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Furoids and kelp in deep eulittoral rockpools

MarLIN – Marine Life Information Network
Marine Evidence-based Sensitivity Assessment (MarESA) Review

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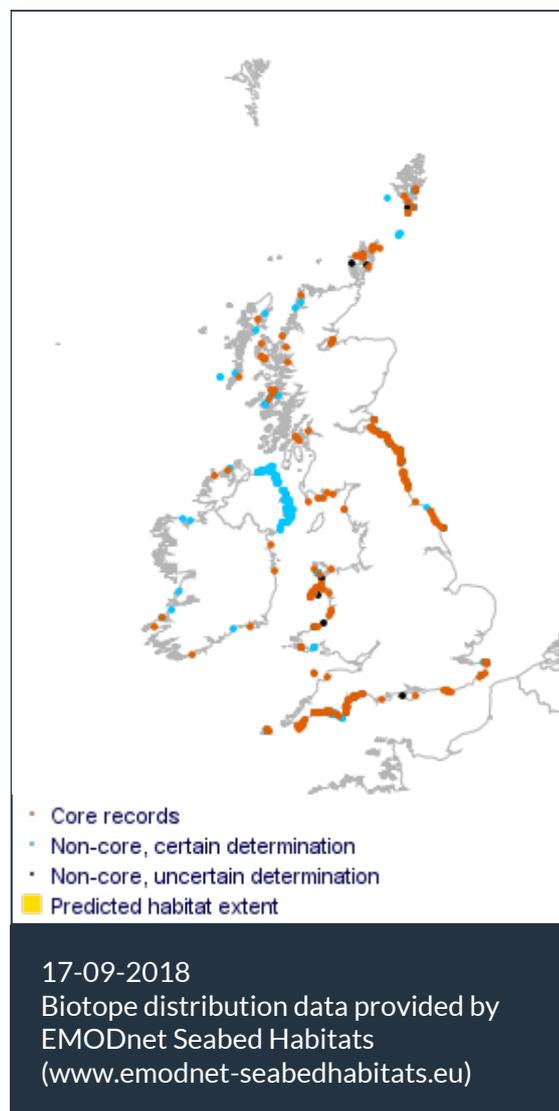


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Fucooids and kelps in deep eu littoral rockpools.
 Photographer: Jon Davies
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Researched by Dr Harvey Tyler-Walters Refereed by This information is not refereed.

Summary

☰ UK and Ireland classification

EUNIS 2008	A1.412	Fucooids and kelp in deep eu littoral rockpools
JNCC 2015	LR.FLR.Rkp.FK	Fucooids and kelp in deep eu littoral rockpools
JNCC 2004	LR.FLR.Rkp.FK	Fucooids and kelp in deep eu littoral rockpools
1997 Biotope	LR.LR.Rkp.FK	Fucooids and kelps in deep eu littoral rockpools

🔍 Description

Deep rockpools in the mid to lower eu littoral zone often contain a community characterized by *Fucus serratus* and *Laminaria digitata*. Other large brown algae, including *Saccharina latissima*, *Himanthalia elongata* and *Halidrys siliquosa*, may also occur. The rock surface is usually covered by encrusting coralline algae. A wide variety of filamentous and foliose algae, which are typical of lower shore and shallow sublittoral zones (e.g. *Palmaria palmata*, *Chondrus crispus*, *Ceramium* spp., *Membranoptera alata* and *Gastroclonium ovatum*) occur beneath the brown algal canopy. Algal-free

vertical and overhanging faces often support the sponge *Halichondria panicea* and anemones *Actinia equina*. The abundance of grazing molluscs varies considerably. In some, large numbers of littorinids and limpets are probably responsible for the limited variety of red seaweeds present. In other pools, fewer grazers may result in an abundance of these algae. Where boulders occur in these pools they provide a greater variety of micro-habitats which support a variety of fauna. Mobile crustaceans (*Pagurus bernhardus* and *Carcinus maenas*), brittlestars (*Ophiothrix fragilis* and *Amphipholis squamata*), encrusting bryozoans and ascidians are typically found beneath and between boulders. (Information taken from the Marine Biotope Classification for Britain and Ireland, Version 97.06: Connor *et al.*, 1997a, b).

