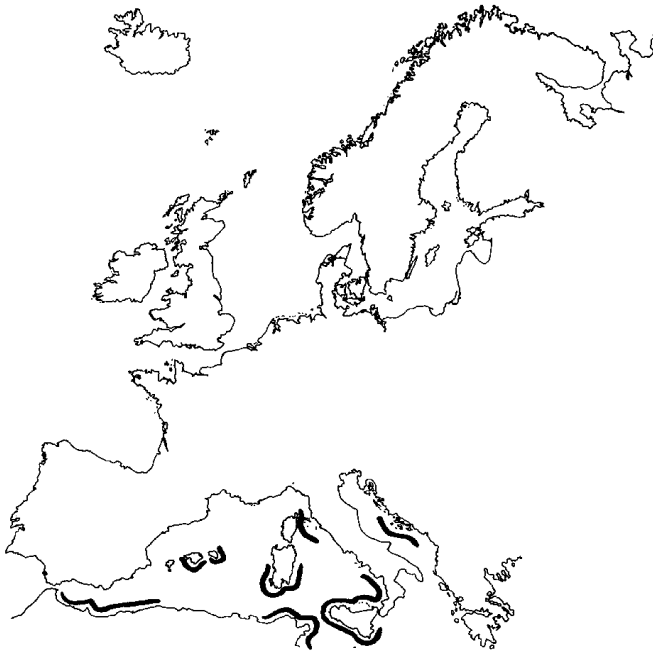
forests fringing the coasts where the substratum and wave regime allow. From the northern part of Denmark its range extends along the Swedish coast and northwards along the Norwegian coast to the Bay of Murmansk. It is not found in the Baltic and there are few records for south-east coasts of England due to lack of suitable substrata.

Laminaria ochroleuca



This is a warm-temperate, Lusitanian species. It is found from Morocco (and possibly the Azores) where it is the kelp forest species in place of *L. hyperborea*, northwards on the Atlantic coasts as far as the English Channel and Lundy in the Bristol Channel. In the northern part of its range it is found with *L. hyperborea* in a mixed kelp forest. Since 1940, this species has been found on the coasts of southern England and is apparently indicative of a slow northward extension of warmer waters. It is also found on the shores of the south-west Mediterranean and in the Straits of Messina.

Laminaria rodriguezii



This species is endemic to the Mediterranean and is found on the coasts of Algeria, Tunisia, Majorca, Corsica, Sicily and the shores of the Adriatic Sea. However, it is restricted to depths of 50 - 120 m where the water temperatures do not exceed 15 °C.

Laminaria saccharina



This species has an amphioceanic heritage and an Arctic-cold temperate distribution. It is found in European Atlantic waters as far south as the coasts of northern Portugal, although it is not recorded from the northern coast of Spain or in the Bay of Biscay. It is found on the southern and northern coasts of Brittany, all around Ireland and north-eastwards to Iceland. It is found on the French and English channel coasts, south-western England, Wales and Scotland but is only found sporadically on the east coast of England. It is not found in the Baltic. Its distribution continues from Denmark, Sweden and the coasts of Norway around the coasts of

the Barents Sea to the western shores of Novaya Zemlya and north as far as the Svalbard archipelago. It is also found outside European waters.

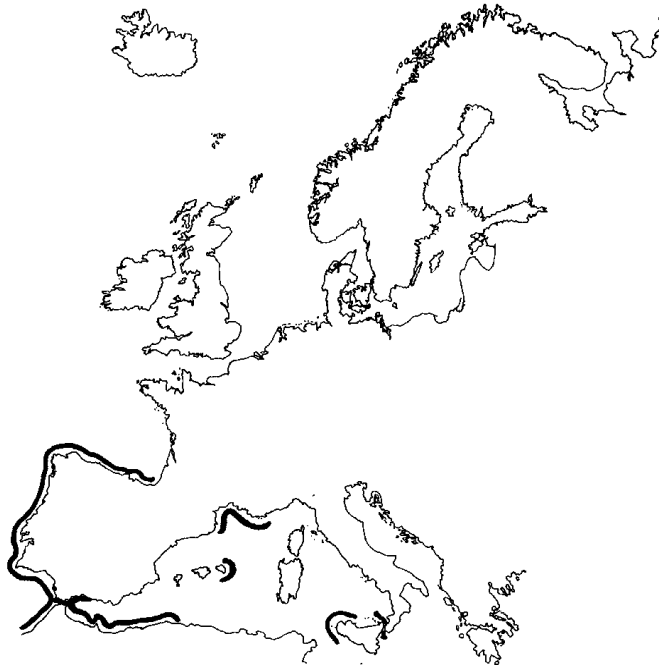
Laminaria japonica

This species has been introduced into the Mediterranean, probably with imported oysters for aquaculture. It is similar in appearance to *L. saccharina*.

Laminaria solidungula

This species is found throughout the Arctic to which it is endemic and, within European waters, it is known only from the Svalbard Archipelago and from Novaya Zemlya.

Phyllariopsis breviceps



A warm-temperate species found in deep water. The southern range ends at the Western Sahara border with Morocco, extending northward on the eastern Atlantic coast to Biarritz. This species is also found in the western basin of the Mediterranean.

Phyllariopsis purpurascens



A warm-temperate species found in deep water. The southern range ends at the Western Saharan border with Morocco, extending northward on the eastern Atlantic coast to the Spanish-Galician coast. This species is found in the southern part of the western basin of the Mediterranean.

Saccorhiza dermatodea



This is a cold water species with an Arctic-cold temperate North Atlantic distribution. In European waters its most southerly habitat is the northern coast of Iceland. It is also found along the Norwegian coast and is reported from Novaya Zemlya and the Svalbard Archipelago. It is also found outside European waters.

Saccorhiza polyschides



This is a European North Atlantic species, which is also found in a few places in the Mediterranean Sea. On the Atlantic coast it is found as far south as Cape Jubi, Morocco, extending northward along the Spanish and Portuguese coasts. It is found on the coast of France, Brittany, south-west England, Wales, Ireland and Scotland. To the north it is found in the Shetland Islands and along the western coast of Norway as far as Rörvik. It is not found in the North Sea or in the Baltic or outside European waters.

Undaria pinnatifida



This species is found in several places within Europe and is increasing its range. The species originated in the Northwest Pacific, where it is harvested and cultivated as a food species (wakame). In recent years it has been introduced into Europe both accidentally (into the northern Mediterranean through the movement of shellfish for aquaculture, and on the hulls of leisure boats to marinas in Southern England) and also deliberately for aquaculture purposes (northern Brittany).

F. KELP BEDS - THE ADVANTAGES AND LIMITATIONS OF THE MNCR BIOTOPE CLASSIFICATIONS

This review makes use of the MNCR biotope classification system in an attempt to group together kelp beds which are similar in nature.

The MNCR biotope classifications use the **easily measured**, stable physical parameters (depth, location, substratum etc.) in combination with observations of **easily found and identifiable** species that are thought to act as **bioindicators** of dynamic physical conditions (subsurface irradiance, sedimentation, temperature & salinity fluctuations, etc.). The broad classifications (higher codes) are further refined in terms of the presence or absence of the easily observed and characteristic plant and animal species within each biotope.

It must be stressed that the marine biotope classification is **not intended** to give any indication of the

- conservation status of a site
- biodiversity of the site
- dynamic patterns of species interactions that may occur at that site.

As an illustration of an equivalent situation on land, a woodland area might be classified on the basis of being upland or lowland, on acidic or calcareous rock, in a high or low rainfall area, being deciduous or coniferous (etc.). The characteristic species might include the larger understorey plants and some of the birds. But a combination of these descriptions would not necessarily give an indication of the diversity and temporal shifts in the insect, bird and plant populations found in the wood, the spring flowering bulbs and autumnal fungi, the complete range of tree species or the maturity of the trees.

Biotope classifications are a **very useful, standardised descriptive tool for the mapping and definition of management areas** and for suggesting the potential species to be encountered within the area of each biotope (based on previous survey experience). They can provide the underlying framework for the structure of a management plan but cannot be expected to contribute to the biological monitoring or management of a site. Due to the gaps in our present knowledge of the species interactions that may be critical to the maintenance of the favourable status of kelp ecosystems (see Chapter VII), species that are normally hidden or cryptic but are characteristic of certain biotopes may not be listed in the present biotope descriptions.

At present there are 51 different biotope codes for infralittoral kelp communities. Within these classifications are included the higher code descriptions. Of the most detailed classifications (biotope and sub-biotope), 45 separate “sub-tidal reef biotopes with kelp” are listed. These classifications are summarised with brief biotope descriptions in Appendix 1. The 5 biotope complexes (with their higher code categories), which together encompass the individual biotopes, are:

- *Exposed infralittoral rock*
- **EIR.KFaR:** kelp with cushion fauna, foliose red seaweeds or coralline crusts (exposed rock)
- *Moderately exposed infralittoral rock*
- **MIR.KR:** kelp with red seaweeds (moderately exposed rock)
- **MIR.GzK:** grazed kelp with algal crusts
- **MIR.SedK:** sand or gravel affected or disturbed kelp and seaweed communities
- *Sheltered infralittoral rock*
 - **SIR.K:** silted kelp (stable rock)

The biological complexity of the kelp beds as habitats and their significance in the marine coastal ecosystems of the UK, can be illustrated by comparing the numbers of distinct kelp biotope descriptions with the numbers of other marine biotope codes.

- Subtidal kelp biotopes are present in 3 of the 23 coastal habitat complexes defined in the MNCR classification,
- Of the 276 biotopes and sub-biotopes defined to date, there are 45 (16%) with kelp as a characteristic component.
- The enormous numbers of species so far recorded from kelp beds around the UK are summarised in Table 4, (see Appendix 5 for complete list). Species numbers (grouped taxonomically) in the MNCR database records for all kelp biotopes in the UK are summarised in Appendix 2. Within the five biotope complexes in the MNCR database (as of March, 1998) the species recorded appear to vary greatly from one site to the next, reflecting the wide geographical distribution of the component biotopes within these complexes as well as the variable quality of the data (D. Connor, pers. comm.) and the intrinsic patchiness and diversity of the fauna and flora found within kelp beds.

Table 4. Numbers of species recorded from the kelp biotope complexes in the MNCR database (as of March, 1998)

code for the complex	number of sites on record	numbers of species recorded from:			
		at least 1% of all sites	at least 5% of all sites	at least 25% of all sites	at least 50% of all sites
EIR.KFaR	769	522	137	19	3
MIR.KR	1,131	590	170	28	2
MIR.GzK	207	366	136	27	8
MIR.SedK	495	658	207	29	4
SIR.K	823	507	144	17	1
All kelp biotopes	3,425	817	266	49	10

- For all the sites included in the MNCR database, a total of 1,819 species (taxa) have been listed (see also Appendix 5).
- Only 10 of these species are regularly found at most sites (more than 50% of sites; see Table 4).
- **The “faithful” species are those which are conspicuous and easily identified, and this may account for their prominence in the database.**
- **Smaller and less readily identifiable species, or species that are hidden within the structure of the biotope, are less frequently recorded even if they are common and abundant at a site. The less conspicuous the species, the fewer the number of records in the database.**
- **In terms of management of biotopes for conservation purposes, these biases within the database and produced by the data collection methods may pose a serious problem by placing emphasis on species which may not be critical to the maintenance of the favourable status of the biotope.**

The “faithful” species (those recorded at more than half of the sites) in the various kelp biotopes are shown in Table 5. That so few large and common species should be recorded on a regular basis from kelp beds, suggests that the faunal and floral variation recorded from different locations as well as from different biotopes with kelp is enormous. The variation in species faithfulness that occurs within a specific biotope is very much less than the variation that occurs between biotopes grouped within a biotope complex. For example, of the suite of 11 species used to characterise the biotope “MIR.Lhyp.Ft”, 8 species are found at more than 61% of all recorded sites of this biotope (T. Hill, pers. comm.)

- **With only 12 demonstration SACs scattered throughout the variety of coastal locations in the UK, it is probable that some of the kelp biotopes will not be represented adequately in the proposed protected areas.**

Table 5. Species or species groups regularly (>50% of sites) and often (>25% of sites) recorded in the kelp biotope complexes				
EIR.KFaR	MIR.KR	MIR.GzK	MIR.SedK	SIR.K
*	*	<i>Alcyonium digitatum</i>		
	*	<i>Gibbula cineraria</i>	*	*
	*	<i>Calliostoma zizyphinum</i>		
*	*	<i>Asterias rubens</i>	<i>Asterias rubens</i>	<i>Asterias rubens</i>
*	*	<i>Echinus esculentus</i>	*	*
Coralline algae, unspecified	Coralline algae, unspecified	Coralline algae, unspecified	Coralline algae, unspecified	*
*	*	<i>Phycodrys rubens</i>	*	*
<i>Laminaria hyperborea</i>	<i>Laminaria hyperborea</i>	<i>Laminaria hyperborea</i>	<i>Laminaria hyperborea</i>	*
	*	*	<i>Laminaria saccharina</i>	<i>Laminaria saccharina</i>
<i>Alaria esculenta</i>				
* indicates that the species is often (>25% of sites) recorded in these biotopes				

It is very important that the following points are noted when referring to the numbers and diversity of species found in kelp forests: The assemblages of species found in kelp forests are probably larger and more complex than our present knowledge would suggest. Much of the information collected during biological surveys has been collected by divers. This is an excellent method of preliminary data collection but it must be noted that it is akin to collecting data on the species diversity of a rain-forest while suspended from a helicopter!

- More than 1000 of the species reported from kelp biotopes were recorded from fewer than 1% of the sites listed under the higher code classifications (see Appendix 5). This might suggest that, of the nearly 2000 total species reported as living in kelp biotopes, more than half are uncommon (or rare) or confined to an uncommon biotope. However, of the species listed as “rare” or only present at a few locations even if locally common, many are either difficult or impossible to see under normal surveying circumstances or hard to recognise *in situ*, or are small and easily overlooked in samples or require specialist skills in order to identify them.
- Based on the patterns of species reported in the MNCR database and on the raw data obtained from several subtidal biological surveys, it is suggested that in many instances one or more of the following may have occurred:
 - samples were sorted and identified by non-specialists (there is a paucity of species indifficult groups, reduced biodiversity, inaccurate or incomplete identification).
 - samples were sorted and identified by a specialist (possible over-emphasis in the biodiversity of the area of expertise).
 - uneven sampling or recording efforts (only the largest, the most easily recognised or the most obvious of the characteristic species of the biotope are reported).
- An understanding of how the samples were collected and identified is needed in order to set the limits of interpretation on the data (D. Connor, pers. comm.).

- For pragmatic reasons, the biotope classification method does not take into account the presence of species which are rare, cryptic, hidden within the biotope or ephemeral. **These may well be the species that are key to the conservation status of the biotope**
- Seasonally migrating species may be key predators within a biotope.
- The grazing activity of the population of *Helcion pellucidum* may control the age structure of kelp forests, but this limpet species commonly lives hidden within the kelp holdfast and is only obvious when newly settled on fronds. This species has been reported (according to the MNCR database) from only about 500 of the 3425 kelp biotope sites in the database yet phycologists report that it is abundant in *L. hyperborea* forests throughout the UK.

G. KEY POINTS FROM CHAPTER I

What is kelp and why is it important?

- Kelp is the colloquial name given to the large, brown seaweeds of the order Laminariales which dominate much of the shallow sublittoral in temperate parts of the world.
- Kelp plants are physically large, metres to several tens of metres tall, and when present in dense stands known as “kelp forests” they form an important habitat for other organisms.

Conservation significance

- The kelp forests that are found fringing the temperate sea shores of the world are possibly the most ecologically dynamic and biologically diverse habitats on the planet.
- Kelp biotopes are identified as a key habitat within the scope of the UK Marine SACs Project, and also in the EU Habitats Directive and the UK Biodiversity Action Plan.
- Kelp beds occur in 8 of the demonstration marine SACs within the UK.
- Many of the organisms that live in kelp habitats are rare, unusual or poorly known; little is known of the ecological interactions between species or between the kelp beds and surrounding biotopes; the biology and the sensitivities of many of the known species are poorly understood.

Distribution

- In almost any UK coastal area where there is a suitable substratum (rock, boulder, cobble, artificial substrata) and adequate water clarity, one or more species of kelp may be found.
- Thirteen species of kelp are found in European waters, of which two are introduced aliens which have escaped from cultivation. Of the remaining species, 4 have a northern (boreal) distribution and 4 have a southern distribution, while the other 3 species are found in both northern and southern waters.
- Species occurring in the UK are *Alaria esculenta*, *Laminaria digitata*, *L. ochroleuca*, *L. saccharina*, *L. hyperborea*, *Saccorhiza polyschides* and the introduced species *Undaria pinnatifida*.

Kelp biotopes

- There are very few “faithful” species (those recorded at more than half of the sites) in the 5 UK kelp biotope complexes, as the variation in fauna and flora between the biotope complexes is large.
- The differences between the specific biotopes are large although different kelp beds within a single classification are superficially similar. The faunal and floral variation to be encountered between similar kelp beds is considerable and the patchiness of species distribution within a single kelp bed is a significant feature of the habitat.
- For all the sites included in the MNCR database, a total of 1,819 species (taxa) have been listed as occurring in kelp biotopes.
- The MNCR database does not necessarily record all species present within a habitat; emphasis is on those species that are larger, do not hide away and are easily identified.
- The biotope classification provides an excellent standardised tool for mapping areas as the basis of a management plan.
- The biotope classifications for subtidal reefs with kelp species may not provide sufficient indication of the diversity and variability within a biotope and *cannot* allow for the dynamic nature of the kelp bed ecosystem.

II ENVIRONMENTAL REQUIREMENTS AND PHYSICAL ATTRIBUTES

A. INTRODUCTION

This section presents an overview of only those fundamental physical attributes and ecological requirements of kelps which affect their basic distribution, with emphasis on information for those species common in UK waters at the present time.

The faunal and floral diversity of kelp biotopes is extremely rich (see Appendix 5). This is in part associated with the diversity of available food sources as primary production (microscopic and macroscopic algae), secondary production (herbivores and subsequent trophic levels) and microbially recycled production but is also due to the physical and structural diversity within the biotopes, with the many and various exploitable niches available.

Any kelp-bearing area will contain a number of habitats available to other biota. Faunal species may be found restricted to, or moving between, any combination of such associated habitats. A large component of the fauna, such as much of the rock crevice fauna or sediment infauna, may occur more or less independently of the presence of kelp. Similarly some fauna may be mainly or entirely restricted to the kelp plants themselves, as is the case with many species found in the kelp holdfasts. The flora found in kelp beds may also not be restricted to this habitat, but the complex interactions of the grazing species found in kelp beds and the several habitats available for colonisation within the kelp bed may lead to a wide diversity of seaweeds being present within a given area.

However, the following points should be noted:

- **For the majority of flora and fauna found within the various kelp biotopes, the specific environmental requirements and the physical attributes of the individual species are not known.**
- **Within the scope of this report it is not possible to consider the specific requirements for any of the many hundreds of species of animals and plants which are characteristic of the given kelp biotopes. It must be assumed that, if a species is present within a kelp biotope, the local conditions are suitable for it. These conditions may be at the upper or lower limits of tolerance for the species the presence of which may be independent of the presence of kelp species.**

B. SUBSTRATUM

The kelp species in the UK are most frequently found attached to submerged bedrock. However, given adequate water movement in the form of tidal currents rather than wave action, large kelp plants may frequently be found attached to cobbles and pebbles. When attached to small solid objects, the life-span of the plant becomes size-limited, since larger plants are more easily washed from their original location if only attached to a small stone. As mentioned in section I.D.2.b, kelps are found in almost all locations where some form of hard substratum is available within the euphotic zone in UK waters; see Table 6.

Table 6. Substrata colonised by kelp species in the UK	
Kelp species	substrata
<i>Alaria esculenta</i>	bedrock, stable boulders, cobbles, pebbles on large gravel, pontoons & moorings, man-made structures. Not in areas where there is sand scouring or siltation.
<i>Laminaria digitata</i>	bedrock, stable boulders, pebbles on large gravel, stones on stable mud or sand, pontoons & moorings, other man-made structures. Not in areas subject to intense sand scouring but can be found in areas of siltation.
<i>Laminaria hyperborea</i>	bedrock, stable boulders, pebbles on large gravel, deeper parts of pontoons and moorings, other man-made structures. Not in areas subject to sand scouring but can sometimes be found in areas of siltation.
<i>Laminaria saccharina</i>	bedrock, stable boulders, pebbles on large gravel, stones on stable mud or sand, pontoons & moorings, other man-made structures. Not in areas subject to severe sand scouring but can be found in areas of siltation.
<i>Saccorhiza polyschides</i>	bedrock, stable boulders, pebbles on large gravel, pontoons & moorings, other man-made structures. Not in areas subject to sand scouring but can be found in areas of siltation.
<i>Undaria pinnatifida</i>	at present, mainly on man made structures, but may spread to bedrock, stable boulders

Where kelp species colonise unstable substrata, the populations are ephemeral. When the lamina reaches a certain area in relation to the mass of the item to which the plant is attached, the plant will be moved by the tide, wave action and current at the site. This frequently results in the plant being removed from the photic zone, either being cast ashore or deposited in deeper water, with the substratum exhibiting a dynamic fluctuation of colonisation and loss of kelp plants. On the shores of the NE Pacific, individuals of the annual kelp species *Nereocystis luetkeana* utilise the local water movement to migrate to deeper water as the plant increases in size (C. Hurd, pers.comm.).

C. LIGHT, DEPTH AND WATER CLARITY

The light quantity and quality that is available to a kelp plant is dependent on the depth of water above the plant (and tidal changes in that depth) and also on the type of water present. Sea water optical types were classified by Jerlov (1951; 1976) into:

- oceanic types (I, II, III), which are relatively clear because of low concentrations of particulate matter (biotic or abiotic); light at the bottom of the photic zone is blue in colour.
- coastal types (1 - 9), which contain higher concentrations of particulate matter (biotic and abiotic); at the bottom of the photic zone light is green in colour.

A detailed explanation of the interactions between light, depth and water clarity and the consequences for algal photosynthesis and growth can be found in Lüning, 1990, pp. 277-320.

The total irradiance that penetrates to different depths will change in different optical water types (summarised in Fig. 1). In addition, the quality of that light (i.e. its spectral composition) will change depending on the coloration and particulate loading of the water.

The irradiance requirements of several species of kelp have been determined experimentally and are known to be different for the different phases of the life cycle (sporophyte and gametophyte - see Chapter 3). In the field, the light requirements of the different kelp species determine the depths at which they may be found within an area with water of any given quality. In areas where the water is clear, light can penetrate to, and kelp plants can grow at, much greater depths (see Table 7) than where water is turbid or loaded with DOM (dissolved organic matter). For example, kelps may be found below 100 m in the Mediterranean, with its clear water which is classed as Oceanic III (Fig. 1), but are generally restricted to a maximum depth of 35 m in Europe (offshore from Ireland, the Scilly Isles, Rockall with water clarity of Coastal 3, Fig. 1., or 47+ m on St. Kilda, D. Connor, pers. comm.), and to as little as 6-7 m depth around Helgoland, which is surrounded by the silt-laden waters of the German Bight recorded as water of type Coastal 7 (Fig. 1). In very turbid waters (e.g. some sites on the east coast of England or in the Bristol Channel), the depth limit for kelp growth may be reduced to about 2 m, and the absence of kelp from even more turbid sites (e.g. south east Kent, inner Bristol Channel) may be attributed to the lack of sufficient light in subtidal habitats (Dring, 1987).

Table 7. Depth distribution of established kelp species in European waters	
kelp species	usual habitat zone & depth ranges (from MLWS) at example locations
<i>Alaria esculenta</i>	Upper sublittoral: Strangford Lough, 0-5 m (pers. obs.); Aran Islands, 15 m; Rockall, to below 35 m (T. Hill, pers.comm.)
<i>Laminaria digitata</i>	Upper sublittoral: Helgoland, 0-1.5 m; Rockall, to 20 m (Lüning, 1990); Brittany, 0-10 m (Gayral & Cosson, 1973); east Kent, 0-2 m (I. Titley, pers.comm.)
<i>Laminaria hyperborea</i>	Mid and low sublittoral: Menai Straits, 0-2.5 m; Norway 0-34 m; southwest England, 0-36 m (Kain, 1971); Hebrides, 0-20 m (Norton & Powell, 1979); Helgoland, 1.5-7 m (Lüning, 1990); St. Kilda to 47 m (MNCR survey)
<i>Laminaria saccharina</i>	Upper sublittoral: Helgoland, 0-1.5 m; Norway, 0-8 m (Lüning, 1990); as <i>L. faroensis</i> & <i>L. longicuris</i> , Shetland, to 25-30 m (I. Titley, pers. comm.)
<i>Saccorhiza polyschides</i>	Carsaig, Argyll, 0-15 m; Isle of Man, 0-24 m; Cornwall, 0-35 m (Norton, 1970)
There is a considerable extension in the depth ranges at which different kelp species may be found when they occur in single-species stands. For example, in the absence of the intense shade of the <i>L. hyperborea</i> canopy (due to harvesting or to severe wave action for example), <i>L. digitata</i> and <i>A. esculenta</i> may be found at much greater depths than normal (as on Rockall).	

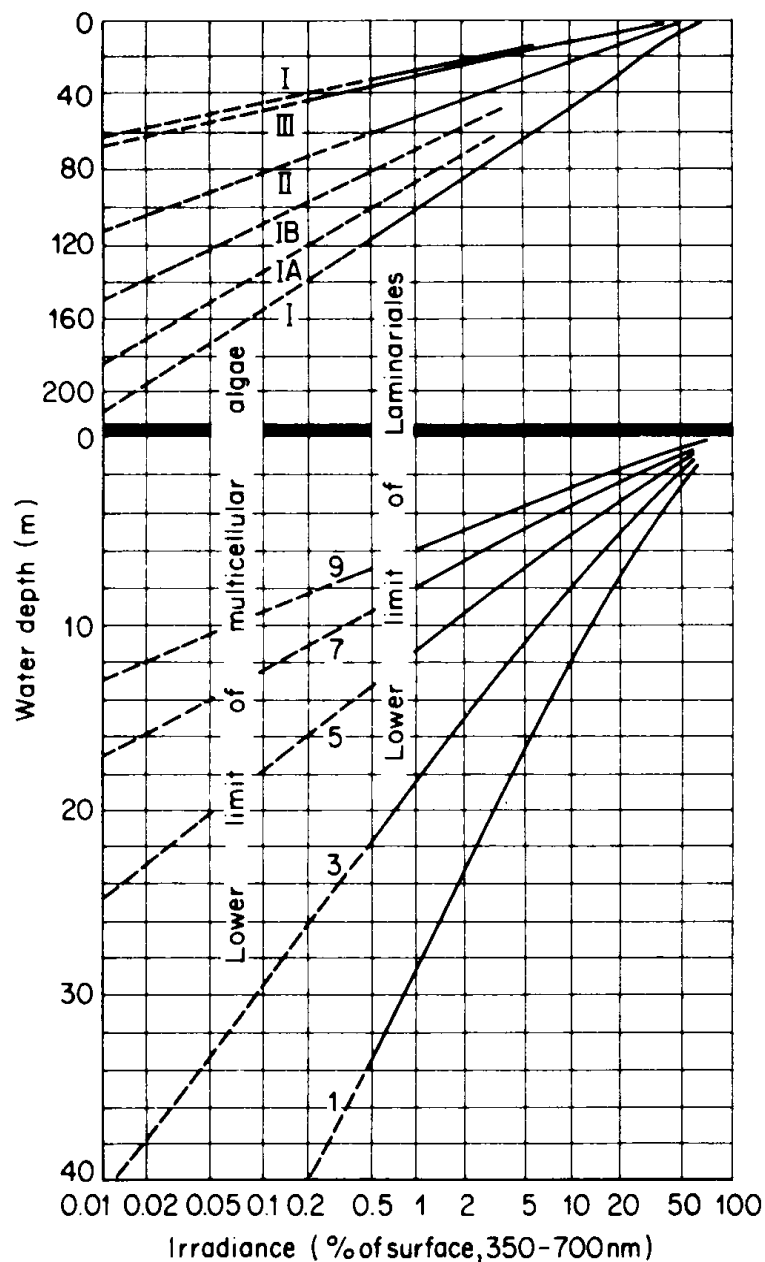


Fig. 2.5 Depth profiles of total irradiance (350 – 700 nm) in a range of water types (oceanic waters above; coastal waters below), showing approximate positions of critical light levels.¹⁴⁶

Fig. 1. Change in irradiance with depth in different Jerlov water types (I, IA, IB, II, III; & 1, 3, 5, 7, 9), showing the lower habitat limits of multicellular algae e.g. coralline crusts, and of kelps (Laminariales).
(Fig. 2.5 from Dring, 1982.)

D. WATER MOVEMENT

1. Introduction

Water movement and the hydrographic regime have a number of effects on both individual kelp plants and on the kelp bed as a whole. In areas where the kelp bed is exposed to heavy wave action (e.g. on an open coast, a headland or at the mouth of a loch), the plants and animals found differ markedly from areas where there is little wave action (within a bay or cove or within a loch). In addition, within sheltered areas there may be kelp beds in regions of high current flow (e.g. at the narrow entrance to a semi-enclosed embayment) or low water movement (within the body of a semi-enclosed embayment). In these different hydrographic regions, a number of major differences may become apparent:

- the species of kelp will vary
- the depth distributions of kelp species may extend or contract
- the structure of the kelp forest may change
- the plants of individual kelp species may exhibit different morphologies
- the understory algal population and species composition may alter
- the fauna covering the bedrock may be different

2. Tidal characteristics

a. Habitat range and population structure

As a general rule, tidal heights and ranges have very little effect on kelp beds, since they are mostly subtidal. Although individual plants which grow at the upper edge of the habitat may on occasion be exposed to desiccation and die as a result, this has little effect on the kelp bed as a whole. In locations where LWST (low water, spring tides) occurs around midday, a period of calm weather combined with high barometric pressure and sunshine can result in a catastrophically low tide exposing the upper band of kelps to severe desiccation stress. The results of exposure can be seen in the form of damaged or dead, bleached tissue in the kelp blade. In contrast, where LWS occur in the morning and evening (such as on the Isle of Man) *L. digitata* may be found as much as 1.5 m above LWS (T. Hill, pers. comm.). Low tide coinciding with severe wave action as the result of storms also has a profound effect, removing larger plants and less flexible species in the surge and swash zones (see also section II.D.3. below). As a result of the episodic exposure and storm events, the population of kelp plants (of whatever species) living to about 1 m depth below MLWS usually has a reduced age range in comparison to deeper parts of the kelp bed. There is some evidence that plants which are only shallowly submerged at midday may be subject to cellular damage as a result of increased UV radiation. However, under field conditions such episodes are of limited duration and plants can repair the damage during the subsequent periods of submergence and darkness (R. Forster, pers.comm.)

b. Growth form and population structure

In areas that are sheltered from wave action, the tidal current may have a critical effect on the appearance and productivity of the kelp plants. Particularly within coastal embayments, strong tidal water movement can result in the growth of luxuriantly large, long lived plants, which lend a degree of stability to the more usual dynamic turnover of the kelp population. This, in turn, can result in a more than usually diverse population of associated plants and

animals within the kelp bed. The tidal flow prevents thick depositional layers of silt building up on the blades of the kelp plants (and effectively reducing productivity through shading) and the water movement over the blades maintains the maximum concentration gradients of external dissolved nutrients (particularly of nitrate and phosphate), which are actively taken up and stored within the kelp tissue. The reduced wave action results in much longer, broader laminae than are found in kelp beds on open coasts.