↓ Depth range

Mid shore, Lower shore

🏛️ Additional information

Factors such as pool depth, surface area, volume, orientation to sunlight, shading, internal topography, sediment content and type, together with wave exposure, shore height, and hence flushing rate, and the presence of absence of freshwater runoff, results in large spatial variation in community structure, even between adjacent pools at the same shore height (Ganning, 1971; Metaxas & Scheibling, 1993). Individual rockpools and the communities that occupy them are highly variable.

✓ Listed By

- none -

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🔄 Ecology

Ecological and functional relationships

The rockpool environment varies depending on factors such as pool depth, surface area, volume, orientation to sunlight, shading, internal topography, sediment content and type, together with wave exposure, shore height, and hence flushing rate, and the presence or absence of freshwater runoff. As a result, no two rockpools exhibit exactly the same physio-chemical conditions and exhibit large spatial variation in community structure, even between adjacent pools at the same shore height (Ganning, 1971; Metaxas & Scheibling, 1993; Metaxas *et al.*, 1994). Any given rockpool is effectively unique (Metaxas & Scheibling, 1993). Therefore, while the organisms detailed below have been recorded in this rockpool biotope, not all of the organisms, and hence the relationships between them, may occur in any one rockpool.

As communities in rockpools remain constantly submerged and the danger of desiccation is absent, it might be expected that rockpools form an easier environment in which to live for marine life than drying rock surfaces, and that species from regions lower on the shore would be able to extend much further up the shore. However, the rockpool environment differs from that of the surrounding emergent rock surfaces, so that not all species that thrive on the surrounding rock occur abundantly in rockpools and much of the lower shore open rock fauna is absent from rockpools (Lewis, 1964). Rockpools constitute a distinct environment for which physiological adaptations by the flora and fauna may be required (Lewis, 1964; Metaxas & Scheibling, 1993). The following description is based on reviews by Lewis (1964), Ganning (1971) and Metaxas & Scheibling (1993), the species listed in the MNCR database (JNCC, 1999) and additional references as cited.

- Macroalgae such as kelps, fucoids, red algae, green algae, encrusting red algae, erect and encrusting corallines provide primary productivity either directly to grazing invertebrates and fish or indirectly to detritivores and decomposers, in the form of detritus and drift algae or as dissolved organic material and other exudates. Benthic microalgae, periphyton and phytoplankton (e.g. diatoms) also add to primary productivity.
- Where present, large macroalgae such as the laminarians (e.g. *Laminaria digitata*, *Saccharina latissima* and occasional *Laminaria hyperborea* and *Saccorhiza polyschides*), *Halidrys siliquosa* and fucoids (e.g. *Fucus serratus*, *Fucus vesiculosus*) shade the substratum (depending on density) so that understory plants tend to be shade tolerant red algae and corallines. Understorey algae, by effectively restricting access to the substratum, may also inhibit or restrict recruitment of other species of macroalgae (Hawkins & Harkin, 1985; Hawkins *et al.*, 1992).
- Macroalgae provide substrata and refuges for a variety of invertebrates and epiphytic algae. The stipes and lamina of *Laminaria* spp. may support bryozoans (e.g. *Membranipora membranipora* or *Electra pilosa*) and grazing blue-rayed limpets (*Helcion pellucida*), while their holdfasts provide additional refuges for meiofauna and small invertebrates. If present, the stipes of *Laminaria hyperborea* may support numerous epiphytes such as *Palmaria palmata*, *Phycodrys rubens* and *Cladophora rupestris* (Goss-Custard *et al.*, 1979). Where present, *Halidrys siliquosa* provide substratum for epiphytes, depending on location, including microflora (e.g. bacteria, blue green algae, diatoms and juvenile larger algae), *Ulothrix* sp. and *Ceramium* sp., hydroids (e.g. *Obelia* spp.), bryozoans (e.g. *Scrupocellaria* spp.), and ascidians (e.g. *Apilidium* spp., *Botryllus schlosseri*, and *Botrylloides*

leachi) (Lewis, 1964; Moss, 1982; Connor *et al.*, 1997b).

- The macroalgae provide refuges for small invertebrates, such as isopods, amphipods, ostracods and copepods. *Corallina officinalis* provides a substratum for small spirorbids e.g. *Spirorbis corallinae*, which is only found on *Corallina officinalis*. Increasing density of *Spirorbis corallinae* was shown to increase the species richness of the epiphytic fauna. The invertebrate fauna of *Corallina officinalis* is detailed in LR.Cor
- Amphipods (e.g. Gammaridae), isopods (e.g. *Idotea* spp. and *Jaera* sp.) and other mesoherbivores graze the epiphytic flora and senescent macroalgal tissue, which may benefit the macroalgal host, and may facilitate dispersal of the propagules of some macroalgal species (Brawley, 1992b; Williams & Seed, 1992). Mesoherbivores also graze the macroalgae but do not normally adversely affect the canopy (Brawley, 1992b).
- Grazers of periphyton (bacteria, blue-green algae and diatoms) or epiphytic algae include harpacticoid copepods, the limpets *Patella vulgata* and *Patella ulyssiponensis*, the blue-rayed limpet *Patella pellucida*, and gastropods such as *Steromphala cineraria*, *Steromphala umbilicalis*, *Littorina saxatilis*, *Littorina littorea*, *Littorina obtusata* and *Rissoa* spp. Limpets and littorinids also graze macroalgal sporelings and green algae especially.
- Coralline algae are probably relatively grazing resistant (Littler & Kauker, 1984) and few species graze the corallines directly except perhaps chitons (e.g. *Acanthochitona* spp. and *Lepidochitona cinerea*) and limpets of the genus *Tectura*.
- Grazing by littorinids and gammarid amphipods has been shown to significantly affect macroalgal abundance and diversity. For example in cage experiments in littoral fringe pools, Parker *et al.* (1993) found that gammarid amphipods significantly reduced the erect macroalgal canopy, while littorinids grazed microalgae and macroalgal sporelings, and prevented the establishment of erect and encrusting algal canopies. Both groups reduced the species richness of the algal canopy (Parker *et al.*, 1993). In tidepools in Nova Scotia, Chapman (1990) and Chapman & Johnson (1990) reported that grazers (especially littorinids) reduced the abundance of *Fucus* spp. sporelings and juveniles but increased the abundance of ephemeral algae, while having no effect on the encrusting red alga *Hildenbrandia rubra* (Metaxas & Scheibling, 1993). Conversely, Lubchenco (1978) noted that the addition of littorinids to mid-shore pools in Massachusetts decreased the abundance of dominant *Ulva* spp. (as *Enteromorpha* spp.) in favour of *Chondrus crispus* (Metaxas & Scheibling, 1993) a less palatable red alga. Wolfe & Harlin (1988a) noted that Rhode Island tidepools with the highest littorinid densities had the lowest abundance of macroalgae. Similarly, removal of the limpet *Patella vulgata* from high tidal pools at Lough Ine resulted in an increased abundance of *Ulva* sp. (as *Enteromorpha*) (Goss-Custard *et al.*, 1979).
- Where present, suspension feeders include the barnacles (e.g. *Semibalanus balanoides*, *Balanus crenatus* and *Verruca stroemia*), the mussel *Mytilus edulis*, hydroids (e.g. the epiphytic *Dynamena pumila*), tubeworms (e.g. *Spirorbis* spp. and *Spirobranchus* spp.), ascidians (e.g. *Botrylloides leachi*, *Botryllus schlosseri*, and *Dendrodoa grossularia*), bryozoans (e.g. *Membranipora membranacea* and *Electra pilosa*) and sponges (e.g. *Halichondria panicea* and *Hymeniacidon perleve*). Deep low shore pools may also support the plumose anemone *Metridium dianthus*. However, the abundance of barnacles and mussels in rockpools is usually low (Lewis, 1964), presumably due to heavy predation on juveniles by the dog whelk *Nucella lapillus* and crabs (e.g. *Carcinus maenas* and *Cancer pagurus*) and poor survival of spat or juveniles.
- Macroalgae compete for space with sessile invertebrates such as sponges, hydroids, ascidians and bryozoans. However, sessile epifauna predominate on vertical rock surfaces, overhangs and under boulders within the pool.
- Scavengers include shrimps (e.g. *Palaemon* spp.), brittlestars (e.g. *Amphipholis squamata*