3. *Wave exposure*

a. **Habitat range and population structure**

Kelp species found in the upper sublittoral (*A. esculenta*, *L. digitata*, *L. saccharina*) may extend their habitat into the lower eulittoral in exposed locations subject to a great deal of wave action. However, a period of calm weather in conjunction with sunshine and a low tide will generally result in the loss of these marginal plants. Consequently, the upper band of kelp plants in areas where there is such an upward extension of the habitat, often have a reduced age range in comparison to plants in deeper parts of the kelp bed. The severity of wave action on a kelp bed in an exposed location will result in a more rapid turnover of kelp plants within the kelp bed. As plants get older, they become larger and more bulky - this is particularly the case for *L. hyperborea* (Kain, 1973). The holdfasts of many of the older plants are also progressively weakened by the browsing and internal tissue excavations of *Helcion pellucidum*. Both these factors render the older kelp plants more susceptible to removal by wave action.

b. **Species distribution**

Laminaria hyperborea is unable to survive where wave action is extreme (such as in coastal surge gullies), since its stiff stipe, topped with a large lamina, is prone to being snapped. In some areas, wave action depresses the upper limit of the *L. hyperborea* habitat to several meters below MLWS (several 10's of meters on St. Kilda, T. Hill, pers. comm.) and, under very severe wave conditions, the species may be absent (as reported from Rockall: S. Hiscock in Lüning, 1990). Those kelps found in the eulittoral and upper sublittoral zone (*A. esculenta*, *L. digitata*, *L. saccharina*) have very much more flexible stipes, and narrow (or at least streamlined) blades. *Alaria esculenta* (and, to a lesser extent, *L. saccharina*) has a thickened midrib or central part of the blade which acts as reinforcement. In very sheltered areas, the upper sublittoral is dominated by *L. saccharina* which combines with, and then gives way to, *L. digitata* as the degree of exposure increases. With ever-increasing wave exposure, *L. digitata* in turn combines with and is then replaced by *A. esculenta* in the lower eulittoral and upper sublittoral zones.

c. **Growth form**

The morphology of kelp plants has been shown to be plastic. If kelp plants from a sheltered habitat are transferred to a more exposed environment, their growth form changes to that typical of plants in the new environment (Svendsen & Kain, 1971).

II. Environmental requirements and physical attributes

The differences in appearance of the same species growing in different exposure regimes can be striking (see Table 8). A brief review of the hydromechanical adaptations of kelp species in response to water movement is given by Lüning (1990, pp 344-346).

Kelp species	growth form in sheltered conditions (or increased depth)		growth form in exposed conditions
	gentle current	strong current	
<i>Alaria esculenta</i>	absent	long plants; fine midrib; broad, silky, thin blade	truncated plants; thicker midrib; narrow, battered blade
<i>Laminaria digitata</i>	thin stipe cucullate* blade, surface silted	long or short stipe long, thin tissue, digitate* blade	long or short stipe deeply digitate, truncated blade
<i>Laminaria hyperborea</i>	thin stipe cucullate blade, surface silted	long, medium to thick stipe long, digitate blade	thick, short stipe; thick, truncated, digitate blade
<i>Laminaria saccharina</i>	long stipe; very broad, thin tissued blade, undulate and frilled, surface silted	variable stipe (may be hollow) long or very long broad, thin tissue blade, undulate and frilled	(rarely present) short, solid stipe; short, narrow, thick tissued blade, strongly and closely wrinkled
<i>Saccorhiza polyschides</i>	if present, large plants with broad, cucullate blades, curved, cordate at base and very flimsy, surface silted	may become enormous plants long stipe, blades cuneate at base, very long at maturity, 30 or more digits	(infrequent) very thick, tough often twisted stipe; short plants, thick, tough blade, 3-10 digits (Norton, 1970)
* A digitate blade is split into many long ribbons; a cucullate blade is cape-like, with few or no longitudinal splits. Information abstracted from Lüning (1990) and references therein.			

E. TEMPERATURE

As a general rule, species of seaweeds with a wide geographical range are *eurythermal* - that is, they are able to tolerate (or adapt to) a wide range of temperature conditions. However, the kelp species of Western Europe have relatively limited geographical ranges, which suggests that these species are *stenothermal* - unable to tolerate large fluctuations in temperature on either a temporal or a geographical basis.

The life cycles of kelp plants consist of two phases: the large, upright sporophyte phase and the microscopic, prostrate gametophyte phase (see Chapter III). For some species, the temperature tolerance ranges for one or both life phases are known experimentally and, for others, the tolerances may be inferred from their geographical distribution with respect to seasonal ocean isotherms. There are a number of temperature constraints on each phase of the life cycle, and lethal temperatures and temperatures that limit vegetative growth and reproduction have been reported for several kelp species (e.g. Table 9). From a metabolic

II. Environmental requirements and physical attributes

point of view, there are upper and lower tolerance limits for growth in both phases of the life cycle, but there are also temperature restrictions for successful gametophyte settlement, spore production by the sporophyte and gamete production by the gametophyte. All these temperature constraints combined may explain some of the different geographical distributions of different kelp species. Where local conditions result in a persistent patch of the kelp forest that is warmer or cooler than the surrounding area, the potential exists for different species of kelp to exploit that area. Localised temperature niches on the south coast of England have enabled several new species of kelp to become established in UK waters in recent times - notably *L. ochroleuca* and most recently, *Undaria pinnatifida*.

Table 9. Temperature tolerance ranges for kelp species in UK waters

(upper and lower lethal limits can be estimated as 1-2°C beyond the growth limits)

* indicates that the temperature restrictions are not known.

kelp species & data source	temperature ranges	
	Sporophyte growth & reproduction	gametophyte growth & reproduction
<i>Alaria esculenta</i> Sundene, 1962	upper: 16°C / * lower: * / *	upper: * / * lower: * / *
<i>Laminaria digitata</i> Gayral & Cosson, 1973	upper: 18°C / 18°C lower: 0°C / *	upper: 17°C / below 13-15°C lower: 0°C / 2-6°C
<i>Laminaria hyperborea</i> Kain, 1964	upper: 15°C / 20°C lower: 0°C / 19°C	upper: 21°C / below 18°C lower: * / *
<i>Laminaria ochroleuca</i> Lüning, 1990	upper: 22-23°C / * lower: * / *	upper: * / 21°C lower: * / 5°C
<i>Laminaria saccharina</i> Lüning, 1990	upper: 18°C / 20°C lower: 0°C / *	upper: 22-23°C / below 18°C lower: * / *
<i>Saccorhiza polyschides</i> Norton, 1977	upper: 24°C / * lower: 3°C / *	upper: 25°C / below 17°C lower: * / 5°C
<i>Undaria pinnatifida</i> Akiyama, 1965	upper: 28-30°C / * lower: * / *	upper: 27°C / below 25°C lower: * / *
	where two figures are shown these indicate seasonal tolerances	

Upper and lower temperature tolerances for UK species are shown in Table 9. Species of *Laminaria* have been shown to have different temperature tolerances (with consequent effects on sporophyte growth) at different times of the year. Increased temperatures during the winter months are less well tolerated than increased temperatures during the summer months (Lüning, 1990). Some species (e.g. *L. saccharina*) form temperature-adapted ecotypes, in which the temperature tolerance of the species varies with location depending on the local conditions to which the plant population has adapted (Davison, 1987).

F. CHEMISTRY

1. Salinity

The salinity of seawater has not varied much over the past 600 million years, so it is not surprising that the majority of the seaweeds will tolerate only a limited range of salinities. The sublittoral seaweeds of truly marine habitats live in an osmotically constant medium of 30-35 psu. Experimental work with a range of species suggests that the tolerance range for salinity fluctuations over periods of up to 24 h may be 16-50 psu (Lüning, 1990). Growth rates of many seaweeds are maximal at an optimum salinity, but this is usually in the range of 30-35 psu. Kelps are *stenohaline* seaweeds, in that they do not tolerate wide fluctuations in salinity; in fact, the growth rate may be adversely affected if the kelp plant is subjected to periodic salinity stress. Localised, long term reductions in salinity (possibly due to coastal construction work and drainage alterations) may result in the loss of kelp beds in the affected area.

2. Nutrients

All kelp species are thought to be efficient absorbers of nitrate and phosphate from seawater. Numerous experiments have been conducted on kelp species throughout the world in order to determine the rates at which kelps are able to take up these major nutrients and to determine the effects of changes in nutrient concentration on the growth rates of kelps (Birkett, 1993). The mechanisms of nutrient uptake are less well understood, as are the mechanisms governing the luxury uptake and storage of nutrients. When nutrients are available to kelps in amounts that are greater than needed to meet immediate metabolic requirements, nutrient uptake will continue (luxury uptake) and the excess is stored in the kelp tissues.

In the laboratory, kelp species respond to increased nutrient levels by taking up the nutrient more rapidly, and the addition of fertiliser to some kelp species (*Macrocystis*, *Laminaria japonica*) *in situ* has been reported to result in increased production (Lüning, 1990). However, all kelp species investigated to date show a similar pattern of responses to excess nutrients in that a maximum rate of uptake is reached at any given nutrient concentration. The maximum uptake rates are governed by the nutrient concentration to which the plant was previously accustomed and by the amount of light available to the plant in the hours preceding the availability of higher nutrient concentrations. There is a complex interaction between nutrient concentrations and their uptake rates, rates of photosynthesis, rates of production of DOM and POM (dissolved and particulate organic matter) and the growth rates of kelps. An increase in nutrient levels in the North Sea and the Irish Sea as well as in coastal waters throughout Europe has been observed over the past 40 - 50 years (long term data sets are few, one is continuing at the Marine Laboratories, Port Erin, Isle of Man).

- The long-term effects of increased nutrient loading on coastal kelp bed communities and the productivity of kelp plants are not known and deserve detailed investigation.

G. KEY POINTS FROM CHAPTER II

- The specific environmental requirements and physical attributes are known for only a few of the species of plants and animals found within the various kelp biotopes.

Substratum

- Kelp species are found in almost all locations where some form of hard substratum is available within the euphotic zone in UK waters.
- On mobile substrata, populations of kelp may be ephemeral.

Light & depth

- In the field, the availability of light and the light requirements of the different kelp species determine the depths at which they may be found (all other conditions being equal).
- In areas where the water is clear, light can penetrate to, and kelp plants can grow at, greater depths. Kelps may be found below 100 m in the Mediterranean, but are generally restricted to 35 m in western coastal waters of Europe and to as little as 6-7 m in the turbid waters of the North Sea.

Water movement

- Tidal currents may have a critical effect on the appearance and productivity of the kelp plants. Particularly within coastal embayments sheltered from wave action, tidal water movement can result in the growth of luxuriantly large, long-lived plants.
- *Laminaria hyperborea* is unable to survive where or when wave action is extreme because its stiff stipes are snapped.
- The morphology of kelp plants has been shown to be plastic. If kelp plants from a sheltered habitat are transferred to a more exposed environment, their growth form changes to that typical of plants in the new environment.

Temperature

- Kelp species of Western Europe are unable to tolerate large fluctuations in temperature on either a temporal or a geographical basis.
- There are temperature constraints on each phase of the life of cycle, and lethal temperatures and temperatures that limit vegetative growth and reproduction have been reported for several kelp species.

Chemistry

- Kelps do not tolerate wide fluctuations in salinity.
- All kelp species appear to be efficient absorbers of nitrate and phosphate from seawater.
- Long term effects on kelp ecosystems of increased nutrient levels in coastal waters are not known.

III BIOLOGY AND ECOLOGICAL FUNCTIONING

A. INTRODUCTION

The biology of kelp species has been well researched but the ecological role of kelp species and the interactions between the kelp beds and the surrounding ecosystems are not at all well known, either in Europe or in the world as a whole. A few long-term research programmes have been undertaken in areas where the health of the kelp based communities has major economic importance (e.g. for the crayfish, lobster and abalone fisheries of the NE Pacific, South Africa and W. Australia). There have also been research programmes where kelp is harvested on a large scale, but these have concentrated on the kelp plants themselves rather than on the ecosystem in which they grow. A comprehensive understanding of the biology and ecology of kelp species, the other species of flora and fauna and the dynamics of the kelp biotopes is essential in order that *efficient* management plans and monitoring programmes can be designed for their conservation.

At present our information on the biology and ecology of the majority of species in the UK kelp beds is such that our understanding of their functioning and ecological interactions is extremely limited, even the basic biological parameters of many of the species are unknown. Despite large numbers of sites having been surveyed, the species that are of key importance to the maintenance of kelp biotopes have not been firmly identified. Because of this, any management and monitoring plans for kelp biotopes will need to be broadly based and encompass all aspects with potential for change *in case* that change turns out to be crucial to the well being of the protected ecosystem. If an intensive, encompassing and co-ordinated research programme is undertaken in the UK, over time the management and monitoring plans for marine SACs may be refined and targeted at specific threats to species identified as key to the maintenance of the ecosystem.

This section will summarise information on the biology and ecology of the kelp species at present reported from UK waters. In terms of the biomass present in UK kelp beds, the most common kelp species are *Laminaria hyperborea*, *L. digitata*, *L. saccharina* and *Saccorhiza polyschides*, and information on these species will form the bulk of this section. Where appropriate, information on other kelp species or associated species found in the UK will be included.

B. BIOLOGICAL CHARACTERISTICS

The kelp species found around the coasts of the UK are all large brown seaweeds composed of a *holdfast* attachment to the substratum, a *stipe* and a *blade*. There are three separate genera - *Laminaria*, *Alaria* and *Sacchorhiza*.

The large blades of kelps form the most conspicuous component of the sublittoral environment. Blades may be simple and ribbon shaped (with or without a conspicuous midrib) or broad and digitate, although the blades of species that are usually digitate can be undivided under some environmental conditions (see section II.D.3.c.). Individual plants are perennial but life spans vary with species and environmental conditions, from just about 1 year to nearly 20 years. The stipes are usually round in cross section and may be stiff or flexible, but they are tough and do not snap easily. The holdfasts consist of numerous haptera (root-like outgrowths at the base of the stipe) which adhere firmly to the substratum and anchor the plant. All kelp species grow from meristematic tissue at the base of the blade and,

if this region of the blade is lost, the plant cannot grow, and the stipe and holdfast decay and are lost.

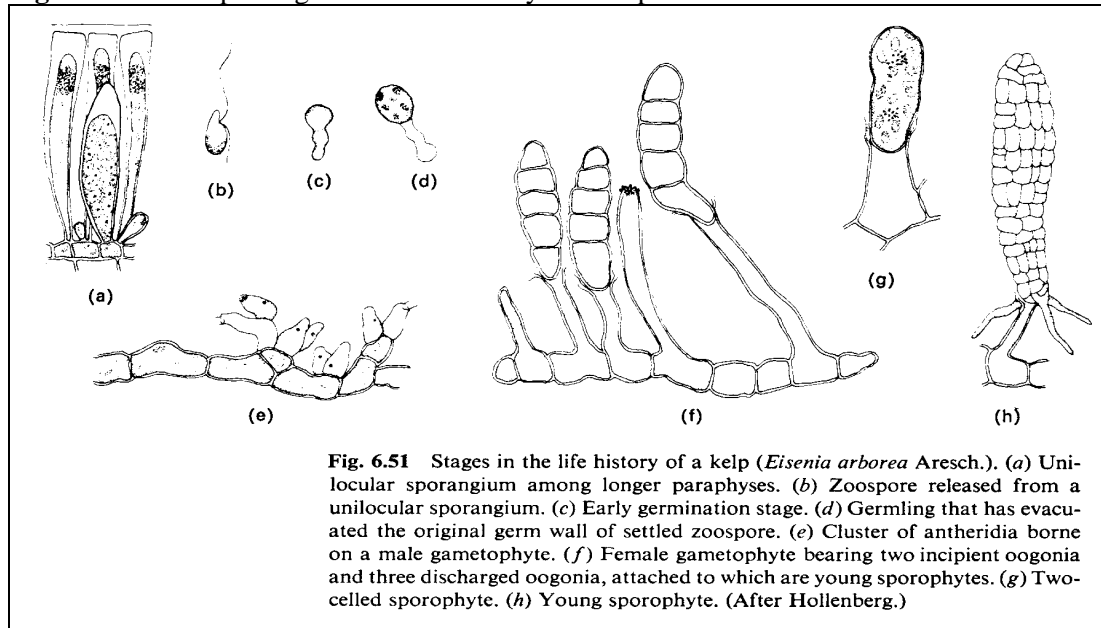
1. Life history and reproduction

a. Life history of a generalised kelp

The life histories of species of the Laminariales are composed of two morphologically distinct phases (heteromorphic), similar in pattern to the life history of pteridophytes (ferns and fern allies). The large, obvious plants are the sporophyte generation (diploid or 2N) which persist for various lengths of time and produce spores. These plants may be regarded as K-strategists since they take optimal advantage of the environmental resources and use a greater part of their annually fixed organic carbon to build up their thallus rather than allocate it to reproduction as the annual algae do. The sporophytes grow rapidly at certain times of the year, fixing enormous amounts of carbon from the coastal seawater while continually releasing DOM and POM (see section III.B.1.b).

b. Reproductive cycle of a generalised kelp

Fig. 2. Microscopic stages in the life history of a kelp



(from Bold & Wynne, 1978).

Within the spore producing tissue (see Table 10), sporangia develop (Fig. 2a.) and haploid spores (Fig. 2b.) are produced in vast numbers, but these represent a very small percentage of the annual biomass production of an individual plant. The zoospores (about 5 µm diameter, Fig. 2b.) may be transported some distance (at least 200 m) from the parent plant but lose their flagella after about 24 h (Sjötun, 1995) and settle out onto any available substratum (Fig 2c.). Male and female kelp spores must settle at a high density (within 1 mm of each other) if the maturing gametangial egg is to be fertilised (Reed, 1990).

III. Biology and ecological functioning

The zoospores develop into the dioecious haploid gametophytes, male plants producing sperm and female plants producing eggs (Fig 2 d,e & f.). The gametophytes of all kelp species are microscopic and may consist of only a few cells before the plants become fertile (Fig.2 e & f.), which can occur in 10 days under optimal conditions. The male gametophyte plants develop antheridia which produce and release sperm; the female gametophyte plants develop oogonia in which the egg develops and on discharge this is fertilised and the young sporophytes start to grow *in situ* (Fig. 2 f, g & h). Under sub-optimal conditions in the laboratory, the gametophytes may be held in a vegetative state for years and this ability may explain why kelp sporophytes are apparently able to “re-colonise” cleared areas so rapidly. On maturation of the gametophyte plants, motile antherozoids (sperm) will fertilise the sessile egg and a new sporophyte plant will start to grow from the zygote.

Table 10. Reproductive notes for sporophytes of kelp species in UK waters			
Kelp species	season of spore production	location of sori on plant	young sporophytes appear
<i>Alaria esculenta</i>	Nov - March	sporophylls on upper stipe	early spring dispersal: to 10 m.
<i>Laminaria digitata</i>	all year, maxima in Jul - Aug Nov - Dec	all of the surface except distal and proximal parts; both surfaces	spring & autumn (all year)
<i>Laminaria hyperborea</i>	winter Sept - Jan - April for 6-7 weeks	old frond; all of the surface except distal and proximal parts; both surfaces	spring dispersal: +200m. Sept - April (all year)
<i>Laminaria ochroleuca</i>	not known for UK coastal waters		
<i>Laminaria saccharina</i>	autumn - winter	central portion on blade	winter - spring
<i>Saccorhiza polyschides</i>	Oct - Mar - May	base of lamina, stipe frills, bulb	spring-summer (all year)
<i>Undaria pinnatifida</i>	spring - summer	sporophylls on stipe	autumn / (all year) dispersal: viable +48h

2. Growth

a. Biomass turnover

As a general rule, the kelp species found in UK waters grow at rates much faster than might be assumed from the size of plants present in the field. The sporophyte phases in the life cycle of members of the Laminariales grow in a manner somewhat like a conveyor belt. The meristematic tissue is at the junction between the stipe and the lamina - the further away from the meristematic region the older the cells. At the distal end of the blade, tissue is being lost continually through decay, abrasion against surrounding plants or wave action, and this represents a significant contribution to the POM (particulate organic matter) in coastal waters

(Wilkinson, 1995). As a result, the biomass that a kelp plant contributes to the coastal ecosystem over a year can be more than 2 to 3 times the biomass of the plant itself. Large portions of the blade of a kelp plant can be removed and regrowth can occur if the basal area of the blade remains, but, as the energy reserves held in the blade have been lost to the plant, regrowth is slow (Lüning *et al.*, 1973). If the meristematic or transition tissue is removed, the stipe and holdfast degenerate and the plant is lost from the population.

b. Rates of photosynthesis

The photosynthetic rate of whole kelp plants varies with the age of the plant and the time of year, but the variations in the rate of photosynthesis among a group of individuals of the same species can be greater than the rate variations of the population due to seasonal changes (Birkett, Dring & Savidge, in prep.). The rate of photosynthesis of different parts of a kelp plant depends on the age of the tissue sampled (i.e. the distance of the sample from the meristem). Net production estimates based on photosynthetic measurements suggest that kelp plants contribute significantly to the DOM (dissolved organic matter) in coastal waters (C. McQuaid, pers. comm.) as well as to the POM and that simple growth measurements in the field or the laboratory may be inadequate estimates of the growth of kelp plants.

c. Effects of light quality on kelp physiology

The absorption of light in coastal waters is much influenced by the amount of particulate matter in suspension (biotic and abiotic) as well as by the dissolved organic components which increase the absorption of blue wavelengths (see section II.C.). Wavelengths of light are attenuated differentially as a result of these factors, altering the spectrum of wavelengths available at different depths. Blue wavelengths are rapidly attenuated in coastal waters. The proportions of red and blue light within the spectrum available to kelp plants has a significant effect on the rates of photosynthesis, development and growth of the plants. Red light favours the accumulation of carbohydrates and blue light enhances protein synthesis, respiration and enzyme activation (Dring, 1988). The light-saturated rate of photosynthesis in blue light may be 50-100% higher than in red light (Dring, 1989). These effects may have a strong influence on kelp distribution and density within a kelp biotope, particularly where land drainage introduces significant concentrations of light-absorbing particles or humic chemicals into coastal waters.

d. Summaries of sporophyte growth for kelp species found in the UK

Alaria esculenta

This is a perennial plant (Table 10) which lives for about 4-5 years in the Irish Sea (T. Holt, pers. comm.) and may live for 7 years in Norway (Baardseth, 1956). Under suitable conditions of strong water flow and low wave action, plants can achieve a blade length in excess of 2 m. (D. Birkett, pers. obs. in the Narrows, Strangford Lough). Maximum growth rates are recorded in April and May (T. Holt, pers. comm.), with plants in the field (Isle of Man) growing by 20 cm a month. Plants in an adjacent rope culture system had average extension rates of 5 cm per day. In June and July the growth rate slows and the continual distal erosion reduces the plant to a holdfast, stipe and a short length of blade, in which state the plants over-winter. In the late autumn and early winter the sporophylls are produced from the stipe at the base of the blade and these persist after sporulation and remain on the plant as thickened, vegetative structures during the summer months, but their total duration is not

known. In the second year of growth, plants may become larger than in their first year (T. Holt, pers. comm.). Slow growth continues during the summer months but cannot compensate for the distal tissue loss.

Laminaria digitata

A relatively short lived perennial plant (Table 10). Mature individuals can produce blade lengths of up to 2.5 m under suitable conditions. On the Calvados coast of northern France, stipe lengths were measured for plants of the same age. In shallower water, the average stipe length was 40 cm and, in deeper habitats, 60-70 cm (Perez, 1969). Maximum rates of growth are reported for the spring and early summer months, with minimum growth rates occurring during the autumn. After their third year of growth, the size of the lamina does not increase, although plants at the end of their fourth year of growth may have laminae that are 1.5 m long, and it has been estimated from the growth of the meristematic region that, over the previous two years, the blades had produced an additional total of nearly 3 m of tissue (Gayral & Cosson, 1973).

Laminaria hyperborea

As a consequence of commercial interests, the biology of this species has been extensively studied over the years throughout its habitat range. Plants are perennial (Table 10) - at least with regard to the holdfast and stipe - and growth follows a distinct seasonal pattern (Kain, 1971b; Lüning, 1971). The period of most rapid blade growth is between December and June, when a completely new blade develops from the meristem. The old blade, delineated by a distinct constriction of the lamina, remains attached to the new, fast growing tissue until it is lost in the spring or early summer. Although the new blade does not continue to increase in size during the summer months, the metabolic activity of the plant remains high (Lüning, 1971). In the first few years of the life of a plant, the blade area and stipe length increase each year until the plant is over 5 years old (Lüning, 1971). The growth rate and length of the stipe may be reduced with depth in the kelp bed. In France and England, stipes are usually about 1 m long but, on open western coasts and in Scotland, stipe lengths in excess of 3 m have been recorded. The length of the lamina depends not only on the time of year but on the local and recent hydrographic conditions. The onset of blade growth during the winter months is an endogenous circannual response mediated by daylength (Lüning, 1990).

Laminaria ochroleuca

Published information is unavailable for this species in UK habitats; growth patterns and reproduction may be similar to *L. hyperborea*.

Laminaria saccharina

These kelps are short lived perennials (Table 10), and the age of the most distal blade tissue rarely exceeds 6-8 months. Maximum growth rates have been measured during the late winter and spring with minimum growth during the late summer and autumn (Parke, 1948; Lüning, 1979). The plants have been shown to reduce their growth rates in response to the onset of shorter days (Lüning, 1988). The overall length of a mature plant in a sheltered locality may not change much during the growth season due to the distal loss of tissue, but extension growth within the blade has been measured as 1.1 cm per day in May with a total length addition of over 2.25 m tissue per year for plants in their second growth season and somewhat less for plants in their third growth season. (Sjøtun, 1993). Many of the larger plants are lost from the population during the late summer and autumn, the annual loss of tagged plants indicating that the normal age of plants did not exceed 4 years (Parke, 1948; Sjøtun, 1995).

Saccorhiza polyschides

The plants of this species are generally described as annuals (Table 10), but would be more accurately described as monocarpic, as the plants which survive to over-winter are those which did not become fertile in their first summer. Young sporophytes appear in the spring and grow rapidly. The blades of individual plants may reach lengths of over 3 m under ideal conditions (D. Birkett, pers. obs.) and the basal “bulb” may reach a diameter of over 30 cm (Norton, 1970). Blade length increases most rapidly in the summer months (6.2 cm per week; Norton, 1970), without allowing for distal abrasion. Growth of the blade ceases at the onset of fertility, and distal decay and abrasion results in the blade becoming progressively smaller; the stipes are finally lost towards the end of autumn. The stipeless bulbs often survive over the winter months, decaying and becoming detached in the spring. The onset of sporophyte growth in the spring appears to be irradiance-dependent rather than temperature-related.

Undaria pinnatifida

This kelp has only recently arrived in UK waters (first reported on the south coast of England in 1994; R. Fletcher, pers. comm.). It is an annual species (Table 10), although possibly monocarpic. The first young sporophytes appear in the autumn and the plants grow rapidly (in suitable conditions) during the winter. Maximum growth rates are reported in the spring, at which time the plants become fertile. The fronds may reach a length of 1.65 m but start to deteriorate during the summer. By the autumn, any fronds that persist are heavily overgrown by colonial animal species.

Table 11. Life expectancy for sporophytes of kelp species in UK waters

kelp species	age to fertility	life expectancy
<i>Alaria esculenta</i>	10-14 months (T. Holt, pers. comm.)	4-7 years (T. Holt, pers. comm.; Baardseth, 1956)
<i>Laminaria digitata</i>	18-20 months, distal parts of blade only 3 years, about 50% of blade surface (Perez, 1971)	4-6 years (Gayral & Cosson, 1973)
<i>Laminaria hyperborea</i>	2-6 years, depending on the location, depth and size of individuals (Kain, 1971)	5-18 years (Kain, 1971)
<i>Laminaria ochroleuca</i>	assumed as for <i>L. hyperborea</i>	
<i>Laminaria saccharina</i>	15-20 months (Sjøtun, 1993)	2-4 years (Parke, 1948)
<i>Saccorhiza polyschides</i>	8-14 months (one year plants) 15-22 months (over-wintering)	8-10 months (bulb 14) 14-16 months (bulb 22)
<i>Undaria pinnatifida</i>	8-10 months	10-14 months

C. ECOLOGICAL ROLES IN KELP BIOTOPES

1. *Diversity of habitats, conditions and species*

a. Diversity of conditions within kelp beds

A small area of a kelp biotope (only a few meters square) may contain a variety of different small habitat areas within it, differentially exploited by various species; the substratum may be generally bedrock but with small patches (less than 1 m²) that are:

- clear bedrock,
- pockets of sediment,
- a mobile boulder,
- open rock that is flat or fissured,
- overhangs of rock,
- steep or vertical faces,

and these different substratum conditions will be advantageous to some species and disadvantageous to others. In addition, the kelp plants themselves may modify the local environment within a biotope. Kelps plants may

- act as energy dampers, ameliorating the surge effects of waves
- reduce current flow in areas of dense kelp forest
- reduce the light available to the deeper parts of the kelp bed
- reduce ambient levels of macronutrients within the kelp beds
- increase levels of DOM and POM within the kelp bed

again enabling some species to flourish at the expense of others on a small scale and leading to a patchwork pattern of species distribution within the biotope.

b. Patchiness of distribution

One of the characteristic features of kelp beds throughout the world is the patchwork of different species and groups of species that occur within the biotopes. This is particularly obvious in areas of low siltation, high water movement, and high kelp productivity (mg C m⁻² yr⁻¹). The bedrock or other substratum in such areas can appear to be covered by a multicoloured mosaic of encrusting algae, sponges, colonial tunicates and kelp holdfasts - with multitudes of other sessile and mobile species on and between them. The inherently dynamic nature of the patchiness of kelp biotopes adds to the difficulty of developing reliable and effective monitoring programmes.

Long term (ongoing) studies in South Africa appear to show that the patches in the kelp beds of are not stable (R. Anderson, pers. comm.), but that the intense competition for space results in slow but continuous changes in the patchwork and the species that form it. The complexity of the environmental structure suggests that small changes in the local conditions might result in a shift in the balance between the competing species and result in more rapid shifts in the patchwork or the development of a different series of dominant species. It is possible that minor environmental changes which allow urchin grazing to increase may permit encrusting algae to dominate for a period but that, over time, the balance would be restored.

The time scales involved in the natural dynamic variation in the species patchwork appear to be on the scale of decades to centuries in South African habitats. The apparently natural development and recovery of NW Atlantic kelp forests from urchin overgrazing also appears to take several decades.

- The corresponding time scales for the species of kelps and urchins and patch forming species of algae and animals in UK waters are not known.

c. Kelp plants as a habitat

Kelp communities are three dimensional in structure. The kelp plants themselves usually become the habitat for other marine species as the mature plants:

- provide a vertical addition to the sea bed, effectively increasing the surface area and habitat variety
- provide a surface to which other seaweeds can attach; other organisms then feed on these seaweeds
- can be grazed directly by organisms such as *Helcion pellucidum*
- provide attachment sites for sessile species of animals which in turn are food for other animals
- holdfasts shelter many species of animals from a wide range of taxa

d. Species present in infralittoral biotopes with kelp.

The most comprehensive data sets available on the species found in UK kelp biotopes are the results of the MNCR surveys that have been undertaken during recent years. The database was consulted during the preparation of this report, in order to obtain some indication of the variety of animals and plants that are found within kelp biotopes. The complete species list as of March 1998 (separated into the 5 biotope complexes) is included as a reference source in Appendix 5. The results of other surveys of kelp beds which may have been undertaken around the UK are not published or not readily available.

The MNCR database aims to provide an indication of the species to be expected within a given kelp biotope and will of course list the characteristic species for that biotope. In addition to the limitations discussed in section I.E., the following specific weaknesses of the species list for kelp biotopes should be noted:

- errors of data entry have occurred (intertidal algae and lichens appear on the list)
- polychaete species are very sparsely reported although they make a major contribution to the biodiversity, biomass and community structure within the kelp bed (Rinde *et al.*, 1992). Since many polychaetes are small, live in burrows or within the holdfast, or are only active at night, it is perhaps not surprising that the frequency with which they are recorded during biological surveys does not reflect their significance or diversity in the kelp biotopes.
- holdfasts were not systematically sampled during MNCR surveys so the database does not reflect the diversity of species within this intensively exploited niche (D. Connor, pers. comm.)
- *Homarus gammarus* (lobster) is reported at only a small percentage of the survey sites, yet lobster fishermen will frequently set pots for preference in areas of kelp forest and reported catches suggest the species is more common than the database would suggest there are some examples of incomplete identification within the database, e.g. coralline algae (as "Corallinaceae") have been recorded at more than 50% of all sites within the kelp biotopes.

However, only 19 of the more than 45 species of coralline red algae present in UK waters have been listed, whereas the taxonomic records (Irvine & Chamberlain, 1994) suggest that few species of coralline algae in the UK are found outside kelp biotopes

An additional weakness is that of the temporary or seasonal presence or absence of some species in kelp beds, either due to a migratory habit or because of a heteromorphic life history. Of the species listed it is possible that some are found in kelp beds only on a temporary basis while other species may not appear in the database having been absent or cryptic during the period of data collection.

2. *Community structure within kelp biotopes*

a. Introduction

As with terrestrial forests, the kelp beds contain a series of stratified habitats within them, and the flora and fauna associated with a kelp forest may occupy one or more of these vertical subdivisions. The relationships within and between the strata are complex because each will modify the water flow and irradiance available to the other layers. Furthermore, the species composition of a habitat stratum will vary not only with the geographical location of the biotope but also with depth within a single kelp bed. It is clear that kelp biotopes often have an extremely diverse fauna and, possibly as a result of this (daunting) diversity, there does not appear to have been any single investigation of the entire range of species in a single location. The epibenthic flora and fauna is now relatively well known and could possibly be used to demonstrate some environmental trends and gradients; the fauna of holdfasts is also fairly well known from a few locations. However, the meiofauna and the ambient plankton populations in kelp beds around the British Isles are more or less unknown.

b. Pelagic habitat in a kelp bed

i. Planktonic

Very little specific information is available about the plankton communities in areas dominated by kelps (or indeed other algae). It can be assumed that these communities will be similar to the general plankton of inshore areas but with larger inputs of larval stages from species with benthic-pelagic life cycles. Additional differences from the plankton in non-kelp biotopes would be the contribution from species with tidal or diurnal behaviour patterns. The former will lead to large seasonal inputs of spores, gametes and larval stages from the biota of the kelp biotopes and this input will be diluted with distance from its habitat of origin. The tidal or diurnal input will add some additional diversity to the plankton of the kelp biotopes on a cyclical basis; but to date this has been documented only in sea-grass communities (Bell *et al.*, 1983) and not in kelp biotopes. It is possible that some planktonic species such as mysids and the arrow worm *Spadella* may be more common in kelp areas than just outside them (P.J.S. Boaden, personal observations). The abundance of filter-feeding and impingement-feeding organisms (e.g. sponges and bryozoans) within kelp biotopes highlights the importance of planktonic input to the benthic community. Wulff & Field (1983) have demonstrated the particular importance of phytoplankton during downwelling conditions in Benguela kelp beds.

ii. Nektonic

There is a paucity of information on the roles of fish, diving birds and mammals in the kelp biotopes of northern Europe, although many divers have observed that conspicuous fish such as wrasse and pollock are common amongst kelp, in addition to more or less benthic and cryptic fish species such as blennies and gobies. Such fish can be important in the diet of diving birds such as cormorants and of seal and some otter populations. Elsewhere, the importance of the sea-otter and of benthic wolffish in the functioning of kelp ecosystems has been documented (Mann, 1982). These animals consume large numbers of sea urchins in the kelp habitats of North America.

c. Kelp forest habitat

The term “kelp forest” is generally used to refer to the part of the kelp biotope which lies between the lowest tides and the depths where kelp plants become less densely distributed. In the main forest area, kelp plants are densely packed and the blades of the tallest plants effectively form a canopy, casting smaller kelp plants, stipe epiphytes and understorey algal species into deep shade. The kelp canopy may intercept as much as 90% of the incident irradiance, with the result that many algal species which are normally confined to greater depths with low irradiances, are able to migrate into shallower waters.

In the upper part of a kelp forest, several kelp species may be found, depending on the wave exposure at a particular site, however, the comments in this section refer to *L. hyperborea* unless otherwise stated.

i. Flora

There is a zonation pattern of the epiphytic algae down the stipes of kelp plants, especially on plants of *L. hyperborea*. and this zonation pattern shifts and the component species change, depending on the stipe length and the depth at which the kelp holdfast is attached to the substratum (Harkin, 1981; Whittick, 1983; see also section III.C.2.e.i, and appendices 3 & 4). The epilithic species that are found vary with geographic location, water depth, canopy density and benthic irradiance, and also as a result of interactions with the grazing species of the site. As a result the species that are found form a diverse population. A list of species is given in the MNCR data set (Appendix 5).

ii. Fauna

Erwin *et al.* (1986; 1990) described six depth-related categories of faunal distribution which could be distinguished among the common species in this densely populated part of a kelp biotope.

Table 12. Common faunal species with different depth distribution patterns within kelp forests in Northern Ireland	
Restricted to shallow water (<10m) and there common Moderately common throughout.	<i>Halichondria panicea*</i> , <i>Amphilectis fucorum</i> <i>Cancer pagurus</i> , <i>Gibbula cineraria</i> , <i>Alcyonidium diaphanum</i> , <i>Membranipora membranacea</i> , <i>Henricia oculata</i> , <i>Aplidium punctum*</i> , <i>Dendrodoa grossularia*</i> , <i>Botryllus schlosseri</i>
Present throughout but commoner with increasing depth Ubiquitous and very often abundant	<i>Electra pilosa</i> , <i>Caryophyllia smithii*</i> <i>Obelia geniculata</i> , <i>Calliostoma zizyphinum</i> , <i>Asterias rubens</i> , <i>Echinus esculentus</i>
Present in deeper parts (10-20m) where they may be very common, infrequent shallower	<i>Dysidea fragilis</i> , <i>Alcyonium digitatum</i> , <i>Leptasterias mulleri</i>
Present where kelp forest extends to 20-30m	<i>Tethya aurantium</i> , <i>Polymastia boletiforme</i> , <i>Axinella infundibuliformis</i> , <i>Stelligera stuposa</i> , <i>Lophon ingalli</i> , <i>Halecium halecinum</i> , <i>Sertularella gayi</i> , <i>Abietinaria abietina</i> , <i>Aglaophenia tubulifera</i> , <i>Caberea ellisii</i> , <i>Bugula flabellata</i> , <i>Bugula plumosa</i> , <i>Corella parallelograma</i> , <i>Ascidia mentula</i> , <i>Polycarpa pomaria</i>
* These species were not found in kelp forest located in regions of decreased wave exposure and more turbid water. Data from Northern Ireland survey, Erwin <i>et al.</i> 1986; 1990.	

d. Kelp parkland habitat

In the lower infralittoral, where a suitable substratum continues into deeper water, the density of the kelp plants is reduced, probably as a result of light limitation. The extension of kelp biotopes into deeper water may, however, be prevented by the pressure of urchin grazing or by the increased rate of sedimentation due to reduction of water movement with depth. Individual kelp plants may become very large in this part of the biotope.

i. Flora

In the lower parts of the kelp forest and into the park biotopes there is little change in the patterns of species distribution on the kelp stipes. However, the biomass of individual epiphytic plants increases and in the habitat as a whole (rather than on individual stipes) the diversity of epiphytic algae increases.

ii. Fauna

All the species listed in Table 12, except those in the first category, also occur in the kelp parkland, both on and among the kelp plants. In addition, there are many species which are

more or less characteristic of this lower part of the infralittoral zone and other species which extend upwards from the circalittoral zone. Hence, the kelp parkland biotopes are frequently the most species-rich areas to be found in the sublittoral zone. The precise array of animal species will depend on a number of factors, principal among which are the types and patterns of substrata and the localised hydrodynamic regimes. For example, many species are found more frequently within kelp biotopes that are on bedrock than within those that are on boulders; a few species show the reverse preference. Erwin *et al.* (1986) cite the following examples:

Table 13. Fauna with apparent substratum preferences within kelp parkland biotopes in Northern Ireland	
Bedrock	Boulders
<i>Pachymatisma johnstonia</i>	<i>Galathea nexa</i>
<i>Hemimycale columella</i>	<i>Xantho pilipes</i>
<i>Alcyonium digitatum</i>	<i>Ctenolabrus rupestris</i>
<i>Sagartia elegans</i>	<i>Galathea spinosa</i>
<i>Liocarcinus puber</i>	<i>Parasmittina trispinosa</i>
<i>Polyclinum aurantium</i>	
<i>Polycarpa rustica</i>	
<i>Myxilla incrustans</i>	
<i>Haliclona rosea</i>	
<i>Urticina felina</i>	
<i>Actinothoe sphyrodeta</i>	
<i>Leptasterias mulleri</i>	
<i>Botrylloides leachii</i>	

Data from Northern Ireland survey, Erwin *et al.* 1986; 1990

e. Kelp plants as a habitat

Kelp plants themselves can form the habitat for numerous species of understorey algae, and a large number of invertebrate species exploit the plants as a secure habitat - in much the same way as forest trees support a variety of other forms of plant and animal life.

i. Epiflora

A wide variety of species of algae can be found on the stipes of *L. hyperborea*. Epiphytic algae are not as commonly found on the stipes of other kelp species and only the most rapidly growing of the opportunistic species are able to colonise the blades of kelps. In the upper infralittoral, where the kelp plants are exposed to wave action, surf and surge, where the upper portions of the stipe may be exposed to the atmosphere during periods of low water and where irradiance levels may become high, there are fewer epiphytic algae than may be found in the deeper parts of the kelp bed. In addition to the mechanical disturbance, irradiance and grazing pressure are thought to affect the distribution of epiphytic algae.

Table 14. Kelp species in UK waters as habitats for epiflora and epifauna			
kelp species	holdfast	stipe	Blade
<i>Alaria esculenta</i>	not known	algae; but uncommon	young: not colonised old: <i>Audouinella alariae</i>
<i>Laminaria digitata</i>	holdfast fauna is very diverse: isopods,	algae; uncommon, but (<i>Palmaria palmata</i>)	hydroids & bryozoans
<i>Laminaria hyperborea</i>	polychaetes, crabs, gastropods, bivalves, amphipods, etc.; older plants have larger holdfasts which have more species - 389 reported from one kelp bed (Dauvin, 1997)	algae, esp. on older plants; irradiance related zonation patterns; diverse fauna 82 species from one kelp bed (Dauvin, 1997)	hydroids & bryozoans may cover 20% of the blade
<i>Laminaria saccharina</i>		algae, but uncommon	rarely colonised
<i>Saccorhiza polyschides</i>	> 2,000 individual animals per holdfast	algae, but uncommon	hydroids & bryozoans
<i>Laminaria ochroleuca</i>	not known	not known	not known
<i>Undaria pinnatifida</i>	not known	not known	by end of season blades colonised by tunicates, bryozoans

Blades: In many habitats the blades of kelps are remarkably free from macroalgal epiphytes, however, the blades can be important hosts for microalgae as epiphytes and endophytes. *Myrionema corunnae* is only found on *Laminaria* blades while *Pogotrichum filiforme* and *Chilionema* spp. are mainly restricted to kelp blades. When extension growth of the blade has slowed, a number of opportunistic species may colonise the distal portion of the blades, particularly in areas where there is little wave action. *Enteromorpha* spp., *Ulva* spp., *Ectocarpus* spp. and *Pilayella littoralis* have been noted (D. Birkett, pers. obs. Strangford Lough).

Stipes: The stipes of the long-lived *L. hyperborea* are frequently heavily epiphytised by a wide range of smaller seaweeds, especially foliose red algae. The epiphytic species which are found vary with the geographic location of the kelp bed. The distribution patterns of species on kelp stipes follows a pattern related to the light available on the stipe and the number of species increases with the age and length of the stipe. As a result, the structure of the epifloral community varies with the holdfast depth and the height of the adult kelp plant (see Appendix 3). The spacing of the kelp stipes of the host plants also influences the epiphytic algae - where stipes are closely spaced, the foliose epiphytes are abraded as the stipes are agitated by the waves and currents. The algae are not evenly distributed over the stipes, but there is a biomass concentration in the top 10-20 cm of the host stipe.

ii. Epifauna and endofauna

There are several physically distinct parts of the kelp plant which are exploited by animals as a habitat. Each supports a different type of community consisting of possibly thousands of individuals from hundreds of different species, and all physically supported by a single individual kelp plant. The complexity of the kelp plant as a habitat has long been recognised but little modern research has been published, so the available information is mostly of a descriptive nature. Relatively little information on kelp epifauna is available but it can be assumed the species concerned show niche segregation and competitive hierarchy as does the epifaunal population of *Fucus serratus* (Seed & O'Connor, 1981).

Two important points that should be noted with regard to epifaunal and endofaunal populations are that:

- it is possible that different kelp species support a different selection of epifaunal and endofaunal species.
- it is probable that some if not many of the animal species found have specific sensitivities which would be of use in an environmental monitoring and conservation management role.

Holdfasts: Jones (1971) listed up to 53 macrofaunal invertebrate species obtained from an individual holdfast, and Moore (1971, 1973a,b) listed and analysed the distribution of numerous meiofaunal and other species, especially amphipods from this habitat. Both these authors have considered the possible effects of pollution on this faunal community but experimental results are lacking. Siltation of the holdfast niche is considered to be a particularly important factor which might be detrimental to the species diversity in the holdfast. Other work on holdfast fauna includes papers by Edwards (1980) and Sheppard *et al.* (1980). The bulbous holdfasts of *Saccorhiza* are known to be able to shelter large organisms such as the squat lobsters *Galathea*, and the clingfish *Apletodon* (Moore, 1983).

Stipes: The stipes of kelp plants in the upper part of the forest area are often relatively free of epifauna, possibly as a result of the greater effects of wave action and surf on the shallower plants. This is possibly the reason why kelp species found in exposed biotopes (high wave energy) tend to be "cleaner" than those in more sheltered areas, rather than that the species themselves do not form a suitable habitat.

Apart from often supporting an assemblage of smaller algae, kelp stipes frequently carry an array of epifaunal species, the abundance and composition of which varies with kelp species and location. Sponges, hydroids, bryozoans and tunicates may all be common - especially on plants of *L. hyperborea* in areas of relatively strong currents. Many of the species which inhabit the stipe are colony-forming, but solitary or stolon connected tunicates are also common. The blue-rayed limpet (*Helcion pellucidum*), which is commonly found on *Laminaria* species and sometimes on *Saccorhiza*, feeds on kelp tissue and can weaken holdfasts sufficiently to make them more susceptible to mechanical damage (Kain & Svendsen, 1969). The epiphytic algae on the stipe will, in their turn, play host to an array of meiofaunal species, the abundance and diversity of which will increase with the structural complexity of the epiphyte community (Hicks, 1980).

Blades: In contrast to the stipes, kelp blades are often relatively clear of visible epibiota as the blade tip is constantly abraded and replaced by younger tissue (see section III.B.1.a). However, a number of opportunistic hydroid, bryozoan and other species may settle on the

blade. Thus, the blades of *Laminaria hyperborea* are a preferred settlement site for the bryozoan *Membranipora membranacea* (Ryland & Stebbing, 1971) and *L. saccharina* is settled by the serpulid *Janua pseudocorrugata* (Knight Jones & Knight Jones, 1977). The hydroid *Obelia geniculata* is also common on the blades of kelp plants (Erwin *et al.*, 1986).

Tissue: A few meiofaunal species may actively burrow into kelp. Benwell (1981) has shown how the nematode *Monhystera disjuncta* may help weaken the distal areas of kelp where it feeds on decomposition-associated microbiota.

iii. Microflora and microfauna

Nothing is known of the possible components, associations or ecological importance of the fungi, unicellular algae, protozoans or bacteria which may be associated with kelp plants.

f. Benthic habitat

i. Introduction

Kelps occur under a wide variety of hydrodynamic conditions, hence the substrata may differ widely (igneous or sedimentary bed rock; sand or mud with embedded pebbles, Connor *et al.*, 1995). A number of different substrata often occur within small areas of the sea bed; fissured bed rock may protrude in an area of boulders lying on shell gravel, for example. The benthic fauna in such sites would include species characteristic of rock, rock crevices, boulders (upper and undersides), sediment and phytal habitats.

It appears that no list is available of species which are characteristic of, or present in, areas of sediment within kelp beds, although many of such species can probably be identified from records for epilithic and epiphytic fauna. Further to this, it would seem that the ease of identifying any characteristic species, relates (negatively) to their spatial separation from the kelp. Kelp plants are usually common only where attachment to boulders or bedrock is possible. Hence the majority of records for kelp associated benthos, apply only to areas of hard substrata. The species concerned may be limited to the infralittoral or extend from or into the sublittoral fringe, or may extend from or into the circalittoral.

The principal factor governing infralittoral faunal distributions is thought to be the hydrodynamic regime; this factor has been implicitly used in attempts to classify marine benthic habitats for at least a century (Forbes 1859; Hiscock & Mitchell, 1980). Extensive lists of epilithic macrofauna are to be found in the numerous reports of various authors to the Marine Nature Conservation Review (see JNCC reviews) from 1987 onwards and many species are listed in Appendix 5.

ii. Understorey flora

The understorey flora of kelp beds varies with depth and geographical location and may be depauperate (as in silted habitats) or very rich. The zonation patterns of the understorey algae are related to the available light rather than to the physical depth. Some indication of the complexity of the community is illustrated by Fig. 3, where the kelp forest peters out at a depth of about 7 m. and the lowest depth of algal growth is 15 m. due to the turbidity of the

local water conditions. With few exceptions, algal surveys have been confined to the summer months and, although this is generally a good season for recording algae, there is the drawback that species which are recognisable only during a winter reproductive phase or which have a phase which is most conspicuous in winter (e.g. *Halymenia latifolia*) may not be recorded.

The kelp species forming the canopy will of course vary around the UK as well as with the local conditions of wave exposure and water movement. In the upper fringes of the kelp bed the low shore *Fucus serratus* may be found and in areas sheltered from wave action, the upper regions of the kelp forest may also include large plants of *Halidrys siliquosa*. Throughout the kelp beds of the UK, smaller plants of several species of kelp form a significant part of the understory flora. These are not necessarily young plants (Kain, 1971) but may be small in size due to light limitation below the canopy. A similar phenomenon is well recognised in terrestrial forests, where small trees in the understory are able to take advantage of additional irradiance available when the canopy is lost due to the removal of mature trees.

In the zonation diagram of the understory algae of kelp forests in Helgoland (Fig. 3), Lüning (1970; 1990) illustrates more than 20 species of algae that are commonly found, excluding the kelp species themselves and the several species of encrusting algae. The species present in the understory of UK kelp beds vary tremendously with depth within a site (if the algae are on the kelp stipes) and within a particular kelp bed (Hiscock, 1984). The species which may form part of the understory flora show considerable variation with geographical location in the UK (Maggs, 1986) as is indicated in Appendix 4.

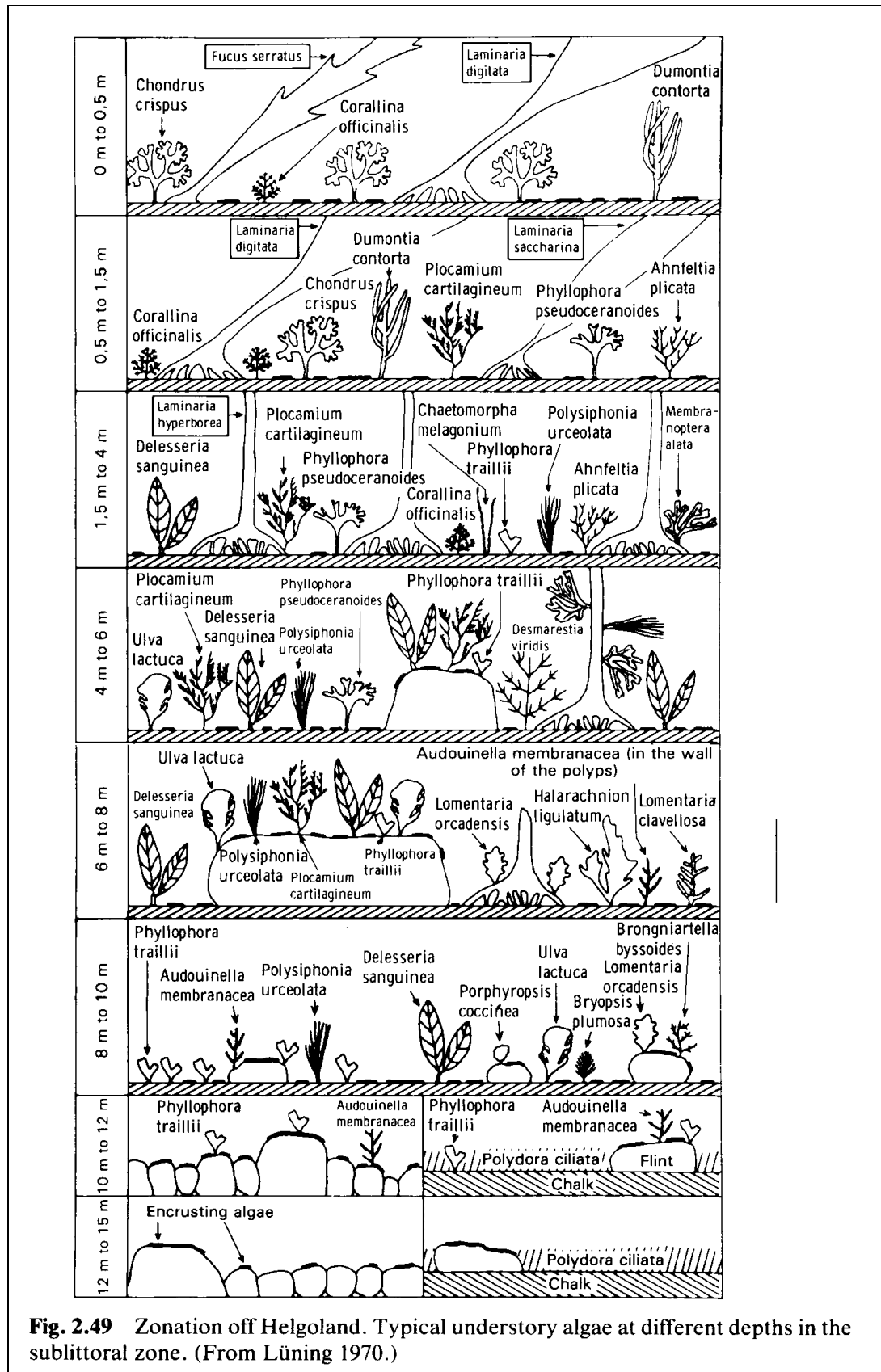
iii. Benthic fauna, attached

There appear to be no species of sedentary fauna which are specific to the kelp biotopes. It is probable that kelp plants and other algae are in direct competition with the colonial tunicates, sponges etc. for space on the substratum. Any coastal marine species which can tolerate the conditions of water movement, siltation and the temperature range within the particular kelp bed is likely to be found there if space is available for attachment. As with the flora associated with kelp beds, there are some species with distinct geographical ranges, which are found in either the warmer or the cooler areas of UK coastal waters. For many of the benthic fauna however, the temperature tolerances have been assumed from recorded distributions. Inadequate reporting of the species range and miss-identification of difficult species may result in incorrect geographical ranges having been suggested. Little experimental work on temperature tolerances of the faunal species has been attempted either for the sessile adults or for the larval forms.

iv. Benthic fauna, mobile

The wide range of habitats, algal species and potential prey species within a kelp habitat enables a wide range of mobile species to be found in kelp beds. It is likely that, for many of these species the records are not representative, mobile species are able to avoid sampling devices and respond to the presence of recording divers by hiding. A true picture of the mobile species present in terrestrial forests has been obtained by patient and intensive recording over long periods of time and seasons. As yet this has not been a practical proposition within kelp beds and effective alternative methods for data collection on mobile species

Fig. 3. Typical understory algae at different depths in the sublittoral zone off Helgoland (from Lüning, 1970; 1990).



have yet to be established. The MNCR database includes 81 listings for amphipods but only 3 species have been identified at more than 1% of the kelp sites recorded. Given the enormous numbers of amphipods which can be obtained by intensive sampling, this would seem to be a classic instance of the under-representation of motile benthic fauna in the records.

v. Fauna associated with other fauna

Most, if not all, animal species provide habitat for further species either via creation of biogenic structures or by carrying epifauna, commensals or parasites. Some of these relationships are very specific (e.g. the hydroid *Hydractinia* on hermit crabs or parasitic copepods in tunicates). Others may be more general, such as the occurrence of meiofaunal species on the surface of epifaunal colonies (as has been shown for *F. serratus*, Boaden 1995). This level of community structure is poorly understood due to the wide range of species involved and the unpopularity of such research with funding agencies and scientific journals.

3. *Keystone and associated species*

The available literature indicates that the keystone species in kelp biotopes are likely (hypothesis only) to be the dominant algae themselves, and the grazers - especially urchins of various species. A great deal of observational work (and some experimental work) exploring the expected interactions between sea urchins and kelp plants has been undertaken in various parts of the world (for example, in Northern Europe, *Echinus*, *Paracentrotus* and *Strongylocentrotus* (Jones & Kain, 1967; Hiscock, 1983; Sivertsen, 1991; Rinde *et al.*, 1992). Predators of urchins, such as lobsters (*Homarus*) and wolffish (*Anarhicas*), have also been studied in detail in several areas. In Alaskan kelp forests, the sea otter has been shown to be the controlling factor for the local populations of urchins (Dayton, 1975). Urchins also graze the understorey algae in kelp biotopes, and some species preferentially graze red algae. There has been little research published on the interactions between kelps and urchin species in the UK and none on interactions between urchins and other algae or urchin predators.

a. Kelp

The population dynamics and biology of several of the kelp species in the UK are relatively well known. *L. digitata* and *L. hyperborea* are species that are harvested commercially and as such considerable research effort has been undertaken in the past into the recovery of the age structure of the population and the growth rates of the plants in areas that have been harvested (see Chapter V). Without kelp plants, not only would there be no kelp biotopes but it is probable that much of the area of the coastal zone which is fuelled by the primary production of the kelp forests would be ecologically damaged.

b. Urchins

A very obvious change that has been noted in kelp forests throughout the world is that, either at a certain depth (Jones & Kain, 1967) or in an area of kelp bed at a certain time, the kelp plants are lost and the bedrock becomes covered with encrusting coralline algae. The populations of the local species of sea urchin increase at the same time. These kelp free areas within or adjacent to kelp forests are frequently referred to as "urchin barrens" and may remain free of kelps for many years. In various parts of the world, the local species of sea urchin are thought to be responsible for much of the grazing of juvenile kelp sporophytes (for

more information see section IV.B.3). Grazing effects on the kelp gametophytes are not known. Where urchins have been removed from an area in which kelps have been replaced by an urchin barren, the area is re-colonised by kelps (Lawrence, 1975).

c. Blue-rayed limpet

Reports and observations of *Helcion pellucidum* on kelp plants in the UK are widespread although the available literature is sparse. A careful examination of the blades, stipes and holdfasts of kelp plants suggests that at any particular site at least half the kelp plants may be hosting one or more of these small, tissue destroying limpets. Since the paper by Kain & Svendsen (1969), only one study on this species has been published (McGrath, 1992) and this is based on studies in the south-east of Ireland. *H. pellucidum* appears as newly settled spat on the encrusting coralline algae of the low shore between February and April, after which period the growing limpets migrate to the fronds of macroalgal species. There is a seasonal pattern to the species that form the habitat for this limpet. Until August, *Mastocarpus stellatus* is the major host species for the juveniles, after which the limpet is more commonly found on *Himanthalia* fronds and on kelps. Growth rates were most rapid for those individuals feeding on kelps. The largest (oldest) limpets are found within the holdfasts of kelps, protected by the whorls of haptera.

d. Predators

Lobsters, crabs and some fish species are known to consume molluscan and echinoderm herbivores, but which species, in what quantities and with what effect on the population structures of the prey species is not known. In some instances, the trophic level and the dietary habits of even the most common and obvious animals in the kelp biotope are not known.

4. Nursery areas

Kelp biotopes, with their enormous numbers of species, high biomass and high rates of productivity will be important nursery areas for a diverse range of species. It is likely that juvenile forms of all the animals that are present as adults in the kelp bed make use of the habitat as a nursery area. Rinde *et al.* (1992) state that the kelp beds in Norway are a nursery area for gadoid species. In addition, unknown numbers of species may make use of the kelp beds during only a part of their life cycle and the temporary nature of their presence may mean that they do not appear in species survey data sets. Specific information on the extent to which UK kelp biotopes are used as nursery areas for animal species is not known.

5. Flora and fauna interactions

a. Introduction

Kelp forests are a very species-rich environment (see Appendices 4 & 5) with more than 1,800 species having been recorded from kelp biotopes in UK waters. It is possible that many of these species are common within a given kelp bed but that due to the patchy nature of species distribution and the difficulties encountered in the detailed identification of species, the true diversity is inadequately reported. The high productivity of kelp forests ($\text{mg C m}^{-2} \text{ yr}^{-1}$) in comparison to other marine biotopes (Mann, 1972b) suggests that the surrounding

coastal areas are dependent on the kelp biotopes as a major source of food energy. 90% of kelp production is estimated to enter the detrital food webs as POM or DOM, being exported from the immediate area of the kelp bed (C. Hurd, pers.comm.).

In terms of direct and possible indirect ecological interactions between species in the kelp beds:

- relatively little research effort, world-wide, has been directed at these topics, although data are available for some interactions of commercial significance
- for the majority of the 1,800+ species listed for UK kelp biotopes, we can only make hypotheses about their ecological interactions

Research conducted in terrestrial habitats has shown that the interactions between species within a habitat are sensitive to relatively small shifts in the populations of interacting species and the natural fluctuations in the physical environment.

b. Herbivory

i. Urchins and understory algae

It has been suggested that the grazing activities of the several species of sea urchin found in UK kelp beds are a critical factor in the maintenance of the heterogeneity of the understory flora. Mixed grazing of terrestrial grassland (sheep, rabbits, horses, cattle) is known to maintain a high diversity of plants in the sward, but some conflicting evidence has been obtained from experiments in kelp beds. Vost (1983) examined the effect of urchin grazing on the understory algae on the rock surface of a *L. hyperborea* forest in the Isle of Man. The understory algae showed a patchy distribution prior to the removal of the urchins, and after 6-10 months this patchiness decreased. Algae with single attachment points became more frequent in the urchin free area and the total biomass and species richness of epilithic species increased.