- and *Ophiothrix fragilis*), cushion stars (*Asterina gibbosa*), gastropods (e.g. *Hinia* spp.), hermit crabs (e.g. *Pagurus bernhardus*) and crabs (e.g. *Carcinus maenas* and *Cancer pagurus*).
- Invertebrate predators include turbellarians, nemerteans and polychaetes (e.g. *Eulalia viridis* and *Harmothoe* spp.) feeding on small invertebrates such as copepods and small gastropods. Lower to mid shore rockpools provide refugia for dog whelks *Nucella lapillus* feeding on barnacles and small mussels within the rockpool and /or leaving the rockpool to forage at high tide. Similarly, crabs such as *Carcinus maenas* and *Cancer pagurus* are generalist predators of gastropods (e.g. littorinids) and bivalves as well as scavengers. Passive carnivores include sea anemones such as *Anemonia viridis*, *Actinia equina*, *Cereus pedunculatus*, *Sagartia elegans* and *Urticina felina*. In addition, intertidal fish such as the shanny *Lipophrys pholis* and gobies prey on small invertebrates such as copepods, amphipods and isopods.
 - As with grazing, predation pressure is potentially higher in mid to low shore rockpools, since predators can continue feeding irrespective of the state of the tide. For example, in New South Wales, whelks were shown to reduce the abundance of barnacles, tubeworms and limpets (Fairweather, 1987; Metaxas & Scheibling, 1993). Dethier (1984) concluded that harpacticoid copepod abundance in mid to low shore pools was low due to the presence of predators such as fish and to a lesser extent anemones. The reduced abundance of barnacles and mussels observed in rockpools (Lewis, 1964) is probably partly due to increased predation pressure.

Seasonal and longer term change

Conditions within rockpools are the consequence of prolonged separation from the main body of the sea, and physico-chemical parameters within them fluctuate dramatically (Pyefinch, 1943; Ganning, 1971; Daniel & Boyden, 1975; Goss-Custard *et al.*, 1979; Morris & Taylor, 1983; Huggett & Griffiths, 1986; Metaxas & Scheibling, 1993; Metaxas *et al.*, 1994). In general, larger and deep rockpools low on the shore tend to correspond to the sublittoral habitat with a more stable temperature and salinity regime. In contrast, small and shallow pools higher on the shore are especially influenced by insolation, air temperature and rainfall, the effects of which become more significant towards the high shore, where pools may be isolated from the sea for a number of days or weeks (Lewis, 1964).

Weather conditions exert a considerable influence on temperature and salinity. Water temperature in pools follows the temperature of the air more closely than that of the sea.

Temperature

The temperature of pools fluctuates with air temperature and sunlight, and tends to warm throughout the day, especially if in direct sunlight (Daniel & Boyden, 1975; Goss-Custard *et al.*, 1979). Shaded pools exhibit less dramatic changes in temperature (Daniel & Boyden, 1975). For example, the temperature of a high shore pool exposed to direct sunlight rose quickly in the morning to a maximum of 25 °C, while a shaded high shore pools only rose by 1 °C, even though air temperatures reached 20 °C (Daniel & Boyden, 1975). In addition, deeper pools may become stratified, with warmer water near the surface and cooler near the bottom (Daniel & Boyden, 1975), primarily due to sunlight. They noted that pool temperatures remained almost constant at night and suggested that pool temperatures would fluctuate slowly during the day under overcast conditions. In deeper pools, the vertical temperature gradation present in summer may reverse during winter owing to density stratification, so that ice may form (Naylor & Slinn, 1958). Morris & Taylor (1983) reported warmer water at the bottom of the pools and cooler at the surface, which they attributed to cooling of the surface water by wind. Examples of temperature ranges reported

for mid to low shore pools include annual maxima and minima of 1-25 °C and 2-22 °C (Morris & Taylor, 1983), a diurnal range of 24 °C (day) and 13 °C (night) for a mid shore pool (Daniel & Boyden, 1975), and surface water temperature ranges of 14-19.25 °C and 15.5-20.75 °C in mid shore pools (Pyefinch, 1943). Smaller (or shallower pools) are more affected by climatic change in temperature than larger and/or deeper ones (Ganning, 1971). Morris & Taylor (1983) noted that temperature showed the greatest seasonal variation of all the physical parameters examined. In summer, the minimum recorded temperatures were greater than the maximum temperatures recorded in winter, and the daily temperature ranges were greater in summer than in winter, in both high and low shore pools (Morris & Taylor, 1983).