The red algae form the bulk of the species in the undercanopy and understory of the UK kelp beds. Aquaculture feeding preference experiments have been conducted with several urchin species around the world, and urchins often show a preference for red algae as food. In the west of Ireland, *Paracentrotus lividus* has been successfully reared using *Palmaria palmata* (P. Heath, pers. comm.). It is possible that the upper stipes of *L. hyperborea* are relatively heavily epiphytised as a result of the lower portions of the stipes being more readily accessible to urchins for grazing. The upper part of the stipe is moved about more by waves and currents and this may dislodge the grazers, or this pattern of biomass distribution on the stipes may be irradiance related (see also section III.C.5.d.).

ii. Other grazing species

Overall, within kelp beds there are relatively few species that are directly grazing either the kelp or the understory algae as the enzymes required to directly utilise algae as food are not common. Those species able to graze directly on the kelp include the gastropods: *Gibbula* spp., *Littorina* spp., *Acmaea* spp., *Haliotis tuberculata*, *Helcion pellucidum*, *Lacuna* spp., *Aplysia* spp. and the Rissoidae, together with some amphipods and isopods that have the necessary laminarinases and alginase-lyases required for this diet (Dauvin, 1997).

c. Predation

Identification of predatory species within the kelp bed biotopes is incomplete. The complex food webs that occur within these ecosystems have not been explored in any detail. Some species are known to prey on others (starfish on mussels for example) but, other than observational records of interactions between a few groups of species, very little else is known of the predator-prey interactions for the diverse assembly of species present in kelp beds. Predator-prey interactions have been studied in depth for numerous groups of species in terrestrial habitats and it has become apparent that the relationships between predator and prey are sensitive indicators of the conservation status of the habitat. More detailed studies in kelp biotopes may therefore have considerable conservation value.

d. Shading

i. Kelps and kelps

The blades of mature kelps in the kelp forest form a canopy layer which, under certain conditions, may cut off as much as 90% of the incident irradiance. Any young sporophytes that are able to establish within the kelp forest are thus able to grow only slowly due to the dense shading. As a result there can be a bimodal size-frequency distribution of kelps in a stable forest, plants of the same age either becoming part of the canopy-forming community or part of the understory flora (Kain, 1963b; 1977). The bimodal (or trimodal, Rinde *et al.*, 1992) population structure does not apply in the deeper kelp biotopes (parkland) where the plants are so well spaced that a dense canopy does not develop.

ii. Kelps and understory algae

The deep shade cast by the kelp forest restricts the development of species with high light demands. Furthermore, those species of algae which would be restricted to the lower infralittoral in kelp-free areas are able to compete more effectively in the reduced light levels of the forest and so are found at lesser depths than. The removal of the canopy results in major changes to the species composition of the understory algae in the area (Rinde *et al.* 1992) and to the relative biomass of different understory species and epiphytic species (Harkin, 1981).

e. Spatial competition and patchiness

In most kelp biotopes there is evidence of strong competition for space, especially for space on a favourable substratum. Competition may occur at a number of levels within the community, for example:

- among kelp species and individual kelp plants of a single species
- between kelps and substratum-colonising species of animals and plants
- between colonial animals and encrusting algae

If a sufficiently large area (hectares) of a pristine kelp biotope is completely surveyed (rather than sub-sampled) at yearly intervals, the species diversity is unlikely to fluctuate greatly over time. At most, the number and variety of species present in the area will vary around a “typical” community structure. However, if the area were sampled on a smaller scale (m²) the spatial interactions between different life forms and different species would be observed, with sample sites showing shifts in species composition and diversity over time. The interactions

between species which are competing for substratum result in the complex patchwork of species that is a characteristic of so many kelp biotopes. Furthermore, this competition for space between individuals and between species is dynamic, resulting in a constantly changing patchwork of species covering any suitable substrata within the biotope. The forces driving the development of these dynamic patterns and the time periods over which the various species and population changes take place are not known.

Natural or human mediated changes in the local conditions within a kelp biotope are thought to result in (often) slow but sweeping changes in the populations and species present, shifting between several extreme patterns of species domination. An understanding of these patterns and the forces driving them would be a very useful tool for the monitoring and management of these complex biotopes.

D. BIODIVERSITY ASPECTS

1. Introduction

There is a remarkable biodiversity within the kelp bed ecosystems of the UK. Over 1500 benthic faunal species have been reported to date (March 1998) from kelp biotopes in UK waters (Appendix 5). In addition, there are possibly 400-500 macroalgal species and unknown numbers of microflora, microfauna, protozoan and fungal species.

Most biological surveys have, of necessity, been restricted to readily observable and readily identifiable species. The difficulty of obtaining statistically representative samples of the flora and fauna within a kelp bed is daunting. With so many different microhabitats within a site, establishing the range of species that might be representative is very difficult indeed.

The MNCR species list (see Appendix 5) provides a good foundation (see section III.C.1.) from which lists of species anticipated at a site within a known kelp biotope may be constructed. However, the species present at a particular location are a reflection of the unique environmental conditions at that site and, as such, the database is only a starting point for the determination of the biodiversity of a site.

The concept of diversity indices may be useful as a preliminary approach to establishing a baseline of diversity for monitoring specific sites. However, the diversity index alone is not a sufficiently sensitive tool for monitoring changes within a biotope as the reproducibility and reliability of the method is strongly related to the time, effort, and specific personnel conducting the survey.

The wide variety of species which are known to be found within kelp biotopes could provide a base-line from which it may in future be possible to select species with known:

- distribution patterns
- chemical sensitivities
- temperature and salinity limits
- seasonal patterns of growth and reproduction
- irradiance requirements
- suspended or settling silt tolerances
- hydrographic requirements

These selected species would then serve as sensitive biological indicators of the conservation status of the habitat within a monitoring programme. Unfortunately, at present the information listed above is known for only a handful of the thousands of species found within kelp biotopes.

- The research into and the development of the use of biological indicator species within monitoring programmes should receive a high level of priority.

2. Taxonomic considerations

Within the kelp biotopes in UK waters are species which are representatives of almost every taxonomic phylum in the classification systems presently in use. The correct identification of species is needed in order to determine the biodiversity of a site, but:

- in many kelp beds, at certain times of the year, it is even difficult to distinguish between *L. hyperborea* and *L. digitata* without taking tissue samples
- the numbers of different but closely related species within kelp biotopes are large
- the consistent recognition and identification of any organisms, other than the most obvious and common, requires extensive taxonomic expertise (in each kingdom and phylum)
- much more attention to species identification will be required if the true biodiversity of species in UK kelp beds is to be monitored
- the levels of expertise required for correct and consistent results are restricted to taxonomic specialists (“an increasingly rare commodity”, J. Breen, pers. comm.).

The most serious drawback of the high levels of expertise needed for species identification is that a monitoring programme needing to distinguish between closely related species can initially be time-consuming and costly. However,

- shifts in the population structure or the distribution of closely related species may be excellent markers of change in the conservation status of a site or of damage related to pollution, etc.

3. Comparisons with other biotopes

a. Other coastal biotopes in the UK

There are no other biotopes in UK coastal waters which display the species diversity, complexity of ecological relationships and net primary productivity ($\text{mg C m}^{-2} \text{ yr}^{-1}$) of kelp beds. Other seaweed dominated habitats such as rocky shores, have equally complex ecological patterns and relationships, but do not have as high diversity and productivity as kelp biotopes. Salt marsh areas dominated by *Spartina* spp. are also productive areas (the lower plant biomass of *Spartina* beds compared to kelp beds is partially compensated for by the higher rates of net primary production, $\text{mg C mg}^{-1} \text{ yr}^{-1}$), but *Spartina* beds are species-poor in comparison to kelp beds. Subtidal beds of *Zostera* spp. (eel-grass) are also relatively productive systems but again, lack the biomass of the kelp forests as well as the diversity of habitat niches that are found in kelp beds.

b. Non European kelp biotopes

Although the species of kelps and their morphology and biology differ in kelp beds throughout the world, there are broad similarities in the ecology of kelp beds and in the range of niches and habitats found within them. Kelp beds:

- have high primary productivity per unit area ($\text{mg C m}^{-2} \text{ yr}^{-1}$)
- export large amounts of POM and DOM
- have a high biodiversity
- have a commercial value based on kelp species
- are the habitat and food source for other commercially valuable species (seaweeds, lobsters, crabs etc.)
- dampen the force of the waves arriving at the shore

4. *Geographical comparisons between kelp beds in the UK*

a. Flora

Maggs (1986) has prepared a biogeographical analysis of marine algae (with emphasis on the Scottish flora but applicable throughout the UK). The British Isles intersect the boundaries of the arctic, lusitanian and boreal floristic provinces and as such, the diversity of algae found within the kelp biotopes of the UK can vary greatly with location. Of the kelp species, *Alaria esculenta*, *L. hyperborea*, *L. digitata* and *L. saccharina* are found throughout the British Isles. In the northern parts of Scotland, *Alaria* (a boreal species) will over-winter as a recognisable plant, whereas on the southern coasts of England this species usually dies back to a nearly unrecognisable holdfast (T. Holt, pers.obs.). *L. ochroleuca* is only found on the south western coasts of England, where winter water temperatures are just high enough for the species to complete its life cycle. As a generalisation, the further south and west a kelp bed is located in UK waters, the more algal species are likely to be found (under ideal local conditions of salinity, silt load and water movement).

b. Fauna

The British Isles also intersect the boundaries of the arctic, lusitanian and boreal faunistic provinces and the species distribution of the marine fauna around the UK reflects these overlaps. Many species in UK coastal waters show a northern or a southern/western distributional bias (Table 15; Briggs, 1974).

Table 15. Examples of geographic bias for some common kelp biotope fauna

Northern	Southern and Western
<i>Leptasterias mulleri</i>	<i>Actinothoe sphyrodeta</i>
<i>Strongylocentrotus drobachiensis</i>	<i>Bispira voluticornis</i>
<i>Pollachius virens</i>	<i>Palinurus elephas</i>
	<i>Paracentrotus lividus</i>

Kelp bed faunas are no exception to this. Indeed, the recently recorded kelp species *L. ochroleuca* is itself limited to south western sites and its associated biota therefore has elements of southern biased fauna (e.g. at Wembury). Sublittoral geographic distributions have been discussed by Hiscock & Mitchell (1980), Hiscock (1980) and Earll & Farnham (1983). The latter present tables listing northern and southern faunal elements and their respective southern and northern boundaries. They also noted how a number of additional factors such as substratum unsuitability may add to the impoverishment of the sublittoral fauna of the English east coast.

5. Seasonal and other temporal changes in biodiversity

The seasonal changes in biodiversity which occur within a single kelp bed have not been studied. With the enormous range of species which are present, such a project would be very labour intensive and time consuming. As far as individual species are concerned, any seasonal changes in distribution are known only if that species has been studied in detail. Some species of algae have seasonally heteromorphic life histories spending a part of the year as a cryptic or encrusting growth form and only becoming recognisable in the foliose phase of their life cycles. Some hydrozoans may be present in the kelp bed in their attached, colonial form only for a part of the year, spending the rest of the year as jellyfish.

Long term fluctuations or permanent shifts in the biodiversity of kelp beds may occur in the UK but the long term monitoring of the species diversity of kelp biotopes has not been undertaken. Long term studies have taken place and are continuing at several locations around the world. A kelp bed on the Atlantic coast of Canada was investigated during the late 1960s (Mann, 1972a) and intensive research continues in the same location. The kelp beds of the south western Cape province (South Africa) and California have been under investigation for more than 20 years now, and some long term data series have been and are being collected. Temporal changes of the biota within kelp beds seem to be on a decadal scale, making long term monitoring projects a necessity.

6. Local variation in kelp biotope biodiversity

The effect of currents on species distributions is fairly well known (Gubbay, 1988) and is well demonstrated in areas such as the Menai Straits and Strangford Narrows as well as in some more open areas. It has been shown that the array of cnidarian species in an area is dependent on current conditions (all other parameters being equal). *Tubularia indivisa* and *Sertularia argentia* are characteristic of very strong currents, *S. argentia*, *Actinothoe sphyrodeta* and *Sagartia elegans* of strong current, whilst species such as *Halesium* and *Kichenpauria* occur in moderate to sheltered conditions.

L. saccharina can cope with fairly strong tidal currents but given adequate substrata its distribution is generally limited to areas with modest or little wave exposure. The conditions under which *L. saccharina* is dominant are often such that large amounts of silt are able to settle on the kelp canopy and on the substrata, which are correspondingly faunistically poor (Hiscock, 1983). This is in complete contrast to the faunistically rich habitat of the *L. hyperborea* kelp forests in non-silty areas (see Table 16). These disparate conditions may be found within a few hundred meters of each other where there is a kelp bed that extends from a sheltered bay to an exposed headland, for example.

Table 16. Tolerances of kelp bed fauna to siltation	
Ubiquitous fauna	
<i>Obelia geniculata</i>	<i>Caryophyllia smithi</i>
<i>Calliostoma zizyphinum</i>	<i>Gibbula cineraria</i>
<i>Crisia</i> spp.	<i>Alcyonidium gelatinosum</i>
<i>Parasmittina trispinosa</i>	<i>Membranipora mebranacea</i>
<i>Electra pilosa</i>	<i>Henricia oculata</i>
<i>Asterias rubens</i>	<i>Echinus esculentus</i>
<i>Clavelina lepadiformis</i>	<i>Aplidium punctum</i>
<i>Botryllus schlosseri</i>	<i>Dendrodoa grossularia</i>
Silt tolerant species	
<i>Amphitrite</i> sp.	<i>Sabella penicillus</i>
<i>Balanus crenatus</i>	<i>Liocarcinus puber</i>
<i>Carcinus maenas</i>	<i>Chlamys varia</i>
<i>Ascidia mentula</i>	
data abstracted from Erwin <i>et al.</i> (1986)	

7. Species that may be confined to kelp biotopes

There are several species which are deemed to be highly typical of kelp beds in the UK, including *Helcion pellucidum* and *Obelia geniculata* (D. Connor, pers. comm.). However, other than the kelp species themselves - which define the biotope - it seems possible that there are no species which are strictly confined to kelp biotopes as their habitat. The list of species that utilise kelp beds at some time as a safe habitat, or for food or as a link in the food web that supports them, may include the majority of all species found in UK waters.

8. Species rarity

The importance of rarity in the marine environment has recently been considered by Sanderson (1997). However, little or no work appears to have been compiled specifically on the rarity of species in kelp biotopes. Some species may be rare at specific sites but not in the UK or Europe as a whole, while others may be rare throughout their biogeographic range as they are an endangered species. Some species may be deemed rare because they are sparsely distributed but may be distributed extensively; others may be deemed to be rare simply because they remain unrecognised by all but the most skilled observers. In an area towards the edges of its habitat range (if these are known) a species becomes less common. In theory, therefore, if a site is known to be on the margins for a specific species, then monitoring the population of that species might be a suitable method of indicating that changes are occurring in the area. The identity and causes of the changes would, however, not be apparent from population monitoring.

E. KEY POINTS FROM CHAPTER III.

Growth

- Kelp plants grow like a conveyor belt; the meristematic tissue is at the junction between the stipe and the blade so the closer to the blade tip the older the cells. At the far end of the blade, tissue is being lost continually by abrasion or decay.
- Most of the upper part of the blade of a kelp plant can be removed and the blade will slowly re-grow, but if the meristematic or transition tissue is removed, the stipe and holdfast degenerate and the plant is lost from the population.
- The biomass that a kelp plant contributes to the coastal ecosystem (as POM and DOM) over a year can be 2-3 times the biomass of the plant itself.
- Each species of kelp has a different growth rate, growth season and life-span and although *Laminaria hyperborea* has been extensively studied throughout its habitat range because of its commercial interest, relatively little information is available for other species.

Life history and reproduction

- Kelps have two morphologically distinct phases (heteromorphic) in their life-cycle; large, obvious plants are the sporophyte generation (diploid) which persist for various lengths of time and produce zoospores.
- Zoospores may be transported for some distance (200+ m) prior to settling.
- Zoospores develop into the microscopic, dioecious gametophytes (haploid), male plants producing sperm and female plants producing eggs, fertilisation sometimes occurring only 10 days after germination and the new sporophyte overgrowing the female gametophyte.

Diversity of habitats, species and conditions

- As with terrestrial forests, the kelp beds contain a variety of different habitat niches in the substrata as well as a series of stratified habitats, and the flora and fauna associated with a kelp forest may occupy one or more of these subdivisions.
- A characteristic feature of kelp beds is the dynamic patchwork of different species and groups of species that form a multicoloured mosaic of encrusting fauna and flora.
- There is a natural, continual shift in the composition and diversity of the species mosaic, with time scales of decades to centuries and spatial scales of square centimetres to hectares.
- Kelp plants themselves often become a habitat for other marine species; epifloral, epifaunal, endofloral and endofaunal species are all found.
- There are many species found in the kelp biotopes of UK waters (1,800+) but no complete lists have been published; kelp beds are the marine equivalent of tropical rain forests in terms of their biological diversity, productivity, population inhabiting or dependent on the habitat, and the species diversity present in the habitat.

Community structure

- Little or no information is available on the pelagic (planktonic and nectonic) components of the kelp beds in the UK.
- In the kelp forest the vertical distribution of the flora is light regulated, as up to 90% of the incident irradiance may be intercepted by the kelp canopy; faunal distribution may be depth related.
- In kelp parkland the biomass and diversity of the associated flora may increase; faunal diversity is also frequently higher than in the dense forest.

- A wide variety of species of flora and fauna can be found on the stipes of *L. hyperborea*, but not on most other kelp species; only the most rapidly growing of the opportunistic species are able to colonise the blades of kelps.
- Kelp plants are exploited as a habitat; the holdfast, stipe and frond each support a different type of community consisting of possibly thousands of individuals from hundreds of species; holdfasts shelter a particularly rich diversity of animals from a wide range of taxa.
- The principal physical factors thought to influence the distribution of species on the substratum are the hydrodynamic conditions and irradiance.

Keystone and associated species

- It is suggested that kelp species, urchin species and *Helcion pellucidum* are among the keystone species of kelp biotopes; characteristic species are listed for kelp biotopes (MNCR biotope classification) but their ecological significance has not been addressed.
- Very little targeted research has been undertaken in the kelp beds of the UK.
- The research into and the development of the use of biological indicator species within monitoring programmes should receive a high level of priority.

Nursery areas

- It is likely that kelp beds support the juveniles of many local species.
- Kelp beds may be important nursery areas for gadoid species and the juveniles of commercial crustaceans.

Flora and fauna interactions

- 90% of kelp production is estimated to enter the detrital food webs of coastal areas, as POM and DOM, supporting habitats beyond the kelp beds.
- Major interactions are thought to be the effects of herbivory, predation, shading and competition for space.
- Complex biological and physical interactions take place within kelp biotopes; some, such as urchin predation, have been studied in detail but others are surprisingly poorly known, particularly in the UK where quantitative studies are few.

Biodiversity aspects

- The specific composition and biodiversity of kelp beds varies from site to site and a complete inventory has not yet been attempted at any site.
- The diversity of species (some of indeterminate taxonomic status) in kelp biotopes necessitate specialist taxonomic skills in comprehensive sampling programmes.
- UK kelp beds are more diverse than any other coastal biotope in European waters as species from the arctic, lusitanian and boreal provinces overlap their distributions on UK shores.
- There are geographical variations in the distribution of species in UK kelp biotopes; in general the further south and west in location, the more species are likely to be found.
- Temporal changes in biodiversity have not been investigated in the UK but it is suggested that, on a large spatial scale, changes may be slow (hectares & centuries) while, on a small spatial scale, changes may be relatively rapid (m² & decades; cm² and years).
- Local variations in the diversity of species may occur on a scale of meters, several kelp biotopes may occur at one depth within a small area.
- Few species appear to be strictly confined to kelp habitats, although it is possible that most species in the coastal waters of the UK may be indirectly dependent on the production from kelp beds.

IV SENSITIVITY TO NATURAL EVENTS

A. DISCUSSION OF SENSITIVITY

All marine benthic communities are subject to natural events which may or may not prove to be catastrophic to the biotopes present. These events may occur on a geological time scale (volcanic activity, tectonic movements, accumulation of sediments) or on a seasonal basis (severe storms, river flooding) or may be single catastrophic changes to biotopes or their components as a result of a wide variety of local events. A local coastal erosion event such as a landslide; unusually warm calm weather resulting in reduced oxygen concentrations in the water; prolonged heavy rain; the outbreak of an algal disease; toxic red tides - all can result in perturbations to a kelp biotope on a local scale. The level of perturbation can be such that surveying a single site in different years can result in the site being classed as a different community type. Hruby (1975) reported that one of his hard-substratum sites in British Columbia changed dramatically due to an "unpredictable environmental perturbation" i.e. the exposure of the fixed quadrat areas he was monitoring to bright sunlight during a series of unexpectedly low tides.

Kelp sporophyte plants are not classed as sensitive according to most of the criteria listed by Hiscock (1997) because they:

- are not fragile, but are capable of surviving enormous mechanical stress from wave action
- are relatively tolerant of pollution (both organic and inorganic - in comparison to many animals tested)
- reach maturity within a few years (e.g. 2 years for *Saccorhiza polyschides*; up to 6 years for *Laminaria hyperborea*; see Table 10)
- show strong recruitment under normal circumstances
- have good "larval" (for kelps, spore) dispersal.

However, kelp sporophyte plants are sensitive by two of Hiscock's (1997) criteria, and an additional one peculiar to *Laminaria*:

- They are long-lived (*Laminaria hyperborea* plants can live up to 25 years).
- They are unable to move away, being fixed to the substratum, and unlike some other seaweeds, cannot reattach and continue growing after removal.
- A particular anatomical feature of *Laminaria*, its formation of a single meristematic zone, make thalli susceptible to damage as they will die if this area is removed (e.g. by storm action, which frequently leaves dying stipes denuded of their meristems) or killed, e.g. by desiccation caused by unusually low tides.

The sensitivities of the zoospores, the gametophyte plants, the gametes and the early stages of the developing sporophyte have been studied under laboratory conditions (Lüning, 1990) but these have not been extended to field conditions. Little research has been undertaken on the chemical sensitivities of the zoospores, gametophytes and gametes of kelp species. In Norway, experiments using sampling devices at varying distances from the kelp forest showed the dispersal range of a population of *Laminaria hyperborea* plants to be at least 200 m (Fredriksen *et al.*, 1995). Large numbers of zoospores were found in samples taken from the water column at a depth of 5 m both within and 50 and 200 m from the kelp forest.

Laboratory experiments showed that spores probably swim as long as they can and thereafter sink passively out of the water column and settle.

The specific sensitivities of other species in the kelp biotopes cannot be addressed in this review. Of the thousands of species which may be present, the sensitivities of only a handful have been investigated. The key species in kelp beds remain to be confirmed. Once established, however, the sensitivities of the key species will define the tolerance of the biotopes in which they are present.

Kelp biotopes have been well studied in regard to two types of natural events. The first is the long-term effect of El Niños in California, and the second, a possibly indirectly related phenomenon, is that of urchin barrens where dense aggregations of various sea urchin species destroy most or all of the macroalgal vegetation, leaving bare crustose corallines. Both these topics are discussed in more detail later in this section. Interactions between different forms of disturbance, such as the complex set of biological relationships and abiotic aspects of the environment that are involved in the formation of urchin barrens, are particularly important for kelp biotopes. For this reason, urchins and their predators are components of kelp biotopes that have been examined in particular detail in several parts of the world.

Caution in interpreting studies showing long-term changes in kelp biotopes was highlighted by Kennelly & Underwood (1992), working in Australia, on a study providing background information relevant to the effects of human and natural perturbations on these systems. Assemblages of macro- and microscopic species in two sublittoral kelp forests at each of four locations on the coast of central New South Wales were variable from site to site, both within and among locations. Complex patchiness was detected at all spatial scales examined. In addition, temporal changes in fauna and flora were variable from site to site. Of 38 taxa which showed detectable fluctuations in abundance, 26 showed trends unique to one forest and 11 showed consistent patterns in both forests within a location. Only juvenile kelp (*Ecklonia radiata*) showed similar fluctuations in abundance in both forests in most locations.

Thus, the structure and dynamics of kelp bed systems vary and do *not* conform to predictions of simple models about processes in habitats dominated by one or a few large organisms. Kennelly & Underwood (1992) concluded that when kelp forests are described using quantitative data at several spatially replicated scales, few general conclusions can be made about the structure of these assemblages.

- It cannot be emphasised too strongly that our present understanding of the natural fluctuations in the species assemblages, populations, distribution and diversity of species in kelp beds is very limited.

B. EXAMPLES OF THE SENSITIVITIES OF KELPS

1. Storm damage

The effects of storm-induced wave damage on kelp forests are frequently obvious, because entire kelp thalli are torn off and are deposited on the strand-line, forming the raw material for low-level algininate industries. Most of the recent detailed quantitative research has been carried out on kelp forests in Australia and California (e.g. by Kennelly & Underwood, 1993). Related studies have not been published for European kelp forests.

The Australian study described below was precise and methodologically sound, using control sites and artificial disturbance. Attempts to classify naturally disturbed kelp communities in Australia (Phillips *et al.*, 1997) were less successful. Macroalgal community structure was investigated in habitats exposed to high, intermediate and low levels of physical disturbance (wave exposure). Community structure was measured by determining the biomass and diversity at both the species level and by assigning algae to functional groups (e.g. crusts, leathery thalli, etc.). Comparisons between the two approaches were made using ANOVA (analysis of variance) of biomass data and derived diversity indices. Multivariate analysis techniques of ordination, Principal Axis Correlation (PCC) and ANOSIM (analysis of similarities) showed that macroalgal assemblages were highly variable, particularly within exposure levels, when examined at both the species and functional group levels.

A less direct effect of storms is the increase in turbidity which occurs due to sediment re-suspension and higher river flows. This affects kelp biotopes because of reduced light penetration (section II.C.) and increased silt deposition. A long period of storms might have serious effects on the quantum budget of kelps living near their lower depth limit, in the same way that unusually thick snow lying over ice greatly reduces annual net growth of *Laminaria solidungula* in the Arctic (Dunton, 1990). Silt is also detrimental to settlement of kelp spores (see section V.D.4.), and to filter-feeding invertebrates.

The interaction between different types of disturbance is emphasised by the observations of Dayton *et al.* (1992) of the giant kelp forest off Point Loma, San Diego, California. A short but intense storm in January 1988 appeared to have been the most severe in perhaps 200 years. It changed age-specific kelp mortality patterns and caused the first large-scale understorey mortality in several decades. By sweeping away drift algae it resulted in intense local urchin grazing which reduced recruitment of kelp plants to the forest.

a. Case studies: UK

Effects of storm damage on kelp biotopes in the UK have not been researched.

b. Case studies: Australia

Kennelly & Underwood (1993) examined the effects of experimental physical disturbances on the assemblages of understorey species living in sublittoral kelp forests in central New South Wales, Australia, across several spatial and temporal scales. Experimental clearing of kelp canopies from 3 replicate patches at four locations in each of two kelp beds mimicked damage done during storms. Subsequent macro- and microscopic sampling of cleared areas, edges of clearings and un-cleared, control areas of natural kelp forest was carried out over a 14-month period. Despite large variations in abundance and temporal fluctuations, there were some similarities in response to disturbance by several taxa in most locations.

- The area of substratum covered by holdfasts of the kelp *Ecklonia radiata* and encrusting algae decreased in the centres of most clearings as the plots became overgrown - first by microscopic filamentous algae and then by macroscopic foliose algae.
- The species of microscopic and turfing algae which colonised clearings were different at different sites, as were the periods after clearing before they colonised.
- The presence of turfing species in the centres of clearings seemed to preclude the successful establishment of some species of sponges and an ascidian species.

- While these changes occurred, there was an increase in the area covered by a layer of sediment and the species richness of the assemblage in the clearings declined.
- At some sites, *Ecklonia* juveniles recruited, but this tended to occur toward the edges of clearings where the covers of microalgae, algal turf and sediment were least.
- Assemblages on the edges of clearings often showed effects intermediate between those in the centres of clearings and those under the natural canopy.
- Species that were fairly uniform in their responses to disturbance were common, occurring in similar abundance in most places.
- Temporal variability showed that some fluctuations occurred over a matter of weeks (e.g. the microscopic organisms), others occurred over several months (foliose algae), whilst the largest time-scale involved the recovery of the disturbed kelp canopy over the full duration of the experiment.

2. Climate change effects

It is only in recent years that the potential effects of climate change (whether natural or anthropogenic) on the natural environment have been considered in depth, because of the enormous amounts of computing power required for modelling global studies. Most research effort has been directed towards the effects of anthropogenic climate change, as natural changes in climate are thought to proceed on a geological time scale and so are unlikely to significantly influence biotopes from one generation of scientists to the next.

Evidence for natural changes in coastal ecosystems has to be separated from the relatively intense effects of anthropogenic impacts, especially those which may occur in heavily populated areas. Data on changes in kelp standing stocks is available from several sites over long periods (decades) because it has been and continues to be harvested for extraction of alginates. In southern California there are highly productive ecosystems based on the primary production of the giant kelp, *Macrocystis pyrifera*, which also support a variety of documented fisheries. The most detailed study on the possible effects of decadal climatic change is that of Dayton and co-workers, e.g. Dayton *et al.* (1992), described below.

a. Case studies: UK

Scottish coasts

Standing stocks of *Laminaria hyperborea* were compared over a period of two decades, from 1946 onwards, as part of a survey of seaweed resources around the Scottish coasts carried out by the Institute of Seaweed Research. Walker (1956) and Walker & Richardson (1957) described how the standing stock varied from year to year, and followed an 11-year cycle that corresponded to a cycle of sunspot activity. Although their methodology was primitive, (spring grabs were used to sample the kelp) their results were surprising and interesting, as more recent ecological studies have shown similar wide-ranging effects which follow sunspot cycles. The cycles of sun-spots may be a visible indicator of solar activity that has a profound effect on patterns of physical changes in the global environment. Increased sunspot activity is thought to have an effect on the climate of the Earth in that the associated increase in the strength of the solar wind is thought to provide additional protection from cosmic rays. This in turn results in a reduction in global cloud cover and a consequent temperature rise (H. Powell, pers. comm. - from p.9 of "The Observer" 12/4/98).

b. Case studies: California

Because of the importance of *Macrocystis* to the diverse assemblage within the Californian kelp forest community, Tegner *et al.*, (1996) focused their research on changes in giant kelp populations. Canopy maps of the Point Loma kelp forest near San Diego show major changes over the last century, which have been ascribed to a variety of different causes, including fluctuations in seawater temperature. To understand the role of physical forcing on interannual variability in the *Macrocystis* canopy at Point Loma, they compared two 31-year kelp data sets with available physical records.

Annual average surface water temperature was significantly correlated with the kelp harvest, but explained only 24% of the variance. Because the canopy of giant kelp is susceptible to disturbances that may not affect plant survival, they also evaluated two subsurface measures: stipe number (as an index of individual plant growth) and stipe density (as a measure of the carrying capacity of the area). Both stipe measures were sensitive to interannual variability in surface water temperature for the period 1983-95 and were more sensitive indicators than the survival of plants.

Plant size and the carrying capacity of the area were very low following the 1992-93 El Niño conditions and the anomalously warm year of 1994. Comparison with historical stipe data from 1957, 1973, and 1974 indicated a reduction in standing biomass of up to two-thirds since 1957. There was a strong inverse trend between median plant size and the sums of anomalies in Scripps Institution of Oceanography Pier surface water temperature, calculated quarterly for three years. Tegner *et al.* (1996) concluded, however, that these large, inter-decadal changes in biomass could be explained by the location of the data sets within multi-year warm and cold periods (i.e. precisely when the samples were taken during the temperature fluctuations). They argued that the sensitivity of stipe counts to surface temperature supported their incorporation into ongoing and future Californian kelp forest research.

The same team also described more community-orientated aspects of this study. Dayton *et al.* (1992) studied the effects of various types of disturbance for three decades on the populations of several species of kelp in the Point Loma kelp forest, with a view to addressing the question “do large-scale episodic events override biological mechanisms as major community structuring processes?” The most sensitive population factors they studied were recruitment, density, and survivorship. There were marked differences between the decades with regard to the intensity of the disturbances. Compared with the 1980s, the two preceding decades were relatively benign. The 1980s had two extreme disturbance events:

- the 1982-1984 El Niño-Southern Oscillation (ENSO) was the most severe El Niño event of the century, and resulted in very warm, nutrient and oxygen depleted water in Californian coastal areas;
- in 1988-1989 a severe storm was followed by a strong La Niña event marked by unusually cool, nutrient-rich water.

The massive disturbances of the 1980s obliterated much of the biological structure in the kelp forest. Certainly the anomalies caused many longer term effects including:

- which, in turn, resulted in between-area variation in recovery rates from the disturbances. outbreaks of understory algae such as the foliose brown alga *Desmarestia ligulata*
- intraspecific competition
- changes in grazing patterns, etc.,

However, in all cases the variation between different sites within the kelp bed was overshadowed by the overwhelming competitive dominance of *Macrocystis pyrifera*. Most of the patches of understory algae on the transect lines (some of which had persisted for 7 years) died out by the end of 1990. The population biology of *Macrocystis* was remarkably similar in most areas, as the cohort longevity and survivorship curves were very similar, and the plant and stipe densities tended to level off in only a few years. Thus large-scale episodic events such as El Niños, La Niñas and rare storms may have dramatic impacts, but small-scale responses such as “density-vague” recruitment (i.e. neither density dependent nor density independent) and survival of robust species allow prompt recovery, often to pre-existing patterns. The one exception was a site which was marked by increased sea urchin grazing and resultant poor kelp recruitment throughout the latter half of the 1980s. A subsequent urchin disease event later reduced the grazing pressure in this area and led to kelp recruitment in the autumn of 1991.

3. Ecological relationships

The relationships between species within kelp beds have rarely formed the basis for scientific research. Other than some work on the interactions between kelps and sea-urchins, presumed interactions are based on field observations rather than statistically valid data.

Sea urchin barrens are found in kelp beds in most parts of the world but the factors influencing their formation and demise are not well understood. It has been postulated that the sweeping action of sub-canopy sporophytes in a kelp bed subject to wave action may dislodge grazing urchins (P. Zoutendyke, pers.comm.) and that mature plants are not directly affected as their longer stipes act as an urchin access barrier to the blade tissue. A change in the population structure of an area of the kelp bed would therefore give urchins the opportunity to develop and maintain a “grazing field”. The interrelationship of urchins with kelps has been studied extensively in California, eastern Canada, Australia and Norway, but some of the earliest work took place in the British Isles (Kain, 1967), and heavily urchin-grazed biotopes are especially common in Scotland. Large areas of barren sea floor are found interspersed with the kelp beds in northern Norway but these barrens are apparently limited to the inner coast - the outer coast is unaffected and supports intact kelp forests. The kelp forests are an important source of zoospores for the potential reforestation of barren areas, and their dispersal range is of vital importance (Fredriksen *et al.*, 1995). In New South Wales, Australia, the formation of urchin barrens is more predictable (and simpler) than in other temperate regions, because the sea urchins (*Centrostephanus rodgersii*) are found in shelters during the day, from which they emerge to forage at night and maintain patches of barren habitat (Andrew, 1993). Artificial provision of shelter (boulders) led to the creation of barrens. Further discussion of urchin barrens in relation to harvesting of kelp is given in section V.B.3.

Other grazers may also reach plague proportions, such as the case of a North Pacific kelp-boring amphipod discussed below, but research on the effects of natural population fluctuations for other kelp bed grazers or their predators is largely lacking.

a. Case studies: UK

Isle of Man

In the Isle of Man, Great Britain, *Laminaria hyperborea* and other algae were absent from the deepest 3 m of the seaward face of Port Erin breakwater (Kain, 1967). Over a 3-year period all sea urchins, *Echinus esculentus*, were removed by hand from a 10-m wide strip. Successful recruitment of young sporophytes of *L. hyperborea* occurred only in the urchin-

cleared strip, young recruits elsewhere being destroyed by grazing. Kain therefore concluded that the lower limit of *L. hyperborea* at this site was determined by urchin grazing pressure.

Scotland

The factors governing the urchin barrens in the Scottish kelp beds are unknown. It is possible that barrens result when urchins take advantage of kelp plants having been removed as the result of a combination of other biological and abiotic factors - such as the stipes having been weakened due to tissue removal by *Helcion pellucidum* and the plants subsequently removed by storms.

b. Case studies: Norway

Leinaas & Christie (1996) examined the stability of the barren state of a kelp forest-sea urchin system in northern Norway. The ability of the sea urchin *Strongylocentrotus droebachiensis* to maintain high population densities and recover from perturbations, and the succession of kelp forest re-vegetation, were studied experimentally by reducing the urchin density on a barren skerry. Additional information was obtained from community changes following a natural, but patchy, sea urchin mortality that varied in degree between sites.

On the barren grounds, high urchin densities (30-50 m⁻²) were maintained by annual recruitment. Severe reductions of urchin densities resulted in the initiation of luxuriant kelp growth, while more moderate population reductions allowed establishment of opportunistic algae (during spring and early summer), but not kelps. After a severe decline in sea urchin densities the succession of algal growth followed a predictable pattern. The substratum was colonised initially by filamentous algae, but within a few weeks these were outcompeted by the fast-growing kelp *Laminaria saccharina*. The slower-growing, long-lived kelp *L. hyperborea* became increasingly dominant 3-4 years after the urchin removal experiment. Increased availability of food after a reduction in urchin density led to increases in the growth of the remaining sea urchin individuals. However, the urchin population density did not increase, either by recruitment or by immigration from adjacent areas with higher sea urchin densities. Leinaas & Christie (1996) concluded that the early phases of the establishment of a dense kelp stand may represent a breakpoint in the ability of sea urchins to maintain a barren state.

The ability of *L. saccharina* to invade and monopolise an area quickly may have both positive and negative effects on the succession towards the climax *L. hyperborea* kelp forest. Competitive interactions between the kelp species may slow the process, but development of a dense stand of *L. saccharina* will also reduce the grazing risk on scattered recruits of the more slowly growing *L. hyperborea*.

c. Case studies: California

Conlan & Chess (1992) reported a new species of amphipod amphipod, *Peramphithoe stypotrurpetes*, which bores into and occupies the interior of abraded stipes of kelps on the Pacific coast of North America. Adult bisexual pairs cohabit the stipes with their offspring of several generations. This amphipod was partly responsible for the creation of an urchin barren following the 1987 El Niño. Infestation of the kelp forest by this species reduced the kelp biomass possibly contributing to the loss of kelp plants which may have triggered damaging urchin grazing.

C. KEY POINTS FROM CHAPTER IV.

- The sensitivities of the many hundreds of species present in any given kelp biotope cannot be addressed in this review.
- Kelp sporophytes are not particularly sensitive in terms of key population features (life-span, recruitment), but their growth from a single meristem makes them susceptible to certain types of damage.
- The sensitivities of non-sporophyte phases of the life cycle are not known.
- The species diversity within kelp biotopes is such that useful quantitative data on the effects of natural events requires multiple replicate sampling at several spatial scales.

Storm damage

- Storm damage to kelp forests (studied by artificial disturbance in Australian *Ecklonia* forest) creates a patchy arrangement of different successional states, as recently cleared areas are settled by ephemeral algae that are gradually outcompeted by the kelps.
- During recovery, macroalgal assemblages in disturbed areas are highly variable even within an exposure level.
- Different types of natural disturbance events may occur simultaneously within a kelp bed - physical disturbances triggering biological imbalances.
- Temporal variability occurs in patterns of recovery from disturbance, some fluctuate over a period of weeks, others over months and full recovery takes years.

Climate change effects

- Seawater temperature changes over periods of several years affect kelp stocks, both in the British Isles (correlation with sunspot cycles) and in California (successions of warm El Niño events); biological interactions may occur in a complex way sometimes resulting in the formation of localised urchin barrens following El Niños in California.
- Long term climate change effects are not yet known, due to the time scales exceeding the duration of present research programmes.

Ecological relationships

- Urchin over-grazing occurs in many kelp beds of the world, possibly triggered by events such as outbreaks of kelp-boring amphipods or limpets and leading to the creation of long-maintained urchin barrens occupied by crustose corallines.
- The environmental and ecological factors that control the initiation, maintenance and demise of urchin barrens are not well understood.
- Artificial or natural (disease-mediated) removal of urchins from barrens leads to recolonisation by the climax community kelp species over a period of several years, due to the competitive dominance of the kelps.

V SENSITIVITY TO HUMAN ACTIVITIES

A. INTRODUCTION

Kelp has traditionally been collected for use as an agricultural fertiliser and to improve soil structure. The change to mechanical harvesting from live kelp beds is the most significant human activity directly affecting the *kelp* in the kelp forests. Other important activities which impact on kelp beds include eutrophication from domestic and agricultural nutrient run-off, which can result in increased turbidity in coastal waters due to blooms of phytoplankton as well as affecting the physiology of the kelp plants. Turbidity increases also occur as the result of increased silt loads in rivers draining agricultural areas and from the particulate components of sewage. The removal of predator species is known to have had major effects in Pacific and Eastern Canadian kelp beds. Effects of predator removal and of the limited harvesting of edible urchins in the UK are not yet known. Very little information is available on the effects of human activities on species other than the kelps themselves and this is a consequence of past research in response to the commercial interest in the kelp species, rather than interest in the kelp bed ecosystems as a whole.

B. DIRECT EFFECTS - KELP HARVESTING

1. Introduction

Around the world numerous kelp species have been exploited over the years as a source of chemicals for industry. Since early times, kelp cast up on the shore has, along with other seaweeds, been collected for use as an agricultural fertiliser (rich in potash and phosphate) and also to improve the soil structure. In more recent times, kelp has been burned to produce iodine-rich ash but now is the basic resource used in the important alginate industry which produces valuable emulsifying and gelling agents. In Europe, kelp is now harvested from living kelp beds, the most commonly harvested species being *Laminaria hyperborea* and *L. digitata*. Commercial interest has also been increasing recently in utilising *Alaria esculenta* and *L. saccharina* as “sea vegetables” and it is possible that these species also will be harvested in the near future. This harvesting may alter or destroy the structure of the kelp forest ecosystem and reduce the POM and DOM available to other biotopes in coastal areas (see section III.B.1.).

As a result of the importance of *L. digitata* and *L. hyperborea* to the chemical industry, several reviews of the effects of harvesting on kelp populations have been produced in recent years in France, Scotland and Norway.

The following brief discussion of the effects of harvesting on kelp biotopes (section 2. a & b.) has been extensively abstracted from the work of Martin Wilkinson (1995): “Information review on the impact of kelp harvesting”.

Examples discussed below include non-European kelp species as these include some useful information on the effects of kelp harvesting on the non-kelp species in the kelp beds. Relatively little work on other species in kelp biotopes has been undertaken in the UK as commercial, mechanical harvesting of kelp has not occurred.

2. *Case studies of the effects of kelp harvesting in UK and European waters*

Impact information comes from two sources: the removal of kelp for scientific experiments, and from observations made on harvested grounds in Norway and Brittany. The observations and data need to be considered in two different ways, the effect of harvesting on the resource itself and the effect of kelp harvesting on the complete kelp forest ecosystem. Not surprisingly most published work concerns the resource rather than the entire ecosystem. The international scientific community recognises the difficulty of determining both the short-term impacts of kelp harvesting and the long-term consequences to the coastal environment. Around the coasts of Brittany 75-80,000 t of seaweed are collected each year and yet there is no data on the effects of this biomass loss from coastal ecosystems (Dauvin, 1997).

a. Experimental canopy removal and clearance experiments

i. Early experiments - effects on the kelp population

Scotland

The earliest manipulative experiments on a kelp forest were carried out in 1936 on the west coast of Scotland by Kitching (1941). He removed canopy plants of *L. hyperborea* with shears and one year later a new canopy of dense plants, 1 m high, had formed. The old holdfasts of the cut plants had gone, showing that they would not survive, along with their own distinctive fauna. The new holdfasts were described as very tight and clean of epibiota. This early experiment shows a standard pattern of response - the forest has considerable potential to regenerate but, when it does so, the age and size structure and plant morphology may be altered with consequent effects on the rest of the ecosystem.

Isle of Man

In 1975 Kain carried out clearance experiments in the Isle of Man which showed that although the *L. hyperborea* forest could regenerate, there might be a temporary domination by other species, notably *Sacchorhiza polyschides*. Concrete blocks at 0.8 and 4.4 m below ELWS were cleared of attached algae. Different blocks were cleared in different years and at different times of the year so that the recolonisation patterns could be related to length of recovery period and responses to seasonal differences in recovery. Blocks at the shallow level cleared in August were re-colonised by *L. hyperborea* but, if cleared in November, February or June, there was initial replacement by *S. polyschides*, *Desmarestia aculeata* and *Alaria esculenta* (in different years). Whatever the replacing species, *S. polyschides* became dominant by the August following clearance of the blocks. However, *L. hyperborea* had always replaced the *S. polyschides* after 2 years and, the biomass of *L. hyperborea* on the blocks was equal to that measured in control areas after 3 years. Colonisation of the blocks at 4.4 m was more variable and it took longer for the *L. hyperborea* to re-establish. On the control blocks at this depth, *S. polyschides* and *D. aculeata* flourished if the block did not hold any plants of *L. hyperborea*. Where blocks at a depth of 1.3 m. were continually cleared at intervals, kelp dominance was lost and the blocks were populated by 41 different species of algae, with reds having maximum biomass in the winter, browns in the spring and greens in the late summer. When sterilised stones were placed in the experimental area they were not colonised by *L. hyperborea* except when the canopy plants were reproductive, although on cleaned but *not* sterilised blocks, new sporophytes grew at all seasons (presumably from microscopic sporophytes or from fertilisation of gametophytes).

ii. Kelp growth rates after clearance

Isle of Man

In further work with cleared areas in the Isle of Man, Kain (1976a) investigated the growth rates of remaining kelp plants. At 0.8 m depth, growth was rapid after canopy removal, indicating the role of the canopy in limiting the light available for the growth of other strata of kelps in the forest. 1-3 year old plants in the cleared areas became larger than those in control areas as a consequence. However, after 3 years the biomass and frond area index of the experimental area was restored. At 4.4 m depth, recolonisation was haphazard and the growth rates of the plants were lower.

The manipulative experiments of Jones & Kain (1967) in which the local population of *Echinus esculentus* was removed showed the potential of urchins to inhibit the regeneration of a kelp biotope after harvesting (see section IV.B.3.).

iii. Epiphyte growth after canopy removal

Harkin (1981) examined the effect of kelp canopy removal on the algal epiphytes of the kelp stipes. There was a rapid increase of red algal biomass in the first summer but brown algae were able to grow better in the first winter. This re-established the previous mixture of red and brown epiphytes. Two years after the removal of the canopy, the biomass of epiphytes had returned to a level similar to that measured before the canopy removal allowed an explosion of growth.

iv. Conclusions

These experiments suggest that some semblance of a kelp forest, in terms of macroalgal biomass and of subsidiary algal species, may be regained within 3 years of canopy removal. However, the size of kelp plants and the age structure of the population in the re-grown forest is different from the untouched forest. Furthermore, the experiments do not directly mimic the effect of kelp harvesting. For example, Harkin's experiments deliberately left intact stipes that a kelp harvesting dredge would have removed. New stipes would not have developed the normal epiphyte flora so quickly. While this work might superficially suggest that 3-4 years is a suitable interval between harvesting to allow regrowth of the macroalgae, a much better picture of the effects of harvesting can be obtained by examining harvested grounds in Norway and Brittany.

b. *Laminaria hyperborea* harvesting

i. Introduction

The stipes of kelp plants cast ashore after storms have been collected commercially for many years as part of a mixed coastal economy in France, Ireland, Scotland and Norway. More recently, methods of dredging *L. hyperborea* on a commercially viable scale have led to this kelp being harvested under strict regulatory conditions in Norway and in Brittany (Arzel, 1996), and harvesting trials were carried out in Scottish waters in 1991 (H.T. Powell, pers.comm.). The commercial harvesting of *L. hyperborea* in French coastal waters was proposed only in 1995-6, as the local industry had previously concentrated on the collection

of *L. digitata* (Arzel, 1996) and consequently, no impact assessments of harvesting have yet been published.

ii. Early assessments of impact

Norway

The earliest assessment of the effect of kelp dredging in Norway was that of Svendsen (1972). He studied kelp beds at depths of 4 to 10 m over periods of up to 3 years after harvesting. These areas were quickly overgrown with new plants of *L. hyperborea*. Within 1 year the population was dense and well-developed. Although he regarded the beds as completely regenerated after 3-4 years in terms of *Laminaria* biomass, the individual plants were only half the height (about 1 m.) of the former mature plants (about 2 m tall). The re-grown biomass was made up by the greater density of smaller plants. From an industrial point of view, the stipes of these new plants were of better quality for alginate extraction because they were less contaminated by epiphytes. From an ecological point of view, even after 3 years, the disturbed biotope was species-poor in comparison to an undisturbed habitat. As in the manipulative experiments described earlier, the forest may regenerate sufficiently after 3-4 years to be harvestable again but it is certainly different in structure, both as regards the kelp plants and the subsidiary flora and fauna. A system of rotation of harvested areas was introduced by the Norwegian government to ensure that each area of kelp forest was harvested only once in 4 years to allow for regrowth of the *Laminaria* plants. It has since been recommended that this time scale be extended to 7-10 years to allow for the partial recovery of populations of non-kelp species.

iii. More recent impact studies of harvesting on kelp populations

Norway

Sivertsen (1991) has compared the regrowth of kelp in areas trawled 1 - 5 years previously with areas freshly trawled and control areas. Large canopy-forming plants were absent until the fourth year after harvesting, but the structure of the kelp population was beginning to stabilise with little change in plant density between years 4 and 5. The age structure of the re-grown areas showed downwardly skewed age distributions in comparison to control areas. At 4 years after harvesting, kelp plants had only reached $\frac{2}{3}$ of full before-harvesting canopy height in the re-grown areas. Sivertsen suggested that harvesting should occur at 6 or 7 year intervals to match the natural growth and recruitment cycles in the kelp population. In addition, the post-harvesting growth data showed that the re-establishment of kelp in harvested areas was primarily dependent on the growth of viable individuals remaining after harvesting. Climax kelp communities, dominated by canopy individuals, provide poor conditions (e.g. light) for new recruitment of sporophytes to the population, so presumably the new sporophytes that grow into the population were present prior to harvesting but were small enough to escape damage. The harvesting dredge used in Norway is designed to leave behind the small kelp plants, only collecting those of canopy height (H.T. Powell, pers. comm.).

A further interesting observation in Sivertsen's report is the temporary post-harvesting replacement (for one year only) of the *L. hyperborea* dominated forest with a population of *S. polyschides* as in the clearance experiments by Kain (1975).

iv. The impact of harvesting on associated flora and fauna

Norway

In a separate survey that was primarily directed at the effects of kelp harvesting on other common organisms in the kelp biotopes (Rinde *et al.*, 1992), the forest structure seemed to recover to something approaching normal after 3-4 years, but with persistent differences from an undisturbed forest. Rinde *et al.* (1992) argue that the forest may be re-harvestable after 4 years but that it does not provide the same physical environment for the other organisms which it shelters. They concentrated on the species thought to be most closely linked to the kelp and considered epiphytes, holdfast fauna and bottom fauna and flora separately. Their report contains a wealth of detail of the species present and the numbers within different animal groups.

The epiphyte community developed in complexity with the increased age of the host stipe. The plants in control areas, at about 10 years old, have a much richer and more extensive epiflora than the younger, replacement plants found in previously harvested areas. The development of a diverse epiflora was deemed to be a desirable feature of kelp biotopes because the physical structure of the epiphytes provides a habitat niche for species of amphipods, isopods, gastropods and small fish.

The epifaunal species present on the kelp stipes were not as diverse as the epiflora, usually consisting of several species of crust-forming bryozoans. Other animals were found only on the older plants; shrubby erect bryozoans and the sponge *Halichondria sp.* on 10-year-old plants, and tunicates on the 6 years post-harvest population. The full development of the epiphyte community of plants and animals seems to need much longer than the advised 4-year interval between trawling.

The holdfast fauna is richer in both species and numbers of individuals for 10-year-old plants from the control area than for younger plants from previously harvested areas. A physically obvious difference between the younger and older plants was the development of large numbers of the large tubeworm, *Filograna*, which forms a visually obvious feature only on the holdfasts of the older plants. As the kelp plants become older the area and the volume occupied by the holdfast increase, with an apparently related increase in the numbers of individual animals, and also in both the biomass and biodiversity of the holdfast fauna. Various larger species were found associated with the holdfasts: shrimps, lobsters, *Hyas sp.*, *Cancer sp.*, hermit crabs, *Echinus esculentus* and *Strongylocentrotus droebachiensis*. These species were absent from recently dredged areas and well established populations appeared only in the undisturbed kelp forest, suggesting that full biological restoration after harvesting may take at least 10 years.

Benthic macrofauna and macroflora were more diverse in the control area (51 species) than the recently dredged area (21 species). The dredged areas tended to have growth of other kelps on the bottom, e.g. *Alaria esculenta*, and also *Desmarestia* spp., while the bottom between the young *L. hyperborea* plants was uniformly covered with coralline algae after 3 years. In the control areas, there was a more diverse bottom community. The coralline algae were still a significant part of the bottom cover but were joined by species of cnidarians, bryozoans and sponges.

v. The impact of harvesting on other species and beyond the kelp beds

There may be consequences for kelp ecosystem components other than those directly associated with the kelp, including fish and lobsters, but these have not yet been investigated in Europe. Sivertsen (1991) suspected that kelp harvesting could have been the cause of dune erosion from adjacent areas. The removal of the kelps reduced the drag caused by the kelp beds, which had had a wave-damping effect. Higher energy waves reaching the adjacent sandy shores and their dune hinterland resulted in increased rates of sediment removal. In the United States, beds of artificial kelp have been used to prevent sand erosion from beaches.

Thrush (1986) refers to the importance of accumulations of laminarial detritus on the seabed of Lough Hyne, County Cork. The POM (particulate organic matter) had a significant input to the energy web of the benthic macrofauna of soft bottoms. The export of both POM and DOM (dissolved organic matter) would be significantly affected by kelp harvesting but the effects of this reduction have not been investigated.

c. Harvesting of *Laminaria digitata*

This information (section 2.c.) has been largely abstracted from Arzel (1996).

Brittany

Around the coasts of Brittany there is a long tradition of seaweed collection. Several species of seaweeds have been harvested on a commercial scale, larger or smaller, since the 1950s and form the basis of a series of flourishing industries. The collection of *L. digitata* around the coasts of Brittany has provided the French alginate industry with feedstock for the production of emulsifiants. The plants are collected from small boats using a device called a "scoubidou". This is a 2-3 m long steel bar with a spiral curved hook at the end which is lowered into the thickest part of the *L. digitata* forests and then twisted, gathering up the stipes like twisting spaghetti on a fork (D. Birkett, pers. obs.). The hook is then winched inboard and whole plants of *L. digitata* are ripped from the substratum, including blades, stipes and some holdfasts.

There is no literature available on the effects of this method of harvesting on the biodiversity and population structures of the kelp bed species. *L. digitata* plants rapidly re-colonise any gaps in the upper infralittoral which result from storm damage and are assumed to respond in a similar way to areas cleared by harvesting. The areas licensed for harvesting represent only a small proportion of the total habitat of *L. digitata* around Brittany, but the substratum area which is effectively cleared each year is not recorded, just the wet mass of the harvest. The complaints of local fishermen that crustacean catches are locally reduced in harvested areas have been dismissed as an example of the historical animosity between fishermen and seaweed harvesters (Dauvin, 1997).

3. Case studies on the effects of harvesting of kelp elsewhere in the world

a. Introduction

The following information (section 3.) has been abstracted from Wilkinson 1995, (chapter 6, prepared by T. Telfer).

Most of the information on kelp harvesting that is available in the literature concentrates on community dynamics of the kelp and the effects on grazers of total or partial canopy removal. This may give an indication of harvesting effects but must be interpreted with great care. The major effects shown by the removal of kelp plants are centred on the influence of grazing populations, particularly the urchins which can increase in abundance and change kelp-dominated areas into coralline "barrens" (Keats, 1991).

b. *Macrocystis pyrifera*

i. Effects of harvesting on the kelp population

The giant kelp *Macrocystis pyrifera* is harvested commercially from Southern California (Barilotti & Zertuche-Gonzalez, 1990) and Southern Chile (Santelices & Ojeda, 1984a, 1984b). *M. pyrifera* is a remarkable seaweed because of the large size and rapid growth rate of the sporophyte generation. Individual plants may measure up to 50 m in length. The stipes arise from perennial, branched holdfasts which may each cover a large area of bedrock and each stipe can bear up to 200 fronds. Individual fronds may grow at rates of up to 7 cm per day. Reproduction is from sporophylls around the base of the plant.

California

Information on harvesting methods from the Pacific Ocean waters of Baja California and California is given in Barilotti & Zertuche-Gonzalez (1990). These methods (North, 1987) are highly mechanised and utilise large boats capable of cutting and lifting 300 to 550 t wet weight in a single load. Harvesting removes only the fronds in the surface canopy to a depth of 1.2 m (operating on the lawnmower principal). This method does not cut the sporophylls located around the base of the plant that provide spores for the next generation, or the meristems that produce the new fronds. The individual fronds have a lifespan of about 6 months (North, 1987). Estimates of biomass removed by harvesting range from 33% to 50% of the total biomass of the plant (Coon, 1987; North, 1987). Such a large amount can be removed from these long plants when cutting at only a shallow depth because most of the mature frond material floats on the water surface, buoyed up by bladders.

North (1968) concluded that little damage is caused to the kelp by harvesting and that in some circumstances harvesting may be beneficial to the plants. These findings were largely confirmed by Coon (1987), who showed that yields and canopy areas in Santa Barbara County, California, remained relatively constant over a five-year harvesting period. Dayton *et al.* (1984) pointed out that the stability of the kelp populations in *M. pyrifera* beds at Point Loma had not been noticeably affected by harvesting. Aerial photographs of Carmel Bay, California from 1971 to 1977 (Barilotti *et al.*, 1985) did not indicate long-term changes in the area of the kelp beds.

Effects of harvesting on the production and recruitment of juvenile plants have not been studied (Barilotti & Zertuche-Gonzalez, 1990). Though removal of 75% of the canopy was shown to reduce the production of sporophylls (Reed & Foster, 1984; Reed, 1987), it is

expected that removal of the canopy will aid recruitment of young plants by increasing the light available, as sporeling growth is thought to be light-limited (Deysher & Dean, 1986).

Chile

Santelices & Ojeda (1984a) found that removal of the canopy resulted in juvenile recruitment in Chilean *M. pyrifera* forests being increased, but there was a significant decrease in interplant distances (a population density increase) showing the change in the population structure of the *M. pyrifera* forest. Removal of the canopy of Chilean *M. pyrifera* forests also resulted in a decrease in the biomass of the understory kelp, *Lessonia flaviscens* (Santelices & Ojeda, 1984b) though the total number of species in the experimental area remained the same.

ii. Effects of harvesting on other species in *M. pyrifera* beds

California

Bodkin (1988) found that the abundance of seven species of fish was significantly decreased after removal of the *M. pyrifera* forest in southern California. Standing stocks of fish are larger in areas with *M. pyrifera* than without, in California, (Larson & DeMartini, 1984) but the abundance of fish was not affected by a decrease in kelp abundance in warmer climates (Stephens *et al.*, 1984).

Grazers such as the sea urchin, *S. droebachiensis*, may modify the pattern of recolonisation (Dayton *et al.*, 1992). Increases in the populations of grazer species may result in the development of "barrens" when the developing and juvenile kelps are removed (Leighton, 1971). This is particularly obvious when large numbers of grazers are congregated in a limited area, such as rocky outcrops from a sandy substratum. These barrens can become a relatively stable community but the kelp forests may recover if the urchins are removed by disease (Elner & Vadas, 1990) or by storm events (Ebling *et al.*, 1985). North & Pearse (1970) associated a population explosion of sea urchins in Southern California with the onset of kelp harvesting, but they also point to other possible causes: the destruction of sea otter populations which prey on the urchins; the depletion of abalone populations which graze competitively with the urchins; enrichment of the coastal waters with partially treated sewage (which may be used as an amino acid source by the urchins).

iii. Effects on kelp of the harvesting of sea urchins

Artificial removal of the red urchin, *Strongylocentrotus franciscanus*, permitted a rapid increase in the biomass of foliose annual algae and the eventual dominance of near-shore perennials (kelps etc.) in laminarian forests (Pace, 1980). *M. pyrifera* communities may therefore change if present densities of urchins are reduced through commercial harvesting or the introduction of a predator such as the sea otter, *Enhydryx lutris* (Pace, 1980). Estes *et al.* (1982) actually associated the destructive levels of urchin grazers with the absence of sea otters. North (1980) showed that the coralline barrens could be re-colonised by dispersing embryonic *M. pyrifera* sporophytes grown in the laboratory.

**c. Harvesting of *Laminaria longicuris*
Nova Scotia**

i. Sizes of plants removed

Laminaria species exist in many of the cool and cold water parts of the world but the major species which is commercially harvested is *L. hyperborea*. The other large *Laminaria* which has been harvested is *L. longicuris*, particularly on the Atlantic coast of Canada (Nova Scotia and Newfoundland). This species can grow up to 12 m long but is commonly 3-5 m in length. It forms dense forests below low-water mark, with the holdfasts always submerged, but with such long plants the fronds can be present on the water's surface at low tide. In Nova Scotia it occurs in the depth range 4-18 m (Mann, 1972a) often in association with *L. digitata*. In south-west Nova Scotia during 1979, over 1,000 tonnes wet weight of *L. longicuris* were harvested for the production of alginates (Pringle & Sharp, 1980) using dragnet harvesting - although this is a reduction on a larger commercial harvest taken in the 1940s (Chapman, 1987). Dragnets harvest whole plants in the larger size ranges. Dragnetting causes bottom perturbation particularly at the beginning of each tow, when the net is in contact with the bottom. Large boulders may be displaced and rocks of up to 7 kg in weight and still attached to holdfasts are removed from the habitat. The optimum sustainable yield of harvest from the kelp population may remove more kelp plants than the minimum cover required for the survival of associated fauna e.g. the lobster *Homarus americanus* (Breen & Mann, 1976).

ii. Effects of harvesting on sporophyte recruitment

In an un-harvested mixed population of *L. longicuris* and *L. digitata* the mean population density of *L. longicuris* remained constant at 1.2 plants m⁻² and the population density of *L. digitata* was around 3.2 plants m⁻² (Chapman, 1984). In this population *L. longicuris* produced 9×10^9 and *L. digitata* produced 20×10^9 spores m⁻² yr⁻¹, of which about 9×10^6 and 1×10^6 sporelings m⁻² yr⁻¹ respectively were recruited (Chapman, 1984). From these millions of recruits only 1 sporeling m⁻² yr⁻¹ of *L. longicuris* and 2 m⁻² yr⁻¹ of *L. digitata* grew to visible size. Removal of macroscopic kelp plants had no effect on the recruitment of the visible stages to the population (Chapman, 1984).

iii. Effects of harvesting on sporophyte growth

After harvesting of *L. longicuris* and its understory of *L. digitata*, faster growth rates of the remaining sporophytes were detected than in the un-harvested area (Smith, 1986). The standing crop had recovered to pre-harvest levels after only one year (Smith, 1986) but it was considered unlikely that the kelp bed had retained its former diversity and population structure. Following the harvest, *L. longicuris* was initially more abundant than *L. digitata* but this pattern altered over the next 3 to 5 years as the proportion of *L. digitata* diminished.

iv. Effects of grazing on post-harvesting recovery

If kelp beds are destroyed or partially destroyed by harvesting, then grazing sea urchins such as *S. droebachiensis* will not allow regeneration and recruitment of the kelp population. Much experimental work has been undertaken in St. Margaret's Bay, Nova Scotia. It is thought that the predators of the urchins such as lobsters, crabs or fish use the kelp forest for cover and protection. A reduction in predator pressure due to harvesting kelp or catching lobsters will permit urchin densities to increase to the point where they form aggregations and

graze destructively on *Laminaria* forming barrens (Bernstein *et al.*, 1981). These barrens become the new community (Breen & Mann, 1976) with urchins able to survive by feeding on algal sporelings and detritus (Warner, 1984; Chapman, 1987).

v. Effect of kelp harvesting on lobster catches

Mann (1977) used fisheries statistics to show that a slow decline in lobster and crab stocks was caused by kelp depletion resulting from overgrazing. This did not fit with normal population patterns. Miller (1985b) used historical reports to show that these depletions of lobster and crab stocks have happened before in this century, associated with kelp bed loss and urchin population increases, and suggested that these slow fluctuations may be part of a long term cyclic succession. Miller (1985b) pointed out that there was a periodic mass mortality of sea urchins in Nova Scotia which enabled the slow regeneration of the *Laminaria* forest. This was confirmed by Novaczek & McLachlan (1986) who showed that the pattern of recovery from barrens was dependent on the substratum depth, since kelp initially re-colonised the shallows but deeper depths had not recovered during the time of the study.