Salinity

High air temperatures cause surface evaporation of water from pools, so that salinity steadily increases, especially in pools not flooded by the tide for several days. Alternatively, high rainfall will reduce pool salinity or create a surface layer of brackish/nearly freshwater for a period. In addition, freezing of surface water increases the salinity of the underlying water (Ganning, 1971; Metaxas & Scheibling, 1993). Daniel & Boyden (1975) and Morris & Taylor (1983) reported little variability in salinity over one tidal cycle, and Ganning (1971) suggested that changes in salinity were of limited importance. However, heavy rain resulted in a layer of low salinity water on the surface of pools. Morris & Taylor (1983) stated that a low salinity layer of 2-10 mm was normal but after one storm the low salinity layer increased in depth, eventually resulting in a homogeneous pool of brackish water. But the deep pools characterized by this biotope are unlikely to become brackish. Morris & Taylor (1983) reported an annual salinity range in mid to low shore pools of 26-36.5 ppt.

The extent of temperature and salinity change is affected by the frequency and time of day at which tidal inundation occurs. If high tide occurs in early morning and evening the diurnal temperature follows that of the air, whilst high water at midday suddenly returns the temperature to that of the sea (Pyefinch, 1943). Rockpools in the supralittoral, littoral fringe and upper eu littoral are liable to gradually changing salinities followed by days of fully marine or fluctuating salinity at times of spring tide (Lewis, 1964).

Oxygenation

The biological community directly affects oxygen concentration, carbon dioxide concentration and pH, and are themselves affected by changes in the chemical parameters. Throughout the day, algae photosynthesize and produce oxygen, the concentration of which may rise to three times its saturation value, so that bubbles are released (Pyefinch, 1943; Ganning, 1971; Daniel & Boyden, 1975; Goss-Custard *et al.*, 1979; Morris & Taylor, 1983; Metaxas & Scheibling, 1993). In summer, rockpools are likely to be supersaturated with oxygen during the day (Pyefinch, 1943). For example, the greatest range of oxygen saturation of 101.7 % occurred in a seaweed dominated, sediment floored pool, which reached over 190 %saturation on some days (Pyefinch, 1943). Daniel & Boyden (1975) noted that a mid shore, seaweed dominated pool reached 194% saturation (ca 15 mg O₂/l) but that oxygenation was also marked in shaded pools. A pool with dense fauna exhibited a maximum saturation of 210 % (Pyefinch, 1943). During photosynthesis algae absorb carbon dioxide and, as concentrations fall, the pH rises. Morris & Taylor (1983) recorded pH values >9 in rockpools on the Isle of Cumbrae.

At night, changes occur in the opposite direction as respiration utilizes much of the available oxygen and pH decreases. Daniel & Boyden (1975) reported oxygen depletion at night, with mid to low shore pools reduced to 8-44 % saturation. They noted that the crab *Carcinus maenas* leaves the pools at night, and that other species with the ability to air-breathe could also do so, e.g. limpets,

littorinids, and the shanny *Lipophrys pholis*. They also observed that shrimps gathered at the edge of high shore pools at night, presumably to take advantage of the better oxygenated surface layer (Daniel & Boyden, 1975). Daily fluctuation in oxygen concentration and pH also vary seasonally, and with the height of the pool on the shore or pool depth (Daniel & Boyden, 1975; Morris & Taylor, 1983; Metaxas & Scheibling, 1993). Morris & Taylor (1983) noted variation in oxygen concentration with pools with pool depth and proximity to pool algae. Again, inundation by the rising tide causes sudden changes in oxygenation, either sudden drops during the day or increases at night.