Where urchins were removed through artificial (Lawrence, 1975) or natural means through urchin pathogens (Miller, 1985c), *L. longicruris* and *L. digitata* quickly re-colonised the area. Miller (1985c) suggested that these virulent, species-specific pathogens may provide an effective natural urchin control within kelp beds, achieved by seeding with urchins infected in the laboratory. Similar methods of germ warfare have been attempted with rabbits in terrestrial forest areas (Myxomatosis) with mixed and uncontrollable results.

Some of the early ideas about the interactions between predator and grazer populations have been questioned. The aggregation of urchins grazing along the edge of the kelp beds has been shown to be purely a feeding response (Vadas *et al.*, 1986) although such aggregations were originally believed to be defensive reactions to predators (Bernstein *et al.*, 1981). Miller (1985a) also maintains that data on stomach contents for lobsters, crabs and fish show that these populations cannot maintain a control over sea urchin populations. Evidence points to the sea otter as being the controlling factor in other temperate sea urchin species. This has certainly been shown to be the case in Alaskan kelp forests (Dayton, 1975).

d. Harvesting of *Ecklonia* species

South Africa, Australia & New Zealand

Ecklonia radiata is the dominant kelp species in southern Australian and in New Zealand coastal waters and *Ecklonia maxima* is the dominant kelp species in South African waters. Neither species is harvested in any great quantity at present but both species have very long stipes and are sources of good quality alginates.

In Australia Kennelly (1987a,b) has shown how the recovery of a kelp forest after the removal of mature plants was dependent on the season at which the mature plants were removed. If plants were removed in the winter months, normal settlement and recruitment of juvenile plants occurred and a new canopy cover was established rapidly. If plants were removed in the spring, summer and autumn, however, the cleared area was initially settled by a dense turf of red algae which inhibited the settlement of gametophytes or the development of young sporophytes in the winter months.

In South Africa a great deal of research has been undertaken into the energetics and population dynamics of the species which forms part of the food web for the commercially

important rock lobster fishery. As a result of this 20-year-long, ongoing, work, it is unlikely that *Ecklonia* harvesting will be allowed due to the key role the kelp has been shown to play in the primary productivity of the coastal ecosystem (R. Anderson, pers. comm.). The stipes of drift-line *Ecklonia* are still collected from the beaches, air-dried, baled and sold on the world market for alginate production (H.T. Powell, pers. comm.).

e. Harvesting of *Lessonia* species.

Chile

Lessonia nigrescens and *Lessonia trabeculata* are important canopy-forming kelp species in Chile which are harvested by cutting the stipe just above the holdfast. It is known that the harvesting method results in the subsequent loss of the holdfast and associated fauna. Harvesting of the kelp is for export, with a total mass of 10,000 t dry weight in 1987 (Vasquez & Santelices, 1990). In harvested kelp beds the plants become more susceptible to grazers both on the outside and within the holdfasts. The increased grazing results in reduced juvenile kelp recruitment and plants of *L. trabeculata* become more easily removed by water currents (Vasquez & Santelices, 1990).

C. MARINE AQUACULTURE EFFECTS ON KELP BIOTOPES

There are both direct and indirect effects of various forms of marine aquaculture on kelp biotopes. These can be summarised as:

- the collection of non-kelp species as feed material or for stock
- nutrient input from uneaten food, faecal and urinary wastes from fin-fish cages, crustacean cages and around shellfish rafts and trestles
- poisoning from chemicals used principally to control disease, sea lice and micro-organisms (Beveridge *et al.*, 1997)
- siltation from detrital waste

Gowen & Bradbury (1987) have reviewed the ecological impact of salmonid farming.

Material used to stock an aquaculture system or given to the farmed species as food and then not removed at harvest, is released as waste material. Food losses vary with species and system, food conversion ratios being a good indicator of loss to the environment. Direct measurements, using video recording techniques, suggest that, in the cages of intensive marine salmon farms, some 5-10% of food is typically not eaten. In poorly run farms the figures may be much higher (Beveridge *et al.*, 1997), due to currents rapidly dispersing the food beyond the reach of the fish. However, organic and chemical wastes are now being reduced. In salmon farming, for example, nitrogen and phosphorus wastes per unit production have been steadily falling thanks to improvements in feeding practices and feed formulation. Food conversion ratios (weight of food fed : biomass of fish produced) have dropped from 2.4 : 1 to 1.3 : 1 over 25 years, while dietary nitrogen and phosphorus levels have fallen from around 7.8% to 6.8% and from 1.7% to 0.8%, respectively, over the same period. Scope for further reductions is limited, however; as phosphorus inclusion levels in many commercial feeds already approximate the dietary requirements and nitrogen levels in diets are, if anything, increasing and so excess nutrients are released into the environment. Although fish cages are usually positioned over sedimentary substrata, plumes of waste could stream into kelp forests, leading to anaerobiosis due to the oxygen demand of the

decomposing material. The detrital rain from the cages could act in a similar way to terrigenous silt, reducing light penetration through the water column and smothering the algal surfaces. As a minimum impact the localised increase in nutrient levels might produce local eutrophication effects, particularly at slack tide.

A wide variety of chemicals are used by the mariculture industry, including compounds employed in and applied to construction materials (e.g. plasticisers and antifoulants), pesticides. (e.g. “Ivermectin” used to control sea lice on farmed salmon) and chemotherapeutants. Potentially the most serious effect of marine aquaculture could be the impact of anti-microbial compounds on benthic ecosystems, in view of the importance of detrital cycling, but as yet the microbial ecology of kelp biotopes is little known.

a. Case studies UK

We believe there are unpublished environmental impact assessments for Scottish fish farms. Such information is regarded as commercially sensitive and is not generally available. There do not appear to be any impact reports on the effects of other forms of marine aquaculture.

b. Case studies elsewhere

None known.

D. INDIRECT EFFECTS

Detecting the environmental impacts of human activities on natural communities is a central problem in applied ecology. It is a difficult research topic because human perturbations must be separated from the considerable natural temporal variability displayed by most populations. In addition, most human perturbations are generally unique and thus unreplicated. This raises the problem of deciding whether observed local effects are due to human intervention or to the natural differences in temporal patterns that often occur among different sites. These problems can be successfully addressed with the Before-After/Control-Impact (BACI) sampling design, in which Impact and Control sites are sampled contemporaneously and repeatedly in periods Before and After the human perturbation of interest (Schroeter *et al.*, 1993).

1. Eutrophication

The marine environment has a capacity to absorb and recycle a considerable amount of natural waste products (those produced by marine animals themselves, for example) via well-developed detritivore communities. The simplest form of marine pollution arises from local or more widespread overloading of this capacity, through disposal into coastal waters or at sea of excessive amounts of inorganic nutrients (from sewage or agriculture) or organic material (from sewage or industry). The addition of excess inorganic fertilisers to cropland where the nutrients cannot be held within the soil results in seepage of nutrients into the groundwater as well as into surface run-off water. Either through ground seepage or drainage into the river systems, these excess nutrients are ultimately delivered to the coastal waters. In addition, nutrient rich sewage water is run off into the river and coastal waters, sewage sludge is dumped in coastal waters (although this will cease in the near future) and large volumes of untreated or only partially treated sewage waste enters coastal waters from the numerous

coastal towns and villages deemed too small to warrant the construction of a complete treatment plant. Industrial organic waste may also enter coastal waters, either through the sewage system or from coastal water dumping of solids.

Excessive nutrient inputs may alter the balance of food chains, eliminate sensitive species, and change the composition of benthic communities, in severe cases completely altering their structure. The increase in the levels of macronutrients (particularly nitrogen and phosphorus) in European coastal waters results in the excessive growth of ephemeral species of macroalgae (commonly referred to as green tides where the effects are visible on the shore). The increased nutrient levels can also result in increased turbidity of the coastal water due to more prolific growth of phytoplankton. Both these possibilities could result in damage to kelp biotopes.

The competitive advantage given to mussels in the vicinity of sewage outfalls (filtering the plume of particulate matter) has significant ecological connotations, especially for marine benthic algae (Fletcher, 1996). For example, reports suggest that mussels are unsuitable substrata for many algae; they compete for available substratum space, have been reported to cover the surfaces of algae, and act as very efficient filters of potentially settling spores. Not surprisingly, therefore, several authors have linked increased mussel populations with declines in algal settlement and establishment, leading to the impoverishment and elimination of the macroalgal biotopes. The effects of eutrophication have been best studied in the Baltic, where there are no kelps, but their ecological role is played by *Fucus vesiculosus*, which grows subtidally there (see below).

a. Case studies UK

None known

b. Case studies elsewhere

Baltic Sea

During the last few decades, eutrophication of the Baltic Sea has increased dramatically. Estimates of nutrient input and measured nutrient concentrations in the open water in the 1990s are many times those in the 1950s - before large-scale nutrient input started. The increased nutrient availability in the photic zone of the open Baltic has led to increased pelagic primary production and consequent sedimentation of organic matter. Studies in locally eutrophicated coastal areas from all over the Baltic Sea region have shown the same general pattern of changes in the macroalgal vegetation:

- decreased occurrence of perennial red and brown algae, especially of *Fucus vesiculosus* - which may affect the entire ecosystem as many epiphytic and free-living invertebrates are dependent for at least part of their lives on these plants for substratum, food and shelter
- increased occurrence of fast-growing filamentous algae
- the formation of loose-lying algal mats, the decomposition of the lower layers of which result in anoxia in the covered substratum

The lower limit of occurrence of *F. vesiculosus* and the depth at which the maximum biomass of the species occurred became significantly more shallow between the 1940s and 1984, but there was little additional change by 1996 (Ericksson *et al.*, 1998). The most probable factor influencing the depth changes in the population distribution was decreased light penetration in the water column, caused by a general increase in phytoplankton production.

2. Pollution

Many chemicals foreign to the marine environment are toxic, whether they are naturally occurring (e.g. crude oil) or man-made (many pesticides). Locally lethal concentrations may have a direct impact on communities by eliminating many or most species. Frequently, toxic compounds become concentrated during progress along a food chain, accumulating in and selectively depleting the top predators; not only are these conspicuous species (such as otters or seals) often of special public or conservation interest, but their removal may have knock-on consequences for the whole structure of a particular ecological community. Only recently has it been widely appreciated that relatively low concentrations of many toxic compounds may affect species through subtle mechanisms leading to, for example, immune system impairment, reduced reproductive success, or developmental aberrations. The toxic effects of oil pollution fall into two categories (Lobban & Harrison, 1994):

- those associated with the coating of the organism
- those due to disruption of metabolism by the uptake of hydrocarbons

Regarding the first of these, the mucilaginous slime covering of kelps is thought to act (serendipitously) as a protective device against coating by oil (O'Brien & Dixon, 1976). Although the oil retained in the canopy of offshore *Macrocystis* beds, following a spill at Santa Barbara, adhered tightly to the kelp blades reaching the surface, removal of the oil layer revealed healthy tissue beneath it. Observable damage to the kelp plants in the beds was negligible, presumably because they were "saved" by mucus secretions.

The metabolic effects of hydrocarbons on kelp physiology may be serious. The application of three different crude oils to the thallus surface of *Laminaria digitata* reduced photosynthetic rates during emersion relative to controls (Schramm, 1972). In *Macrocystis*, 10-100 ppm of unspecified fuel oils in emulsion with sea water reduced photosynthesis by 50% during 4-day exposures (O'Brien & Dixon, 1976). In young blades, the photosynthetic capacity was completely reduced after 3 days exposure to a 1% emulsion of diesel oil in sea water; boiler fuel, containing a higher proportion of toxic components, was even more algicidal. More recently it has been found that reductions in rates of photosynthesis vary with the type of crude oil, its concentration, the length of exposure, the method of preparing the oil-seawater mixture, and the irradiance used during the experiments (Lobban & Harrison, 1994). Although *Macrocystis* fronds may be exposed directly to floating oil because of their buoyancy, *Laminaria hyperborea* fronds, being almost exclusively subtidal, would not come into contact with freshly released oil, but only to sinking emulsified oil and oil adsorbed onto particles.

The kelps are relatively insensitive to the dispersants used in oil-spill cleanups, but faunal elements of kelp biotopes may be seriously damaged by oil pollution. Oil is known to interfere with the ability of lobsters to detect the sex pheromone that triggers mating, and with the normal feeding behaviour of sea-anemones (Beveridge *et al.*, 1997).

a. Case studies UK

Early oil-spills in the UK, such as that of the Torrey Canyon on the Scilly Isles, are now not particularly relevant as it is widely believed that much of the ecological damage was due to the use of highly toxic dispersants which have now been replaced by relatively non-toxic chemicals.

Information on the effects of the Milford Haven oil spill (Sea Empress) on kelp biotopes are due for publication in late 1998.

b. Case studies elsewhere

Norway

In Norway, *Laminaria digitata* grown in large concrete basins was continuously exposed to diesel oil for two years. With diesel oil at 130 µg per litre, lengthwise growth was reduced by about 50% (Lobban & Harrison, 1994). At the lower concentration of 30 µg per litre there was no overall inhibition of growth. After two years of continuous exposure, the plants completely recovered during a subsequent oil-free growing season.

The Amoco Cadiz oil spill in Brittany had no significant effects on *Laminaria* spp. (Lobban & Harrison, 1994). The consequences for other faunal and floral components of the kelp biotopes are not known.

3. Channel dredging and coastal alteration

In order to renew or enlarge navigational channels, extensive dredging may take place. This involves removing the seabed, which results in the suspension of the fine silt and clay fractions of the sediment. This fine sediment may be deposited by the inshore currents either locally or at a considerable distance from the dredging operation. The additional sediment load will increase local turbidity. The addition of breakwaters, promenades and sea defences to EU coasts is becoming commonplace. These constructions inevitably result in changes in the depositional and erosional patterns of the local coastal area. These changes may be gradual and continuous or may be catastrophic (storm-related) but intermittent. Gradual but continuous changes are the norm on mobile depositional shorelines such as much of the east coast of England. Where an area of shore is protected with solid defences, erosional scouring increases adjacent to the ends of the protected area. Where constructions result in the formation of tide driven or wind and wave driven eddies, the scouring may take place at a considerable distance from the structure.

There have also been a number of reports of coastal eutrophication problems arising as a result of hydrographical alterations, construction work, sand movement etc. limiting tidal interchange (Fletcher, 1996).

a. Case studies UK

None known. However, in the North Sea the construction of sea defences and other man-made structures provide additional substrata which are colonised by kelp species.

b. Case studies elsewhere

South Africa

Changes within kelp beds as a result of increased silt load have not been studied. Within Saldanha Bay (South Africa) the construction of an ore-loading facility resulted in a major increase in the silt load within the bay which led to the loss of the commercial harvest of *Gracilaria* sp. Despite the return to normal sediment loads in the water column, this species had not recovered to harvestable populations after 10 years (J. Bolton, pers.comm.).

Italy

The previously dominant large brown algae in the Venice Lagoon were adversely affected when channel excavations limited the water exchange patterns and this led to a build up of nutrient levels and eutrophication within the lagoon. The sewage-related floristic changes included a decline or disappearance of a number of algae belonging to the *Cystoseira* association, and their replacement by green algae such as *Codium fragile* and *Ulva fasciata*, which are more readily adaptable to the high nutrient loadings.

4. Sediment loading

The deposition of organic matter (acting like silt) is increased in the vicinity of sewage outfalls and this can exert a number of detrimental influences on marine benthic algal communities (Fletcher, 1996). The sediment can:

- cover all available substrata interfering with the processes of spore (and larval) attachment and recruitment
- smother young germlings resulting in their growth and development being inhibited.
- in combination with water movement, abrasively scour surfaces settled with spores.
- (as deposits on algal thalli) reduce photosynthetic activity while at the same giving competitive advantages to species and life-forms of algae that are better adapted to life in areas of siltation

All the above-described detrimental influences of increased sedimentation on benthic communities have been well-recognised and have been offered as explanations for the decline of kelp beds off the coast of southern California. Devlinny & Vorse (1978) showed that sediments interfere with *Macrocystis* gametophyte development. A similar detrimental effect of silt on zoospore development was demonstrated for *Laminaria saccharina* by Burrows (1971). The kelp *Saccorhiza polyschides* is tolerant of sediment layers, however, when the substratum is not too steeply sloping (Santos, 1993). Changes in algal zonation patterns and depth distributions as a result of increased sediment loading have been reported (Fletcher, 1996). For example, a reduction in the kelp depth range has been reported in the vicinity of sewage outfalls with plants generally restricted to shallow water and very few new kelps present under the canopy of the older plants.

a. Case studies UK

There are sediment traps at Skomer and in the Menai Straits, where long-term monitoring programmes have been initiated. The results of these continuing studies are not yet available.

b. Case studies elsewhere

California

Schroeter *et al.* (1993) examined the ecological effects of the cooling water discharge from a coastal nuclear power plant in southern California on *Macrocystis* forest. Relative to control populations, there were statistically significant reductions in density of snails, sea urchins, and starfish, all of which occurred primarily on rocky substrata. All of the reductions were larger at the impact station about 0.4 km from the discharge than at a second impact station 1.4 km away. The most plausible mechanisms for the declines seem to be linked to the turbidity plume created by the power plant and the resultant increase in suspended inorganic and organic materials (+46% at the impact site nearest to the discharge). Any associated flux of fine particles on rocks would have deleterious effects on many of the species inhabiting the

hard substrata. Populations of two filter-feeding species, a gorgonian coral and a sponge, showed relative increases in density.

5. *Effects of the removal of predator species.*

The harvesting of one or more species from a biotope may result in an ecological imbalance. If this is not ameliorated by the influx of replacement individuals of the harvested species, then long-term shifts in the composition of the biotope may occur. The Californian giant kelp forests provide the best-known examples of the effect of predator removal on kelp biotopes. With the near-extinction of the sea otters for their fur by the mid-nineteenth century, sea urchins were no longer controlled and urchin barrens were created, as already discussed. The sea otter is now making a comeback under protection, but does not appear to be having any effect on urchins as yet. In eastern Canada, the lobster fishery was similarly implicated in the explosion of urchin barrens in the 1970s but definitive evidence is still lacking.

a. Case studies UK

None known

b. Case studies elsewhere

California

A fishery for red urchins, *Strongylocentrotus franciscanus*, which became extensive in the Californian kelp forests in the late 1970s, has resulted in a decline in their density since the mid 1970s. A study by Dayton *et al.* (1992) found that the Point Loma (San Diego) kelp forest showed significant recovery during the year after the 1982-84 El Niño, although a similar degree of recovery had taken more than 5 years in the 1960s. The reduction in the urchin population was cited as an important contributor to the faster recovery of the kelp forest. Dayton *et al.* considered that, in the absence of evidence for increased recruitment or temperature effects on urchin grazing demand, the destructive grazing observed during and after the El Niño of 1957-59 resulted from reductions in kelp standing stock and productivity below levels necessary to satisfy the existing grazing demand.

6. *Effects of introduced species*

The increase in non-native marine species, introduced principally by aquaculture and in ballast water, is causing concern in Europe. One introduction of potential significance to kelp biotopes is the Japanese kelp, *Undaria pinnatifida* (wakame). This species has recently spread to the south coast of England from northern Brittany, where it was introduced for aquaculture, and it is thought likely to compete with the native *Saccorhiza polyschides*. The brief introduction of *Macrocystis pyrifera* to French waters in the 1970s, which was stopped by international pressure, could have had disastrous effects on all the native kelps and their associated biotopes. *Macrocystis* fronds can reach 60 m in length, and a single frond can gain 36 g per day, and thus would have competed with native species for space, light and nutrients.

a. Case studies UK

None known

b. Case studies elsewhere

None known

7. *Global warming*

Even in the relatively short term, global warming by the anticipated 1-3°C within the next century, could have an effect on distribution of the kelp species that occur in the UK. For example, *Laminaria ochroleuca* could extend its distribution northwards up the western coasts of the British Isles (see section I.C). Some research work has been undertaken on the effects of the periodic short-term temperature anomalies known as El Niño which impact on the kelps of the western Pacific (see section IV.B.2). Unfortunately, global warming effects span multiple generations of scientists and governments and the need for very long term monitoring and research has only recently been appreciated.

a. Case studies UK

None known

b. Case studies elsewhere

None known

8. *Ozone layer depletion (leading to increased UV penetration)*

Studies on the effects of UV-radiation on macroalgae have been rather scattered, both geographically and taxonomically (Dring *et al.*, 1996). Germination of zoospores and the growth of gametophytes in several *Laminaria* spp. were reduced after exposures of more than 1 h and gametophyte photosynthesis did not recover after exposures longer than 4 h. Although photosynthesis in sporophytes was reduced after exposure, recovery took place during the following 24 h period. Sensitivity to UV decreased from gametophyte to sporophyte and with increasing age of the sporophyte (Dring *et al.*, 1996). Some effects of increased UV-A and UV-B on the survival and physiology of other species of seaweeds have also been investigated (see Lüning, 1990). Changes in survival and growth patterns in natural kelp populations as a response to increased UV-radiation have not been monitored. UV light has been implicated in the kelp disease of infection with the brown algal endophyte *Streblonema aecidioides* (Schaffelke *et al.*, 1996). This causes deformation of host thalli, but damage was worse at 2 m than at 5 m, and this was interpreted as being due to lower levels of UV at 5 m depth.

a. Case studies UK

None known

b. Case studies elsewhere

None known

E. KEY POINTS FROM CHAPTER V

Direct effects - kelp harvesting

- Drift weed was traditionally collected in Europe but now living kelp forests are the main harvest.
- The most significant human activity directly affecting kelp biotopes is mechanical, commercial scale kelp harvesting for alginates.

European, experimental

- Canopy removal of *Laminaria hyperborea* stimulates the growth of small plants.
- Canopy cleared areas are colonised first by the rapidly growing *Saccorhiza polyschides* and after a few years *L. hyperborea* again dominates.
- Recolonisation of *L. hyperborea* in cleared areas at the Isle of Man led to biomass equal to control plots after 3 years but the population and community structure differed.
- Experimental harvesting appears to be less damaging than commercial harvesting, so research results must be extrapolated cautiously.

European, commercial

- In Norway a harvested forest of *L. hyperborea* recovered kelp biomass within 3-4 years, but individuals were only half the size of those in the pristine forest.
- Harvested kelp biotopes in Norway were species-poor compared with control sites. Older kelp plants, which are removed by harvesting, support very much more diverse and populous epiphyte communities.
- *L. digitata* forest is extensively harvested in Brittany although little information is available on the overall consequences of the harvest on the ecological balance within the kelp beds.
- The effects of kelp harvesting on the complete ecology of European kelp beds, especially in relation to commercially valuable species, are not known.
- The effects on associated coastal biotopes of the removal of biomass from coastal ecosystems by kelp harvesting, are not known.

Non European

- Harvesting of *Macrocystis pyrifera* in California is non-destructive of individual plants and appears to stimulate kelp recruitment.
- Complex and poorly understood interactions have been shown to occur in California and eastern Canada between kelps, urchins and urchin predators (lobsters, wolf-fish and sea otters).
- Each different kelp species shows particular responses to harvesting and the effects of harvesting or other causes of kelp removal must be determined for each target species.

Marine aquaculture

- Releases of uneaten food and faeces contributes to eutrophication but effects may be mitigated by tidal flows.
- Chemicals used as therapeutic agents for the fish may be toxic to other components of coastal ecosystems - including species that may be key to the health of kelp biotopes.
- Anti-microbial agents could be particularly harmful to kelp biotopes because of the importance of bacteria in recycling of kelp detritus.

Indirect effects

- Indirect effects of human activities are difficult to detect and may require the use of Before-After/Control-Impact design experiments.
- Eutrophication is due largely to sewage discharges and agricultural run-off and has some obvious effects, raising depth limits of large brown algae such as kelps and subtidal (Baltic) *Fucus* due to reduction of light penetration by persistent phytoplankton blooms.
- Polluting chemicals such as spilled oil and clean-up dispersants may not be directly damaging to kelp plants but may adversely affect kelp physiology and may have serious short and long term effects on invertebrates in kelp biotopes.
- Increased sediment loading due to dredging etc., sewage discharges, changed agricultural practices, and power station effluent, affects kelps at the spore settlement stage; filter-feeding invertebrates may increase in density and compete for space with the kelps.
- Harvesting of kelp grazing species (particularly urchins) permits recovery from urchin barrens; harvesting of urchin predators may initiate urchin barrens. The effects of human activities on barrens formation are poorly understood.
- Introduced kelp species (such as *Undaria*) may compete with the native species for space, light and nutrients. More research is required.
- Global warming could affect the distribution of kelps, which are primarily cold-temperate species. Very long term (multiple generation) research programmes are required to monitor these changes.
- Increased UV levels caused by ozone depletion have been implicated in a kelp disease; UV light is damaging to all kelp species tested, but long term field research has not yet been undertaken.

VI MONITORING AND SURVEILLANCE OPTIONS

A. INTRODUCTION

In the context of this report, “monitoring” is defined as:

- ‘surveys undertaken to detect departure from agreed or predicted amounts of disturbance’

whereas “surveillance” is considered to mean:

- ‘an attempt to detect unanticipated impacts, particularly ones that may be wide ranging, subtle or that only slowly become large and obvious’ (Hiscock, 1998a).

The development of methods for such ‘monitoring’ and ‘surveillance’ of marine conservation areas in the UK are at a relatively early stage of development.

The fundamental difficulties involved in the monitoring or surveilling of kelp biotopes can be highlighted from the following selected examples:

- Kelp biotopes are underwater, and may extend offshore into areas with dangerous currents and exposed to storm action, and in depths of up to 25 m.
- Many of the species of plants and animals found in kelp biotopes are small and difficult to distinguish.
- There is a high level of spatial and temporal variability in kelp biotopes, which means that trends are difficult to establish against the high background of natural variation.

The marine environment is not a simple or relatively safe one in which to work, and in comparison to other complex biotopes on this planet, very few people are working on coastal marine ecological topics. Unfortunately, long term environmental projects require skilled scientists and are expensive, requiring a continuity of expertise and personnel, with both legislative and financial support. In the early 1970s, investigations of ecological interrelationships in marine habitats became deeply unfashionable (with regard to research funding) and this has left us with considerable gaps in our basic understanding of the ecology of coastal habitats (see Chapter VII).

In any monitoring programme, the above factors will need to be accepted and budgeted for. It must also be recognised that there are few short cuts or high technology solutions (e.g. aerial survey, satellite imagery) available for the derivation of detailed, accurate and reliable biological data, and that even simple sample collecting can be very time consuming, especially from remote locations.

Biological data apart, there are accepted methods and practices for monitoring changes in the physical and chemical nature of coastal waters. The routine and regular collection and analysis of data from representative locations within and without the designated area of an SAC should be planned. Weather data, seawater temperatures, salinity, wave height and direction, turbidity and irradiance at depth should all be collected, collated and analysed, ideally on a semi-continuous basis. Regular collections of standard measurements such as nutrient levels, chlorophyll concentrations in the seawater and scans for possible traces of pollutants should also be made. Monitoring devices deployed *in situ* should be used for data collection wherever possible.

Wherever possible standard measurements of a physical and chemical nature should be collected simultaneously at all SACs and the data analysed and published through a central laboratory. All biological data collection programmes should also liaise and report through to the central laboratory. This would enable the rapid transmission of information on potentially dangerous conditions or population fluctuations to be notified to all other UK marine SACs and the laboratory would also serve as the liaison point with other participants in European wide marine SACs.

B. OVERVIEW OF OPTIONS

The morphology of kelp plants makes them relatively easy to study in the field because the individual plants are large and easy to count, and because the basal meristem permits the growth of plants to be measured *in situ* by following the movement of punched holes away from the base of the blade. Consequently, kelps have probably received more scientific attention than any other group of seaweeds, and the habitats dominated by them have also been fairly well studied (see details described and references cited in Chapter III). Nevertheless, there are significant gaps in our knowledge of the ecology of even the commonest kelp species, and much larger gaps in the information available about the animal and plant species that are associated with kelps in kelp forests.

- It is still not possible to define which of these associated species are really diagnostic of, or endemic to, kelp ecosystems, as opposed to those which are favoured by the physical, chemical or biological conditions that a kelp forest creates.

Clearly, the kelp species, themselves, are diagnostic of kelp biotopes, and they would certainly be selected for inclusion in an 'ACE' survey (Abundance scale, Check list and Exact location; Hiscock, 1998a) as 'important' or conspicuous species, as 'keystone' species, as 'indicator' species and, possibly, also as 'sensitive' species, in view of their susceptibility to human impact (see Chapter V). However, in spite of the wealth of information about the ecology of kelp species, it is not easy to select one or two attributes of kelp plants (e.g. density of plants per unit area, stipe dimensions, blade dimensions, growth rate of blades) that could be easily measured in the field and used as an indicator of the health of a kelp forest or ecosystem.

It is also possible that some of the floral and faunal species associated with the blades, the stipes or the holdfasts of the plants, or the substratum or water within the kelp forest, could provide an indication of impending changes in the forest *before* the large, perennial kelp plants, themselves, begin to react. However, our knowledge of these associated species has barely got beyond the descriptive phase, and we are not yet in a position to say which species should be targeted as potentially sensitive indicators of change (see Chapter VII.B.3.d).

- The identification of the keystone species in kelp biotopes should receive the highest priority.

Much of the basic research on kelp biotopes that has been undertaken so far, particularly in Europe, has not been directed to the management of these biotopes in their entirety although, as discussed in Chapter V, some recent work has sought to examine the effects of harvesting the kelp on the subsequent recovery of the kelp and its associated species.

In view of the global paucity of management-directed studies on kelp beds, it is difficult to answer even the simplest of management questions. Monitoring options suggested here can, therefore, be based on little more than informed speculation. Firm recommendations could be offered only when the agencies responsible for managing kelp biotopes had reached

decisions, based on biological and environmental evidence or legal obligations imposed by statutory bodies, about precisely *what* is to be monitored and *why* it should be monitored.

Given adequate background and species specific information, scientists will be able to develop optimal methods for the provision of reliable, reproducible, accurate and relevant data to contribute to the management of the biotope. Conservation and management agencies should make full use of CASE (or CAST in Northern Ireland) research studentships as a cost-effective way of tackling specific management issues in co-operation with marine biologists based in universities.

- The precautionary principle should be adopted until such time as dependable, scientific methods for monitoring and surveilling all necessary aspects of the ecology of kelp biotopes have been developed.

C. CASE STUDIES

Apart from the studies of the effects of kelp harvesting discussed in Chapter V, there has been almost no scientific work in European kelp forests that has had the objective of monitoring or surveying change within kelp biotopes. In other parts of the world, and notably in California, South Africa and Australia, however, scientists have been interested in or funding has been available for examining the effects of some environmental impacts on the inhabitants of kelp forests. Two methodological examples deserve mention here.

California

Schroeter *et al.* (1993) conducted a case-study of the impact of human activities on the invertebrates of kelp forests in Southern California, which attempted to separate human perturbations from the considerable natural temporal variability displayed by most populations, using the Before-After/Control-Impact (BACI) sampling design, in which Impact and Control sites are sampled contemporaneously and repeatedly in periods Before and After the human perturbation of interest.

In systems where plants and animals are long-lived and recruit only sporadically, the rates of change in population density are often so low that sampling more than a few times per year will introduce serial correlations in the data. As a result, for studies of only a few years' duration, few samples will be taken. The resultant small sample size means that the tests of the assumptions underlying the statistical analyses (e.g. independence and additivity), will have low power. This injects uncertainty into the conclusions. Small sample size also means that the power to detect any but very large effects will be low.

In this study, sampling periods of 2-3 years both Before and After the impact were not long enough to detect a halving or doubling of population at the impact site. Nevertheless, the authors concluded that there were significant environmental impacts because:

- the effect size was generally very large (almost 75%);
- there was a consistent pattern among species;
- there were two Impact sites, and effects were larger at the site nearest the discharge;
- the observed effects accorded with physical changes that could be linked with the source of impact;
- a number of alternative mechanisms, unrelated to the source of impact, were examined and rejected.

Relative to control populations, there were statistically significant reductions in density of snails, sea urchins, and sea stars, all of which occurred primarily on rocky substrata, although populations of two filter-feeding species, a gorgonian coral and a sponge, showed relative increases in density. The authors concluded that:

“... monitoring studies of relatively long-lived organisms will often have low power to detect ecologically significant changes in density”.

Although their study of kelp forest organisms extended over nearly 6 years, the resulting statistical tests generally had power of <30% to detect a doubling or halving in density at a significance level of 0.05.

“In such a community it would be a mistake to conclude that there were no significant ecological effects based on conventional hypothesis tests. Unless there is a willingness to accept the fact that changes in natural populations of the order of 50% will often go undetected, the standards and types of evidence used to demonstrate environmental impacts must be changed”.

Australia

On the basis of a study of the fluctuations in the distributions and abundance of species in sublittoral kelp forests in New South Wales, Kennelly & Underwood (1992) concluded that the structure and dynamics of such systems

“... vary, and do not conform to predictions of simple models about processes in habitats dominated by one or a few large organisms. When kelp forests are described using quantitative data at several spatially replicated scales, few general conclusions can be made about the structure of these assemblages”.

- The implications of the above results for monitoring the effects of human and natural perturbations on the European kelp ecosystems are considerable.

D. METHODOLOGY ILLUSTRATIONS

The UK Marine SACs Project is conducting and publishing the proceedings of a series of workshops devoted to the development of monitoring and management programmes for marine SACs (Worsfold & Dyer, 1997; Hiscock, 1998a). Methods that should be included as part of a monitoring programme would include the following.

1. Mapping the extent of the biotope

a. RoxAnn.

At Newcastle University, the BioMar project (Davies *et al.*, 1997) has developed a survey protocol for mapping the sea floor using acoustic techniques, validated by biological sampling, with the data stored and analysed using geographic information systems (GIS). A *RoxAnn* processor was used for acoustic mapping. Acoustic data have no biological meaning unless they can be related to biological assemblages, determined from direct observations or samples of the seabed at predetermined point locations (see Worsfold *et al.*, 1997 for further discussion).

Based on the video samples, grab samples, diver surveys and previous detailed records of biological surveys in a Scottish sea-loch (Howson *et al.*, 1994), a map of the sea-bed showing the predicted distribution of a total of 23 biotopes was constructed. Acoustic mapping using a *RoxAnn* system provided data on the physical nature of the sea-bed (depth, smooth/rough, soft/hard), and biological information was then added to the acoustic data. It was not found practicable to relate each biologically based biotope classification to a particular acoustic pattern. Instead, the biotopes determined from a biological approach had to be grouped into 15 much broader categories in which the species component was generally lost and in which there was no possibility of indicating a gradual change from one life form to another.

The recent deployment of the *RoxAnn* method for a few days in Strangford Lough confirmed its value in mapping the distribution and extent of beds occupied by different benthic animals (M. Service, pers. comm.) and it is possible that the *RoxAnn* method could be further developed to allow the identification of areas where kelp forests are present. Without subsequent checking by more labour-intensive (and expensive) methods, the method would not differentiate among different kelp species, and neither could it provide useful information on density, growth rates or overall health of the biotope, but it may offer the most cost-effective way of mapping the extent of the kelp forest in an SAC.

b. Aerial surveys

It has often been suggested that subtidal kelp beds could be identified from aerial photographs. This method could then be used to make a very broad-scale, rapid assessment of the extent of kelp forests in inshore areas. Attempts to put this idea into practice in Strangford Lough, Northern Ireland (A. Portig, pers. comm.), have largely foundered on the virtual impossibility of getting sunny, calm conditions and a low spring tide to coincide with the availability of an aircraft. The images are also difficult to interpret quantitatively if the orientation of the photograph departs significantly from the vertical. In practice, therefore, and especially given the prevailing weather of the British Isles, it seems that this approach is unlikely to yield detailed, quantitative information, although it could be used to provide a broad over-view of inaccessible areas of coastline.

2. Sampling for species diversity and population abundance

The methods being developed for monitoring marine SACs (Hiscock, 1998a) which are relevant to kelp biotopes are summarised below but, as with all benthic habitats, the patchy distribution of flora and fauna creates difficulties for objective sampling. The main questions raised are:

- what is the minimum sample area?
- should samples be distributed randomly or systematically?
- how many samples are needed in order to obtain an adequate representation of the species diversity and biomass of the site?

Hiscock(1998a) provides a discussion of all of these aspects, with particular reference to marine habitats, and also covers the additional question of when is the most appropriate or efficient season to sample a particular type of habitat.

a. Grab samples

Much of the early work on the extent and biomass of kelp beds in Scotland and Norway was based on samples obtained with a spring grab lowered from a boat (see Chapter III). The major disadvantages of this technique are that the surface area sampled is uncertain, and the grab leaves an unknown (and probably variable) proportion of the kelp population behind. Nevertheless, several of the ecological relationships established by this technique have been confirmed in subsequent work by divers, and it may appear to be a cost-effective way of monitoring kelp plants in relatively dense forests. However, the limitations mentioned above are so serious as to rule it out for detailed, quantitative work on the kelps, and the technique also fails to provide useful data on any of the associated species in the biotope.

b. *In situ* surveillance using abundance scales and check lists at exact sites (ACE surveys)

Quadrats of known size at an exactly located site are surveyed by divers and the occurrence and abundance of all species on a check list are recorded. This technique has been developed during the workshops preparing methods for the marine SACs project (Worsfold & Dyer, 1997), and is described in detail by Hiscock (1998b). Its efficiency in monitoring sublittoral biotopes has yet to be tested, but it is probably the only technique available for the quantitative recording and monitoring the species associated with kelp biotopes on a broad scale. The development of this technique with specific reference to identifying keystone species in kelp biotopes would make a suitable topic for a CASE/CAST research studentship.

c. Quantitative surveillance using photographs

Diver-operated cameras are used to record fixed quadrats at suitable time intervals, and the percentage cover of the most conspicuous species is subsequently determined using a grid of point quadrats over the enlarged or projected photographs. The application of this technique to sublittoral rock biotopes in marine SACs is described in detail by Hiscock and Bullimore (1998). In kelp biotopes, it would only be practicable for monitoring the more obvious flora and sedentary fauna of the substratum below a kelp canopy. The cover of the kelp plants, themselves, could not be determined using this technique because of their size and mobility in water currents.

3. *Monitoring rates of growth and production of kelp plants*

Measuring the growth rates of individual kelp plants by the “punched-hole technique (i.e. following the movement of punched holes away from the base of the blade) is an elegant method of monitoring the performance of plants *in situ*, and management agencies would be well advised to make use of it when they are carrying out underwater surveys. A random sample of 20-25 plants in a representative area of kelp forest or parkland should be marked by tagging the lower part of the stipe or the holdfast. A hole (3-5 mm diameter) should then be punched through each blade at a measured distance above the blade-stipe boundary. At intervals of 2-3 months during the spring and summer (depending on the growth rates of the plants) and less frequently at other times, the sites should be re-visited and the distance from the hole to the blade-stipe boundary re-measured. Once the hole is half-way along the blade, a new hole should be punched near the base. Using this technique, the growth rates of plants at different depths, or at different sites, within an SAC can be compared (yielding valuable basic information; see Chapter VII.B.3.b), and the effects of environmental changes (e.g. eutrophication, pollution, temperature or turbidity changes) on growth rate can be quantitatively established (Chapter VII.B.5).

The productivity of kelp plants can now be measured in the field using underwater fluorometers (“Diving PAM”; Beer *et al.*, 1998) or submersible recording oxygen electrodes (Birkett *et al.*, in prep.). Such measurements may provide a more rapid indicator of environmental change, but the need for technically elaborate and expensive equipment restricts the number of plants that can be examined. Nevertheless, academic work is continuing with the aim of modelling kelp productivity from continuous measurements of surface irradiance, combined with data on light penetration through the water, and such models may soon require *in situ* growth data for validation. Once this stage is reached, a broad picture of kelp performance may be obtainable from physical measurements made from the surface, verified by spot checks during diving surveys.

E. KEY POINTS FROM CHAPTER VI

General points

- The development of methods for such ‘monitoring’ and ‘surveillance’ of marine conservation areas in the UK are at a relatively early stage of development.
- A central laboratory for the analysis and assessment of data for all UK marine SACs would facilitate consistency of monitoring methods and promote the dissemination of information.
- Long term environmental projects require a continuity of expertise and personnel, with both legislative and financial support.

Overview of options

- There are significant gaps in our knowledge of the ecology of even the commonest kelp species, and much larger gaps in the information available about the animal and plant species that are associated with kelps in kelp forests.
- In spite of our extensive knowledge of kelp biology, it is difficult to pin-point variables that can be measured on plants *in situ* to monitor the health of a kelp forest or biotope.
- Our knowledge of the animal and plant species associated with kelps is at present too limited for us to be able to identify keystone species in kelp biotopes.
- Firm recommendations with respect to monitoring and surveillance can be offered only when decisions have been made, based on biological and environmental evidence, about precisely *what* is to be monitored and *why* it should be monitored.
- The precautionary principle should be adopted in all cases where there is inadequate data available, until such time as dependable, scientific methods have been developed for the monitoring and surveillance of kelp biotopes.
- There is a global paucity of management-directed studies on kelp beds. Basic research on kelp biotopes needs to be directed towards the development of the management of these biotopes in their entirety.

Case studies

- Monitoring studies of relatively long-lived organisms will often have low power to detect ecologically significant changes in population density.
- Changes in natural populations will often go undetected, unless the standards and types of evidence at present used to demonstrate environmental impacts are changed.
- When kelp forests are described using quantitative data at several spatially replicated scales, few general conclusions can be made about the structure of these assemblages.

Methodology illustrations

- The application of acoustic techniques for mapping kelp beds should be explored further.
- Large-scale surveys of the extent of the biotope are limited to acoustic survey or aerial photography, neither of which yield straightforward data.
- The patchy distribution of flora and fauna within kelp beds creates difficulties for objective sampling in order to estimate species diversity and population abundance.
- Of the monitoring methods developed to date for the UK marine SACs Project, only the semi-quantitative ACE surveys can encompass the kelps as well as the associated species in kelp biotopes.
- The development of methods for estimating the physiological “health” of selected species *in situ* within kelp biotopes may, in future, provide a sensitive tool for use within a management scheme.

VII GAPS AND REQUIREMENTS FOR FURTHER RESEARCH

A. INTRODUCTION

Subtidal coastal habitats are one of the least well researched biological subject areas in Europe. The kelp forests in particular cover vast areas of the near-shore environment and yet, because we were unable to investigate these habitats until relatively recently, we are still at the stage of making observations and listing the species that inhabit these areas. Most people in Europe can visit a terrestrial forest and appreciate the natural beauty of their surroundings, if not the ecological complexity that surrounds them. Even now, more than half a century since SCUBA was invented, very few people are able to enjoy the privilege of visiting a kelp forest, and only a fraction of those visitors can begin to assess the environmental complexity through which they are swimming!

Many of the gaps in our present knowledge of the biology and ecology of kelp biotopes will need to be filled before specific management questions can be answered and efficient and effective monitoring programmes be established. A few of the topics suggested below (section VII.B.) are already being addressed within the EU, if not with specific reference to UK waters.

Some management questions may be specific to kelp biotopes within UK waters but might be best addressed, at least initially, by consultation with national, regional and local conservation bodies elsewhere in the world. The problems of kelp biotope conservation in the UK are by no means unique and may have been addressed (at least in part) by nations with a longer history of the development and management of marine nature conservation. Much information on the legislative requirements, monitoring implementation and problems encountered in the protection of kelp biotopes elsewhere in the world will be equally applicable to the UK and EU. It is probable that other topics may be answered at least partially on the basis of published and unpublished work on kelp bed species from other parts of the world.

Kelp plants, particularly *Laminaria hyperborea*, which is the most common species in UK waters, are very long lived individuals in comparison to most of the marine plants and animals in the kelp biotopes (see Table 10). As such, the kelp plants themselves are not necessarily the best species to study for clues as to the well being of the kelp biotope. Any changes in the population of kelp within a kelp bed is likely to be the result of cumulative processes which have been continuing for several years, if not decades. The effective monitoring of the ecological health of a habitat usually involves selecting a range of sensitive species and studying these in some detail. At present, such species have not been identified for UK kelp biotopes.

Much of the basic biological and ecological information pertaining to the flora and fauna within UK kelp biotopes is at present unknown and it is probable that extensive research will be required in order to answer some of the most basic and specific management questions. The demands which may in future be required of the management of UK SACs are unknown. However, where a useful and potentially commercial species, such as kelp, and commercially important species, such as lobster, form part of a protected biotope, the preparation of a management plan must take into account that scientific evidence in support of conservation measures may need to stand up to scrutiny in a court of law.

As a result of the historical time and financial constraints on basic coastal ecosystem research, there is a serious shortage of information with which to provide detailed answers to questions of habitat conservation, monitoring and management. This section cannot attempt a comprehensive assessment of all the gaps in our understanding of the biology and ecology of the species found in kelp biotopes or the ecology of the biotopes as a whole. Nor can the requirements for further research be given in any degree of completeness or order of priority.

B. SOME SPECIFIC GAPS IN OUR UNDERSTANDING OF UK KELP BIOTOPES

1. *Introduction*

The more information that is available on the sensitivities of the key species and the species interactions that occur within kelp biotopes in different locations around the UK, the more effective and efficient will be the monitoring programmes devised for the SACs. With the present gaps in our knowledge, monitoring programmes may have to be devised which are initially much more complex, comprehensive and time consuming than would be the case under ideal circumstances.

Some of the readily identifiable gaps in our understanding are presented below in the form of a series of questions. The gaps are divided up into major groupings of questions on associated topics with a brief description of the problem and why this information is needed, followed by a brief suggestion on how the question might be addressed. The answers to some of these questions may already be known in part, and the methods which could answer such questions in UK waters may have been developed and used elsewhere in the world. Given the difficulties associated with data collection from subtidal ecosystems and with experimental work - both in the field and in the laboratory - using subtidal species, it is not surprising that our understanding of the kelp beds as ecosystems is very patchy. The questions identified have not been placed in any order of priority as this will vary with the perspective of the reader. Macroalgal physiologists, marine ecologists, population biologists and conservation agencies will all have a different range of questions and research priorities.

2. *Kelp biotopes*

a. Where are all the kelp beds?

The most comprehensive information available on kelp bed distribution in the UK is currently held in the MNCR database (D. Connor, pers. comm.). During the Second World War (1939-45), a team of four phycologists led by V.J. Chapman was provided with a small petrol allowance and an even smaller living allowance and, under some remarkably difficult conditions, attempted to estimate the standing stock of large, brown seaweed species useful to the war effort ("Strictly Marginal", G.E. Fogg. Published by the British Phycological Society). Since that time, no concerted effort has been made to plot the distribution of kelp beds around the UK. In coastal areas adjacent to University field stations or to marine research laboratories, information has been collected piecemeal over the years, but rarely analysed and published. More recently, and especially around Scotland, intensive subtidal surveys of parts of the coastline have been undertaken under the aegis of the JNCC (Marine Nature Conservation Review) and Scottish Natural Heritage.

Our present information on the distribution of kelp beds could be extended using high resolution satellite images to identify coastal areas with high chlorophyll signatures. These areas could then be surveyed for the presence or absence of kelps using a system such as RoxAnn. A combination of satellite images and geological survey maps with the kelp distribution maps might illustrate areas of coastline that appear suitable for kelp bed development but where, nonetheless, kelps are absent. Investigations of such areas might provide information on conditions which are detrimental to the development of kelp beds.

b. What are the geographical distributions of the different kelp biotopes?

In some areas of the UK, there have been major submarine biological surveys. Some of these surveys are recent and were conducted with the object of describing areas in the broad terms of the biotope complexes devised for the UK. Other surveys were conducted prior to the development of the marine biotope concept and, 20-30 years later, attempts are now being made to fit the old data into the new categories. It may be that some of the kelp biotopes defined to date are restricted to distinct geographical locations. If this were the case, it would be important to identify such areas and afford them the highest level of management and protection in order to conserve the habitat diversity within UK coastal waters.

A survey of the coastal waters throughout the UK would be needed in order to map the distributions of the biotopes. This project could initially be based on information gathered in order to answer question **a.** (above), and could be combined with other surveys already undertaken or planned. Surface based methods which will allow classification of benthic communities to the biotope level would need to be developed. The ideal equipment might be a remote controlled miniature submarine equipped with very high resolution remote video devices capable of broadcasting data to trained personnel.

c. Which species are found in kelp biotopes and where?

The MNCR database represents an excellent starting point for the construction of a complete list of species to be found in the various kelp biotopes of UK waters. Due to its youth and the infrequency of major surveys, this database cannot provide a complete list. Some gaps are present because the particular niche within the kelp biotope was not sampled (e.g. for holdfasts) or because expertise was not available to identify the flora and fauna accurately (e.g. section III.D., encrusting coralline algae).

The geographical variation in the component species for each biotope and species distribution limits would form a powerful tool for use in the conservation management and ecological monitoring of kelp biotopes in Marine SACs. Once the species composition of a site is known, shifts in the distribution patterns or the population dynamics of species can be identified and linked to local environmental changes, biotope exploitation or use, and to management practices.

It may not be practical to attempt to survey the entirety of a biotope at one time. A more complete list of species for a site might be acquired if specific niches within the biotope were investigated in some detail at each site. Thus, records of the epilithic flora and fauna could be obtained by trained divers; holdfasts, stipes and blades of kelp plants, sediment pockets etc. could be sampled separately; large, mobile species which are sensitive to human presence might be monitored from a fixed camera; the epifauna of attached understory algae or of

other faunal species might be collected using a contained anaesthetising method, such as has been previously used in terrestrial and pool habitats.

d. What species use kelp biotopes as nursery areas?

The biological surveys which have been undertaken within kelp biotopes have, of necessity, been limited to a single time of the year at most sites. As a result any species with a seasonal presence within the biotopes may not have been recorded. The juvenile forms of many species tend to be small, cryptic or are hidden within a habitat and again may not be recorded.

The presence or absence of juveniles of species within a biotope may be indicative of the stability of the ecosystem or of changes beyond the kelp biotope that may have a local effect. The juveniles of some species may form an important seasonal food supply for permanent inhabitants of the biotope. The kelp biotopes may form nursery areas for species of commercial importance such as lobster, crawfish, crabs, octopus etc. and, by careful management and conservation of the kelp beds, it may be possible to improve local catches.

At selected sites (possibly the candidate Marine SACs) around the UK, regular samples throughout the seasons (possibly monthly but at least quarterly) should be collected. These should be from the different niches within the kelp biotopes, which should be sampled specifically for the presence of juvenile species whose adults are known to live beyond the boundaries of the kelp bed. This could form part of a larger, more intensive survey or a separate, commercially slanted investigation. If the latter, the commercial species and their food supply species (possibly lobsters & juvenile bivalves) would need to be included.

3. Kelp biology and ecology

a. Distribution of kelp species

i. Which species of kelp are present at each location?

Although the locations of kelp beds around the UK have been approximately known, and the limits for kelp species have been determined by early researchers in the field, the coastal water temperatures of the UK are increasing relatively rapidly (Port Erin Marine Laboratory data set, Isle of Man). Therefore, much previously collected information may be out of date. The present extent of any migration of kelp species needs to be established, particularly with reference to species that have arrived relatively recently in the UK.

The distribution patterns of kelp species within biotopes may provide an indication of local conditions where these confer a competitive advantage to one species over another, and distribution patterns may therefore be a useful tool for monitoring long term changes at specific sites.

At specific locations around the UK, preferably representative of all the kelp biotope classifications, a regular check of the population structure and distribution of all kelp species should be made. This could then be compiled - together with local physical and chemical conditions - into a central database. Long term shifts in the patterns could be looked for. An annual check would be sufficient (provided that records were collected at the same developmental season at all the sites).

ii. Does the depth distribution of kelps change with geographical location?

It is normally assumed that, in the absence of a biological or geological factor controlling the lower limit of kelp growth, the attenuation of irradiance with depth - both in terms of total irradiance and in the total quanta of blue light available to kelp gametophytes - will determine the maximal depth at which kelp plants can grow. However, it is possible that other physical factors (e.g. pattern of daylengths during the year, water temperature, etc.) may affect this maximal depth. In Brittany, plants of *L. digitata* are the dominant species down to 6-10 m. below chart datum (Arzel, 1996). In the UK however, *L. digitata* is normally found to no more than about 2 m below chart datum; this difference is thought to be related to the differential competitive abilities of these two species near their temperature margins.

The establishment of a depth distribution pattern for the different kelp species with reference to geographical position could be a useful management tool. Fluctuations in the long term distribution patterns of kelp species within an SAC for example, might follow a pattern similar to that found on a geographical basis and act as a bio-indicator that the changes may be the result of environmental fluctuations on a global scale and beyond the control of the local management. Alternatively, the data could serve as a continual measure of the long term stability of a site against which short term fluctuations could be measured.

This data could be obtained as part of a long term, National project to monitor the ecological health of UK coastal waters, or as part of the kelp biotope monitoring programme. A series of permanent transect sites distributed in the different kelp biotopes around the UK would need to be inspected at regular intervals by teams of divers observing stringent data quality control, including the accurate identification of *L. digitata* and *L. hyperborea* growing in shallow water.

iii. Do kelp species compete with each other?

Different combinations of kelp species may be present at different depths within a given biotope, but the physical or biological factors which influence the mixture are not known. If an area of kelp is cleared, the substratum (in some UK waters at least, see section V.B.2.) may be colonised by the fast growing kelp *Saccorhiza polyschides*. After the first year, *L. hyperborea* begins to be re-established and, after the end of the second year, it has regained its dominance. Investigations on the effects of removing other kelp species have not been published and may not have been undertaken for the non-commercial UK species. There is a latitudinal difference in the outcome of competition between *L. digitata* and *L. hyperborea*, the latter apparently being more successful in northern and western parts of the UK (H.T. Powell, pers. comm.). This may explain the differential depth distributions between the French and British kelp populations.

It is likely that one of the results of monitoring the kelp biotopes in SACs would be that short term local fluctuations in the kelp species would be detected. It would be helpful for management to have access to the "normal" pattern of recovery from a change in the balance of species. Additional monitoring to detect possible abnormal conditions might then be avoided if the pattern of recovery were shown to be similar to reports from experimental sites. Experimental designs similar to those used on the Isle of Man by J.M. Kain during the 1970s could be used within the different kelp biotopes and at different geographical locations around the UK. This might be achieved as a series of short, repetitive, joint contracts with local research institutes, the data from which could be collated, analysed and published by a central agent.

b. Age and growth of kelps

i. What are the age structures of kelp populations in different kelp biotopes?

The age profile of the population of *L. hyperborea* is known from a few locations around the UK (notably on the Isle of Man and from some sites in Scotland). The differences in age structure that occur with depth are also reported from the Isle of Man (Kain, 1973). The age structure of populations of other species of kelps are not known, and changes in age structure of other kelp populations in different biotopes have not been reported.

It is likely that kelp plants in a habitat that is sheltered from strong wave action live longer than plants in an area where the larger plants are subject to greater damage. A useful tool in long term monitoring programmes would be to predict the expected age profile of a population of a given kelp species within a specific biotope. This could be used to estimate the normal turnover of plants to be expected within a habitat and to measure any changes that might take place in future decades. If any SAC were expanded to include more kelp areas, an age profile of the new population might indicate the similarities or differences between populations within the SAC. This data would also provide the management with an estimate of how long any environmental change affecting kelp species would take to effect loss of cover within a specific biotope.

Unfortunately, the determination of the age of kelp plants is a destructive process because the stipe has to be cut at the holdfast and the rings of light and dark tissue (like tree rings) counted. Specific instructions on how to do this are given in Kain (1973) but it is technique that requires skill and practice. The initial survey of kelp populations at all UK SACs should therefore be carried out by an expert team who could be consulted later when problems arose or were anticipated. A central agent could be made responsible for quality control, statistical integrity and data collation and publication.

ii. Do the age profiles of kelp species in different biotopes vary with geographical location?

This question follows on from the one above. It is possible that, in areas of different irradiance and temperature regimes, the kelp species have different life expectancies. There is some evidence to suggest that *L. hyperborea* may live longer in the more northerly part of its distribution, whereas, in the centre of its geographical range, it is growing optimally. More data are required in order to confirm this and complete data sets are needed for the other UK kelp species. Again, this information would be useful in determining the length of time between a major environmental incident affecting the recruitment of juvenile kelp plants and the loss of kelp cover.

If a nation-wide study were implemented in the manner outlined above (i), this information could be obtained at the same time, provided that the data sets were sufficiently large to be statistically robust.

iii. What are the growth rates of kelp species in different biotopes?

The growth rates of kelps have been measured in UK waters, but data have been published from only a few sites (see section III.B.1.d). It is likely that kelp species grow at different rates in different local conditions, but also possible that there is a biotope related pattern. Local changes in the growth rates of the kelp species will result in changes to the energy input from the kelp biotopes to the surrounding coastal areas. If the growth rates of marked kelp

plants are monitored within different kelp biotopes in an SAC, this data may be used as a biological indicator of local conditions at that site.

Growth rates of marked kelp plants should be measured within each of the biotopes for each of the UK species of kelps. This would need to be conducted simultaneously in the different biotopes and the study should continue for at least 2 years. At intervals of 5-10 years, the study would need to be repeated in order to detect any changes that might take place. Sufficiently large data sets would be needed from each site for statistical analysis and, in addition, growth rates might need to be normalised to the available irradiance for each plant.

iv. What are the geographical patterns of kelp growth rates?

This question follows on from the one above. It is possible that the kelp species have different growth rates in areas of different temperature regimes or nutrient levels. Certainly, the growth rates given by Parke (1948) for *L. saccharina* on the southern coasts of the UK were much slower than rates measured in Strangford Lough (Birkett, 1993). More data is required in order to confirm this and complete data sets are needed for the other kelp species. Changes in the growth rates of kelps will affect the energy export from the kelp biotopes to the surrounding coastal areas. This information would be useful in determining changes in local conditions which directly affect the kelp plants. If kelps start growing more rapidly or more slowly it may be an indicator that local conditions are shifting within the geographical range of growth rates for that species.

The necessary data could again be obtained as part of any nation-wide study that was implemented along the lines outlined above (iii), provided (again) that the data sets were sufficiently large to be statistically robust and the study were repeated at intervals in order to monitor any possible shifts in the geographical patterns.

c. Kelp productivity

i. What are the rates of biomass production of different kelp species?

The contribution of *L. hyperborea* to coastal ecosystems can be estimated as 1.5 - 3 times the standing stock per year. Productivity estimates based on growth rates or rates of photosynthesis measured under laboratory conditions appear to give much reduced estimates as compared to mesocosm field experiments with whole plants (Birkett, Dring & Savidge, in prep.). The biomass production for *L. hyperborea*, *L. digitata* and *L. saccharina* has been estimated from rates of photosynthesis measured in the field, but not for other UK species of kelp. The productivity of the kelp bed is likely to have a direct impact on the survival of many if not most of the other species in the area, as the kelp plants may be responsible for more than 60% of the primary productivity in coastal ecosystems (to a depth of 10 m., Birkett, Dring & Savidge, in prep.). If a statistical relationship between the local growth rates and production estimates could be established, then measurements of growth rate could be reliably transformed into production estimates.

Additional measurements of productivity for other kelp species and production rates linked to growth rates are required in order to establish how much of the production of kelp species may be released as DOM, not appearing in the form of plant tissue first (see section III.B.1).

ii. Do productivity rates vary with geographic location?

This question follows on from the one above. Growth rates of a kelp species vary with geographical location, but are the proportions of production allocated to growth (as opposed to losses of POM and DOM) similar throughout the range of a kelp species? This information would enable management to determine if changes in growth rates (linked to production) resulted in the shift of population structures within a biotope to a population pattern resembling an adjacent geographical area.

Additional experiments would be needed at a series of different sites around the UK.

iii. How much POM and DOM is generated from different kelp biotopes?

At present, we have no clear idea how much of the production generated by kelp beds is cycled into the DOM (used by heterotrophic organisms such as bacteria) or through POM into the detrital food webs. Estimates have been made for phytoplankton blooms and some kelp work was done in South Africa (Jarman & Carter, 1981). The POM and DOM from kelp beds fuels the surrounding coastal area and so any changes in the production of the kelp bed are likely to have serious repercussions on the local benthic communities. Some work was undertaken to determine the extent of the influence of kelp beds in South African coastal waters, using immuno-sensitivity methods to identify kelp components in seawater samples. This sensitive method was able to detect kelp components in seawater samples collected more than 7 km from the kelp beds (C. McQuaid, pers. comm.). It is probable that reduced kelp production would affect the population structures of other commercial species such as crabs and lobsters, as was reported from Canada (Mann & Breen, 1972). There is no literature available for the kelp beds of Europe.

Experimental determination of these data will require time and expertise, and the methods developed would not form part of any monitoring programme. However, this type of hard evidence of the significance and commercial value of large, healthy areas of kelp biotopes would strengthen the case for rigorously protecting kelp beds.

iv. What are the links between kelp generated POM and DOM and other coastal biotopes?

This question covers the wider links within coastal waters. There is little point in enforcing stringent rules and management programmes to protect sensitive species or biotopes if the local kelp beds that support them (with a food supply) are not adequately protected, on the grounds that kelp plants are “less sensitive” to perturbations. These questions were first addressed in Canada and South Africa but have not been investigated in detail. In Europe they have not been investigated at all.

This sort of investigation requires to be planned, funded and executed as part of a long term and detailed project, in a similar manner to the offshore UK and Antarctic Ocean research programmes of the last decades. It is a serious gap in our understanding of the significance of kelp biotopes in coastal ecosystems.

d. Epiflora and epifauna

i. Do the epiphytic animal and plant species show geographical distribution patterns?

There is some evidence to suggest that a few of the species which are found as stipe epiphytes have distribution patterns that differ from the kelp species on which they grow. These epiphytic species would form useful and accessible indicators of changes in local conditions if those epiphytic species that were close to their distribution or tolerance limits were monitored within each marine SAC. A continuation and expansion of the sporadic distributional and species survey work that has been undertaken in the past is required.

ii. Are epiphytic plant and animal species specific to kelps?

Most of the understorey algae within a kelp biotope are found on the substratum as well as growing as epiphytes on the stipes of kelps. There are numerous species of algae that are not found on the substratum but may be found on kelp stipes. It is possible that these species are using the stipes as a refuge from grazing pressure, as a habitat niche with slightly higher irradiances, or, it may be that these species are more intimately associated with the kelp species on which they grow. Similarly, some animal species occupy parts of kelp plants as a common or preferred habitat, but, again, little is known of the exclusivity of habitat for these species.

If a species is selected for inclusion in a monitoring programme as an indicator species, due to its sensitivity to changing local conditions, it would be advantageous for that species to be readily accessible from the stipes of plants rather than being ubiquitous within the biotope. Information to answer this and an associated suite of questions would require extensive and detailed sampling of the epiphytic species throughout the UK and comparison with epilithic survey data. Furthermore, those factors influencing the distribution and the sensitivities of epiphytic species would need to be determined.

4. Ecological interactions in kelp beds

Very little work has been published on the interactions between the multitudes of species found within kelp biotopes. The habitat is not conducive to field research and many of the species of interest will not survive or are difficult to maintain in aquaria. The majority of the topics outlined below require intensive research work over periods of several years, but ideally should be undertaken within a network of collaborating researchers. It is to be hoped that the information requirements of bodies responsible for the management and monitoring of marine SACs will be an encouragement to research groups and funding agencies alike and that the most significant relationships between trophic levels in the kelp biotopes will be established and investigated over the coming years. Such information would also allow the interactions between species and the environment, and between different species and the food webs, within each biotope to be suggested and then developed to the level, perhaps, of biomass and energy transfer. This would enable management of, for example, lobster fishing to be put on a scientific basis for the first time.

a. Non-kelp macroalgae: which are the key species within kelp biotopes?

Large numbers of juvenile animals and small invertebrates appear to live in and feed on the understory algae and, in particular, on several species of red algae. Some of these seaweeds may form a key part of the diet for significant animal species within the biotopes, but such linkages have not been investigated for many species. It is known, for example, that *Helcion pellucidum* feeds on *Mastocarpus* as a juvenile (McGrath, 1992), but the effects of removing favoured algal species from the juvenile diet is not known. If it can be established that certain seaweeds are important in the diets of herbivores identified as key species in the kelp biotopes, then monitoring effort can be directed toward those algal species which are most significant rather than having to take a broad brush and less efficient approach to monitoring the status of the specific biotope.

This topic would require intensive research for a period of years and might be a suitable subject for a suite of doctoral theses. The following questions are examples which might be addressed at the same time or as subsequent topics of research:

- What factors are the macroalgae sensitive to?
- What factors influence their population dynamics?
- What are the effects on the kelp biotopes of their loss or their increase?

b. Herbivore species: which are the key species in each kelp biotope?

The importance of sea urchins in kelp beds and the consequences to kelp beds of changes in their population dynamics have been discussed in chapters IV and V. *Helcion* is known to graze kelp plants, but the linkages between this limpet and the kelp population are not well documented. Data on the grazing preferences and trophic interactions of other common herbivores are needed in order to answer this question. Filter feeding species should not be excluded from this topic, although many species may be dependent on DOM rather than directly interacting with the seaweeds. Different species of herbivores may be of greater or lesser significance in the different kelp biotopes and the geographical distribution of key species (once identified) need to be established. Further questions associated with this topic include:

- Which species do they graze?
- What environmental factors are they sensitive to?
- What factors influence their population dynamics?
- What are the effects on the kelp biotopes of their loss or their increase?

Again, using the information gained from research into these topics would enable any monitoring programme to be targeted at key interacting species and at species that are sensitive to environmental and ecological changes.

c. Predator species: which are the key species within the kelp biotopes?

Sea otters have been identified as a key predator species in the kelp beds of North America, but they do not live in European waters. The key predator species in UK kelp beds have not been identified. Research programmes to identify the key predators should be combined with research to answer the additional questions about predator species suggested in the list below.

- Which species do they prey on?

- What factors are they sensitive to?
- What factors influence their population dynamics?
- What are the effects on the kelp biotopes of their loss or their increase?

This topic will require a great deal of research effort in order that efficient monitoring programmes can be developed. It is probable that the key predator species in kelp biotopes will be species with a commercial value. Because of this, it may be necessary to restrict or ban local collection of these species, if the natural balance between trophic levels is to be maintained. If this should become a necessity within a marine SAC, a body of statistically robust evidence in support of the critical importance of the SAC as a refuge for the predator species would be useful to the management programme. The long term consequences of predator removal could also be brought in as supporting evidence if robust data were available.

d. What are the effects on kelp biotopes of the introduction of alien species of kelp, other algae, grazers or predators?

In places on the south coast of England, the traditional zonation pattern of the intertidal fucoid algae has been masked and disrupted by the establishment of *Sargassum muticum*. In Tasmania, kelp beds in the vicinity of the port where *Undaria pinnatifida* became established have become dominated by the alien species. With the arrival of *Undaria* in the south of England and the apparent tolerance that this species has for a wide range of temperatures, a similar shift in kelp population patterns may develop. Despite the controls on the movement of aquaculture species within Europe, and the care taken to avoid the introduction of alien species, such introductions are common and widespread (Eno *et al.*, 1997).

The arrival of new species within a kelp biotope that is subject to regular, biodiversity monitoring is likely to be spotted quickly unless the new species is small, cryptic or difficult to identify. The potential ramifications of the arrival of that species need to be anticipated or understood, in order for targeted monitoring programmes to be introduced. The effects of introduced species within kelp biotopes should, therefore, be investigated, particularly if the alien species threatens to replace or interact deleteriously with any of the local key species.

5. Effects of changes in physical and chemical parameters

a. What are the effects of increased nutrient levels on kelp biotopes?

Increased nutrient levels at times of the year when kelp plants are growing rapidly may not be detrimental to the kelp plants or to the associated food webs. The possibility exists that the increased DOM in the environment will result in an overloading of the soft bottom benthic communities and the development of anoxic conditions, or that the zone of influence of the kelp bed may be extended - resulting in an increased biomass throughout the local coastal area. Given the differential rates at which different species grow at different seasons, however, the addition of nutrients may result in opportunistic species becoming dominant within the biotope. Some preliminary experimental work has been undertaken on the effects of adding nutrients during productivity during experiments (D. Birkett, unpublished data) but further methodological development is required before useful data can be obtained.

In order to follow such effects, frequent chemical monitoring should be instituted until such a time as any long term biological or ecological effects can be shown to have a significant correlation with changes in the nutrient supply. A programme of experimental work to determine the changes in productivity expected from a nutrient enriched kelp biotope should

be started. Naturally encountered nutrient levels should be used and experiments conducted under field conditions, using enclosed mesocosms.

b. What are the effects of increased temperature on kelp biotopes?

The warming of the oceans on this planet is a distinct possibility in response to natural fluctuations in the climate of the world or as a consequence of modern production rates of CO₂. Kelp species may, in the long term, shift their pattern of distribution in response to seawater temperature shifts. Any such changes would be detected if some (or all!) of the above suggestions were included in the monitoring programmes for marine SACs. It is more probable that species with a shorter life span and greater temperature sensitivity than the common kelp species would be affected by higher temperatures. However, it is thought that *L. ochroleuca* arrived on the southern shores of England during a phase of slightly warmer water in the Channel during the 1940s. As with many of the physical and chemical parameters, temperature is best checked on a semi-continual basis as part of a routine programme of monitoring, ideally using remote devices and long term deployments.

c. Changes in the available irradiance

i. What are the effects of increased turbidity?

Water that is either permanently or periodically turbid will reduce the total irradiance, and change the quality of the light available to the seaweeds. Changes in the turbidity of the water within a kelp biotope could result in shifts in the depth distribution of kelp species, of associated algae and of the rates of development of the blue-light sensitive gametophyte plants (see section II.C.). A comparison of the depth distributions of kelp species in biotopes with a range of mean turbidity measurements (over a year) would provide a database against which comparisons could be made.

ii. What are the effects of decreased surface irradiance?

Climate change predictions are at present in very early stages of development. It is possible that the skies of northern Europe may become more cloudy as a result of global warming. A decrease in the annual irradiance at the surface would result in depth profile changes for many algal species. Further development of models relating to kelp productivity at different depths to surface irradiance and the clarity of seawater would provide a database against which future changes could be compared.

C. KEY POINTS FROM CHAPTER VII

General points

- Much of the basic information on the biology of the kelp species in the UK has been researched, particularly with regard to those kelp species that have a commercial value.
- The ecological role that kelp species fill in UK waters (or in other parts of the world) has been studied in far less detail than their biology and is not well understood.
- Basic information, such as complete species lists for kelp biotopes, species distributions and their environmental and ecological sensitivities, are lacking.
- The key species in the ecology of kelp biotopes have not as yet been confirmed.
- Interactions between kelp species and the component species within the different kelp biotopes are very poorly understood.
- Some of the gaps in our information about kelp bed ecosystems are highlighted in this section but the suggestions listed must not be taken as a complete list.

Some specific gaps in our understanding

kelp biotopes

- The location and dimensions of kelp beds throughout the UK.
- Geographical distributions of the different kelp biotopes.
- Species lists for the different kelp biotopes in their geographical contexts.
- The importance of kelp beds and specific biotopes as nursery areas.

kelp biology and ecology

- The detailed geographical distribution of each kelp species, together with the variation in patterns of depth distribution and inter-specific competitive outcomes within each biotope.
- The age structure and profiles of kelp populations in different biotopes and geographical variations in these patterns.
- The growth rates of kelp species in different biotopes and geographical variations in these data.
- The biomass production of each species of kelp and variations in these rates with biotope and geographic location.
- Estimates of the production, utilisation and exportation of POM and DOM from different kelp biotopes and linkages to other coastal ecosystems.
- Geographical distribution patterns of epiflora and epifaunal species within kelp biotopes and the specificity of these species to the various biotopes.

ecological interactions

- The sensitivities of the non-kelp macroalgae, identification of key species within this group and the factors that influence their population dynamics and the effects of these fluctuations on other species in the different kelp biotopes.
- The sensitivities of the herbivore species, identification of key species within this group, identification of key food species, identification of the factors that influence their population dynamics and the effects of these fluctuations on other species in the different kelp biotopes.
- The sensitivities of the predatory species, identification of key species within this group and their prey species, identification of the factors that influence their population dynamics and the effects of these fluctuations on other species in the different kelp biotopes.

- The sensitivities of the alien species within kelp biotopes, identification of key species within this group and the factors that influence their population dynamics and the effects of these fluctuations on other species in the different kelp biotopes.

effects of physical and chemical changes

- The effects of changes in concentrations of nutrients on kelp biotopes.
- The effects of water temperature changes on kelp biotopes
- The effects of changes in the irradiance within kelp biotopes on kelp and non-kelp species both as a result of increased turbidity or as the result of decreased surface irradiance.

Notes

- Many of the current gaps in our knowledge are the result of the present global unpopularity of such basic research topics with funding agencies and scientific journals rather than lack of interest or resources.
- In the absence of so much basic scientific information, *valid* biological and ecological monitoring plans cannot be constructed at present and *efficient* management plans therefore cannot be implemented, necessitating the adoption of the precautionary principle with respect to the ecological management of marine SACs.

VIII CONCLUDING COMMENTS ON THE APPLICATION OF INFORMATION FOR CONSERVATION MANAGEMENT RELEVANT TO MARINE SACs.

A. INTRODUCTION

This report has covered an enormous amount of information on numerous topics associated with our present understanding of the biological and ecological structure and function of the kelp biotopes around the UK. As has been mentioned previously, for a variety of reasons little research data is available which can be specifically and directly applied towards the construction of management plans for kelp beds within marine SACs. Where such information has been available, specific attention has been drawn to it within the context of each chapter. The intention of this present chapter is to add a final perspective to this extensive review.

The Habitats Directive requires member states to identify and designate SACs which will eventually form part of a network of conservation sites across the EU. It is expected that, where selected SACs correspond to areas previously designated as SSSIs or ASSIs, any management measures required will usually be implemented through the existing management. However, with kelp biotopes, this will generally not be possible. Most of the existing management structures do not contain adequate available skilled personnel to undertake the additional work load that will be needed. Even where a local authority has some jurisdiction over the seashore and seabed, recent court cases suggest that, due to common law and to historical practices, no effective protection of species with commercial value within a marine SAC will be possible in future without specific, scientifically supportable legislation to separate protected areas from the general shore and seabed areas in UK waters.

B. BASIC MANAGEMENT GUIDANCE

1. Time scales

The time scale over which a management plan for a kelp forest is to operate has to be decided. Unfortunately, political and biological time spans are often quite distinct. With the exception of direct harvesting of kelp, little is presently known about the long term effects of many present day human activities on kelp biotopes. The primary productivity of some kelp ecosystems is thought to be among the highest per unit area of all global vegetation (Mann, 1972b), but this is not reflected, as in tropical rain-forests, in accumulation of biomass. Much of the net production of kelp plants is exported from the kelp forest to coastal ecosystems as a whole, and is generally thought to sustain many inshore fisheries. Any deleterious impact of human activities on kelp production could, therefore, be translated into decreasing landings of fish before changes in kelp density or standing stock could be detected.

2. *Maintenance and restoration*

Kelp biotopes should be managed so as to contribute to the maintenance or restoration of the favourable conservation status of the natural habitat and species composition of the biotope. Each kelp forest, and possibly each area within a kelp forest, may have a different biological composition, and our knowledge about the associated flora and fauna is too sketchy to permit broad generalisations to be drawn. Amongst the other gaps in our detailed knowledge, are the time scales of the natural variability of the kelp habitat and the extent of temporal variation in species composition.

3. *Integrity of sites of kelp biotopes*

The conservation status of the kelp beds within SACs must be considered before any activity, plan or project is undertaken that is likely to have a significant effect on the kelp biotope. Effectively, this requirement of the Habitats Directive prohibits most activities, uses and changes in management practices as applied to kelp habitats, due to the paucity of applicable biological information that is available.

4. *Monitoring requirements*

As discussed in Chapter VI, monitoring the marine environment is a time-consuming and expensive task, requiring high levels of expertise in a wide range of techniques. Kelp biotopes are renowned for their species richness and diversity and, as such, present a challenge with regard to monitoring their status. The monitoring of kelp biotopes needs to be conducted in a manner that permits biologically significant changes to be linked to changes in local conditions, management practices or human activities, if any management plan is to be effective. Among the highest priorities in the management strategy for kelp biotopes should be ***the identification of the keystone species*** among the associated fauna and flora of kelp biotopes. Population levels of these species should then be monitored. In contrast to the rocky intertidal zone, where the dynamic relationships between the principal biota are well understood (because they are easier to study!), ***we do not yet have sufficient basic information on the ecological relationships within kelp biotopes*** to enable these species to be selected with any confidence.

5. *Avoidance of habitat deterioration*

This requirement of the Habitats Directive implies that whatever monitoring programme is implemented must be adequate to enable the present status, the optimum status and any changes in the status of kelp biotopes to be detected.

- Physical parameters should be checked regularly, such as
- the dimensions of the kelp forest or parkland
- the degree of light penetration to the depth of the kelp bed
- Water quality, salinity and temperature need to be monitored with sufficient regularity and accuracy to identify any natural or anthropogenic events which might be detrimental to the kelp biotopes.

6. *Local human needs*

Despite all the strictures within the Habitats Directive with regard to the conservation of the environment and the species that they contain, the economic, cultural, social and recreational needs of the local people are also to be taken into account.

- International experience demonstrates that local co-operation and voluntary systems *alone* are, in practice, inadequate to protect habitats and the biota that they sustain.
- Any management scheme will be dependent on the quality of the monitoring programmes to provide adequate *scientifically robust data* to support any legal cases which may arise in the course of defending the kelp biotopes against “local needs” prejudicial to the conservation of these biotopes.

C. PARALLEL CONSERVATION MANAGEMENT ACTIVITIES

1. *UK biodiversity action plan for kelp species*

No information is available, although action plans are unlikely for these very abundant species.

2. *Other networks that focus on kelp*

None known

D. KEY POINTS FROM CHAPTER VIII

- A coherent system of habitat conservation legislation is required in the UK.
- Kelp biotopes require more research into management-related aspects in order to permit efficient management plans and monitoring programmes to be developed.
- The optimum approach to the management of kelp biotopes within marine SACs is, for the present, to prohibit any additional environmental or ecological stresses and to reduce or remove - by legislative means if need be - any such stresses presently extant.
- The level of long term commitment, by Government, to marine conservation should be reassessed with regard to fulfilling the requirements of the Habitat Directive.

BACKGROUND READING AND LITERATURE CITED

Literature cited in the text of this review is listed below, together with a selection of other articles and books relevant to the ecology of kelp beds.

The publications indicated by underlining the citation are, in our opinion, sources of useful background information for readers who are unfamiliar with kelp beds and their ecology. In particular, Lüning (1990) is an excellent source of information and contains an extensive bibliography.

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APPENDICES

APPENDIX 1.

MNCR biotope codes with definitions, for biotopes with kelp in the British Isles		
Habitat and outline description of the biotope	higher code	biotope code
INFRALITTORAL ROCK (and other hard substrata)	IR	
EXPOSED INFRALITTORAL ROCK	EIR	
Kelp with cushion fauna, foliose red seaweeds or coralline crusts (exposed rock)	EIR.KFaR	
<i>Alaria esculenta</i> on sublittoral fringe bedrock	EIR.KFaR	Ala
<i>Alaria esculenta</i> , <i>Mytilus edulis</i> and coralline crusts on very exposed sublittoral fringe bedrock	EIR.KFaR	Ala.Myt
<i>Alaria esculenta</i> and <i>Laminaria digitata</i> on exposed sublittoral fringe bedrock	EIR.KFaR	Ala.Ldig
<i>Alaria esculenta</i> forest with dense anemones and sponge crusts on extremely exposed infralittoral bedrock	EIR.KFaR	AlaAnSC
<i>Laminaria hyperborea</i> forest with a faunal cushion (sponges and polyclinids) and foliose red seaweeds on very exposed infralittoral rock	EIR.KFaR	LhypFa
Sparse <i>Laminaria hyperborea</i> forest and dense <i>Paracentrotus lividus</i> on exposed infralittoral limestone	EIR.KFaR	LhypPar
<i>Laminaria hyperborea</i> with dense foliose red seaweeds on exposed infralittoral rock	EIR.KFaR	LhypR
<i>Laminaria hyperborea</i> forest with dense foliose red seaweeds on exposed upper infralittoral rock	EIR.KFaR	LhypR.Ft
<i>Laminaria hyperborea</i> park with dense foliose red seaweeds on exposed lower infralittoral rock	EIR.KFaR	LhypR.Pk
Mixed <i>Laminaria hyperborea</i> and <i>Laminaria ochroleuca</i> forest on exposed infralittoral rock	EIR.KFaR	LhypR.Loch
<i>Laminaria saccharina</i> and or <i>Saccorhiza polyschides</i> on exposed infralittoral rock	EIR.KFaR	LsacSac

MODERATELY EXPOSED INFRALITTORAL ROCK	MIR	
Kelp with red seaweeds (moderately exposed rock)	MIR.KR	
<i>Laminaria digitata</i> on moderately exposed or tide-swept sublittoral fringe rock	MIR.KR	Ldig
<i>Laminaria digitata</i> on moderately exposed sublittoral fringe rock	MIR.KR	Ldig.Ldig
<i>Laminaria digitata</i> and under-boulder fauna on sublittoral fringe boulders	MIR.KR	Ldig.Ldig.Bo
<i>Laminaria digitata</i> , ascidians and bryozoans on tide-swept sublittoral fringe rock	MIR.KR	Ldig.T
<i>Laminaria digitata</i> and piddocks on sublittoral fringe soft rock	MIR.KR	Ldig.Pid
<i>Laminaria hyperborea</i> and foliose red seaweeds on moderately exposed infralittoral rock	MIR.KR	Lhyp
<i>Laminaria hyperborea</i> forest and foliose red seaweeds on moderately exposed upper infralittoral rock	MIR.KR	Lhyp.Ft
<i>Laminaria hyperborea</i> park and foliose red seaweeds on moderately exposed lower infralittoral rock	MIR.KR	Lhyp.Pk
<i>Laminaria hyperborea</i> forest, foliose red seaweeds and a diverse fauna on tide swept upper infralittoral rock	MIR.KR	Lhyp.TFt
<i>Laminaria hyperborea</i> park with hydroids, bryozoans and sponges on tide-swept lower infralittoral rock	MIR.KR	Lhyp.TPk
Mixed <i>Laminaria hyperborea</i> and <i>Laminaria ochroleuca</i> forest on moderately exposed or sheltered infralittoral rock	MIR.KR	Lhyp.Loch
Grazed kelp with algal crusts	MIR.GzK	
Grazed <i>Laminaria hyperborea</i> with coralline crusts on infralittoral rock	MIR.GzK	LhypGz
Grazed <i>Laminaria hyperborea</i> forest with coralline crusts on upper infralittoral rock	MIR.GzK	LhypGz.Ft
Grazed <i>Laminaria hyperborea</i> park with coralline crusts on lower infralittoral rock	MIR.GzK	LhypGz.Pk
Sand or gravel-affected or disturbed kelp and seaweed communities	MIR.SedK	
<i>Saccorhiza polyschides</i> and other opportunistic kelps on disturbed upper infralittoral rock	MIR.SedK	Sac
<i>Laminaria saccharina</i> , <i>Chorda filum</i> and dense red seaweeds on shallow unstable infralittoral boulders and cobbles	MIR.SedK	LsacChoR
Mixed kelps with scour tolerant and opportunistic foliose red seaweeds on scoured or sand covered infralittoral rock	MIR.SedK	XKScrR
<i>Sabellaria spinulosa</i> with kelp and red seaweeds on sand influenced infralittoral rock	MIR.SedK	SabKR
Ephemeral red seaweeds and kelps on tide-swept mobile infralittoral cobbles	MIR.SedK	EphR
<i>Halidrys siliquosa</i> and mixed kelps on tide-swept infralittoral rock with coarse sediment	MIR.SedK	HalXX

SHELTERED INFRALITTORAL ROCK		SIR
Silted kelp (stable rock)		SIR.K
Mixed <i>Laminaria hyperborea</i> and <i>Laminaria saccharina</i> on sheltered infralittoral rock	SIR.K	LhypLsac
Mixed <i>Laminaria hyperborea</i> and <i>Laminaria saccharina</i> forest on sheltered upper infralittoral rock	SIR.K	LhypLsac.Ft
Mixed <i>Laminaria hyperborea</i> and <i>Laminaria saccharina</i> park on sheltered lower infralittoral rock	SIR.K	LhypLsac.Pk
<i>Laminaria saccharina</i> on very sheltered infralittoral rock	SIR.K	Lsac
<i>Laminaria saccharina</i> and <i>Laminaria digitata</i> on sheltered sublittoral fringe rock	SIR.K	Lsac.Ldig
<i>Laminaria saccharina</i> forest on very sheltered upper infralittoral rock	SIR.K	Lsac.Ft
<i>Laminaria saccharina</i> park on very sheltered lower infralittoral rock	SIR.K	Lsac.Pk
<i>Laminaria saccharina</i> , foliose red seaweeds, sponges and ascidians on tide-swept infralittoral rock	SIR.K	Lsac.T
Sparse <i>Laminaria saccharina</i> with <i>Codium</i> spp. and sparse red seaweeds on heavily silted very sheltered infralittoral rock	SIR.K	Lsac.Cod
<i>Echinus</i> , brittlestars and coralline crusts on grazed lower infralittoral rock	SIR.K	EchBriCC
<i>Laminaria saccharina</i> on reduced or low salinity infralittoral rock	SIR.K	LsacRS
Sparse <i>Laminaria saccharina</i> with dense filamentous red seaweeds, sponges and <i>Balanus crenatus</i> on tide-swept variable salinity infralittoral rock	SIR.K	LsacRS.FiR
<i>Laminaria saccharina</i> and <i>Psammechinus miliaris</i> on reduced salinity grazed infralittoral rock	SIR.K	LsacRS.Psa
<i>Laminaria saccharina</i> with <i>Phyllophora</i> spp. and filamentous green seaweeds on reduced or low salinity infralittoral rock	SIR.K	LsacRS.Phy
In addition to the above biotopes which have kelp plants in them, there are 4 biotopes where, although included in the “kelp” higher codes, there is no kelp present in the biotope description. There are no biotope classifications which include kelp gametophytes		
data abstracted from JNCC report no. 229 Marine Biotope Classification for Britain and Ireland, 1997		

APPENDIX 2

Numbers of different species (arranged in taxonomic groupings) listed in the MNCR database as being recorded as present within the 5 higher code biotopes with kelp

Total species reported from kelp biotopes around the UK: 1,819

Where only a *genus* name has been listed in the database, it is assumed that the specimen recorded was *not* one of the listed *species*. However, this will possibly overestimate the numbers of species recorded as present in each biotope. Where a listing occurs only at a taxonomic level above genus, it has not been included.

Taxonomic group	commonly referred to as:	species
Protozoa	microscopic, one celled animals	2
Porifera	sponges	107
Cnidaria	jellyfish (sedentary and heteromorphic life-cycles)	158
Ctenophora	comb jellies	3
Platyhelminthes	flatworms	8
Nemertea	ribbon worms	13
Nematoda	threadworms	?
Entoprocta		3
Sipunculida		2
Echiurida		3
Annelida		
Polychaeta	worms (many bristles, most species are marine)	173
Oligochaeta	worms (few bristles, few species are marine)	3
Chelicerata Pycnogonida	sea-spiders	13
Crustacea		
Cirripedia	barnacles	15
Ostracoda		2
Mysidae		2
Amphipoda	sand hoppers	81
Caprellida	skeleton shrimps	8
Isopoda	sea lice	14
Epicaridea	sea slaters	6
Caridea	shrimps, lobsters, hermit crabs, porcelain crabs	40
Brachyura	crabs	30
Xanthoidea	more crabs	4
Mollusca		
Polyplacophora	chitons	12
Gastropoda (Prosobranchia)	limpets and snails	114
(Opisthobranchia)	sea hares, sea butterflies, sea slugs	98
Pelecypoda	bivalves	99
Cephalopoda	squid and octopus	3
Teuthoidea	giant squid	3
Brachiopoda	lamp shells	2
Phoronidea		2
Bryozoa	sea mats	101

Echinodermata		
Crinoidea	feather stars	3
Asteroidea	starfish	22
Ophiuroidea	brittlestars	21
Echinoidea	sea urchins	9
Holothurioidea	sea cucumbers	18
Tunicata	seasquirts	70
Chondrichthyes	sharks, skates & rays	6
Osteichthyes	bony fish (round and flat)	89
Mammalia	mammals	3
Cyanobacteria		2
Rhodophyta	red seaweeds	289
Chrysophyta		?
Phaeophyta	brown seaweeds	107
Chlorophyta	green seaweeds	53

APPENDIX 3.

Distribution of algal species epiphytic on <i>L. hyperborea</i> (Sherkin Island, Co. Cork, Ireland; D. Birkett, unpublished data)	
depth of kelp holdfast, m.	dominant species distribution pattern (from top of stipe down) on average plants, with length of stipe section colonised
1	<i>L. digitata</i> 10 cm; <i>Palmaria palmata</i> 50 cm
2	<i>L. digitata</i> 15 cm, <i>P. palmata</i> 50 cm
3	<i>L. digitata</i> 25 cm, <i>Phycodryis rubens</i> 5 cm, <i>Cryptopleura ramosum</i> 5 cm, <i>P. palmata</i> 20 cm
4	<i>C. ramosum</i> 5 cm, <i>Membranoptera alata</i> , 5 cm, <i>P. rubens</i> 30 cm, <i>P. palmata</i> 30 cm
5	<i>M. alata</i> 5 cm, <i>C. ramosum</i> 5 cm, <i>P. palmata</i> 5 cm, <i>P. rubens</i> 75 cm.
6	<i>P. palmata</i> 5 cm, <i>M. alata</i> 5 cm, <i>C. ramosum</i> 10 cm, <i>P. rubens</i> 50 cm.
7	<i>Nitophyllum</i> sp. 5 cm, <i>L. hyperborea</i> 10 cm, <i>Dictyota dichotoma</i> 5 cm, <i>Callophyllis laciniata</i> 5 cm, <i>C. ramosum</i> 20 cm, <i>P. palmata</i> 25 cm, <i>P. rubens</i> 30 cm.

APPENDIX 4

Common understorey algae of UK and nearby kelp beds (no depth affinities shown for each species)					
species	Aran Isles to 25 m.	Inner Hebrides to 22 m.	SE Scotland to 16.5 m.	Brittany to 20 m.	Helgol and to 15 m.
<i>Acrosorium uncinatum</i>	*	*		*	
<i>Aglaozonia</i> sp.	*			*	
<i>Ahnfeltia plicata</i>					*
<i>Audouinella membranacea</i>					*
<i>Bonnemaisonia asparagoides</i>				*	
<i>Brongniartella byssoides</i>					*
<i>Bryopsis plumosa</i>					*
<i>Callophyllis laciniata</i>	*	*		*	
<i>Chaetomorpha melagonium</i>					*
<i>Chondrus crispus</i>		*			*
<i>Corallina officinalis</i>	*	*			*
crustose Corallinaceae	*	*	*		*
<i>Cryptopleura ramosa</i>	*	*		*	
<i>Delesseria sanguinea</i>	*	*	*	*	*
<i>Desmarestia viridis</i>					*
<i>Dictyopteris membranacea</i>	*			*	
<i>Dictyota dichotoma</i>	*	*		*	
<i>Dilsea carnosa</i>		*	*		
<i>Drachiella spectabilis</i>	*			*	
<i>Dumontia contorta</i>					*
<i>Halopteris filicina</i>				*	
<i>Heterosiphonia plumosa</i>		*		*	
<i>Hypoglossum hypoglossoides</i>	*				
<i>Kallymenia reniformis</i>	*			*	
<i>Lomentaria clavellosa</i>					*
<i>Lomentaria orcadensis</i>					*
<i>Membranoptera alata</i>	*	*			*
<i>Mereditha microphylla</i>				*	
<i>Myriogramme bonnemaisonii</i>				*	
<i>Myriogramme heterocarpum</i>	*				
<i>Nitophyllum punctatum</i>					
<i>Odonthalia dentata</i>		*	*		
<i>Palmaria palmata</i>	*	*	*		
<i>Phycodrys rubens</i>	*	*		*	
<i>Phyllophora crispa</i>	*	*	*		
<i>Phyllophora pseudoceranooides</i>					*
<i>Phyllophora traillii</i>					*

<i>Plocamium cartilagineum</i>	*	*	*		*
<i>Polydora ciliata</i>					*
<i>Polyneura laciniata</i>	*			*	
<i>Polysiphonia urceolata</i>					*
<i>Porphyropsis coccinea</i>					*
<i>Pterosiphonia parasitica</i>	*				
<i>Ptilota plumosa</i>	*	*	*		
<i>Radicilingua thysanorhizans</i>					
<i>Rhodophyllis divaricata</i>				*	
<i>Rhodophyllis</i> sp.	*	*			
<i>Rhodymenia</i> sp.	*				
<i>Sphaerococcus coronopifolius</i>				*	
<i>Sphondylothamnion multifidum</i>				*	
<i>Ulva lactuca</i>					*
Abstracted from Maggs, 1986					

APPENDIX 5

Species recorded in kelp biotope complexes.
(24 pp.)

This information was compiled from the MNCR database (February, 1998) at the request of the authors of this review. Despite the length of this appendix, we feel that this information is a useful inclusion as it illustrates our present knowledge of the identity and diversity of species to be found in kelp habitats. As such, it may serve as a useful reference list within the context of Task 1.1.

Column headings

Taxons listed	biotope complexes (codes: see Appendix 1)				
	EIR.KFaR	MIR.KR	MIR.GzK	MIR.SedK	SIR.K

Letter codes entered in each column indicate if the taxon was recorded as:

Common	Frequent	Present	Occasional	Rare
---------------	-----------------	----------------	-------------------	-------------

Numbers in the columns indicate the percentage of sites at which the taxon was recorded and the **horizontal bar** illustrates this percentage. Where no number appears in a column, the taxon is found at fewer than 1% of all sites under that classification code. The **number of site records** are shown at the start of the column.