Ganning (1971) noted that the temperature of sediment at the bottom of pools showed little variation in temperature, and noted that diurnal fluctuations of greater than 1°C were rarely observed in bottom sediments of pools deeper than 0.5 m, although a temperature of fall 0.5-1 °C was observed at the water/sediment interface. The presence of sediment in pools increases the risk of scour, which is likely to vary seasonally, increasing in winter storms. In addition, anoxic conditions within the sediment could potentially cause significant and sudden decreases in oxygen levels if the sediment was stirred up by wave action, although no evidence of this effect was found.

Seasonal change in communities

Tidepool community structure has been shown to vary markedly over time, particularly with season (Metaxas & Scheibling, 1993). However, most studies have examined tidepools overseas, or different tidepools communities to those that occur in LR.FK (Dethier, 1984; Wolf & Harlin, 1988a,b; Kooistra *et al.*, 1989; Metaxas *et al.*, 1994) so that the species concerned are very different. Seasonal changes in macroalgal cover and diversity were associated with changes in water temperature, light intensity and day length, and reduced grazing pressure from littorinids in winter, although the community types were relatively stable over time in Rhode Island pools (Wolfe & Harlin, 1988a,b). Metaxas *et al.* (1994) noted that sheet forming algae (e.g. *Ulva lactuca*) were found throughout the year, filamentous forms (e.g. *Cladophora* and *Ceramium*) were present in late spring and summer (although other studies found them to be present from late spring to late autumn) while thick leathery and encrusting forms did not vary seasonally. However, macroalgal diversity was lowest in summer and autumn, especially in mid shore pools, probably due to grazing. Metaxas *et al.* (1994) also noted that the abundance of mussels, littorinids and whelks in Rhode Island peaked in summer due to recruitment but varied significantly between pools.

Many of the macroalgae within the biotope are perennial. However, they show seasonal variation in reproduction, with *Halidrys siliquosa* releasing spores in the winter months, potentially enabling them to colonize free space opened up by increased wave action in winter storms and the dying back of annual species (see Kain, 1975). Growth rate of *Laminaria digitata* is seasonally controlled with a period of rapid growth from February to July and one of slower growth from August to January. *Saccharina latissima* grows fastest from late winter to spring then growth declines from June onwards and may cease in late summer. Increased wave exposure and storms in winter months are likely to erode *Laminaria* blades so that they appear tattered in winter months and overall standing biomass is reduced. Annual species, e.g. *Chorda filum* are likely to proliferate in spring, reaching maximum abundance in summer (high insolation and temperature). In *Fucus serratus* reproduction commences in late spring/early summer and continues through summer and autumn, peaking in August - October, and in the summer months it can reach 95% cover on emergent rock (see review). In England, *Fucus vesiculosus* has a protracted reproduction period of about six months which varies only slightly in timing between a population at Wembury on the south coast of Devon and one at Port Erin, Isle of Man (Knight & Parke, 1950). Gametes may be produced from mid winter until late summer with a peak of fertility in May and June.

Red algae exhibit seasonal variation in growth and reproduction and red algal turf declines in abundance during the winter months, partly due to die back and abrasion during winter storms. Although protected from wave action in deep pools, macroalgae will be susceptible to damage and abrasion by wave action and winter storms near the surface or in shallower pools. For example, *Delesseria sanguinea* exhibits a strong seasonal pattern of growth and reproduction. New blades appear in February and grow to full size by May - June becoming increasingly battered or torn and the lamina are reduced to midribs by December (Maggs & Hommersand, 1993). The maximum growth of *Furcellaria lumbricalis* occurs in March/April (Austin, 1960b) and release of carpospores and tetraspores occurs in December/January (Bird *et al.*, 1991). Reproductive bodies are present on the gametophytes of *Ahnfeltia plicata* between July and January and mature carposporophytes occur between October and July (Maggs & Paschal, 1989). Dickinson (1963) reported that *Chondrus crispus* was fertile in the UK from autumn to spring, but that the exact timing varied according to local environmental conditions. In the Bristol Channel, Bamber & Irving (1993) noted that the biomass of *Corallina officinalis* increased steadily through spring and summer and began to decline after July. *Mastocarpus stellatus* (as *Gigartina stellata*) was reported to have a perennial holdfast, losing many erect fronds in winter, which grow back in spring (Dixon & Irvine, 1977). *Osmundea pinnatifida* also shows seasonal variation in growth, expanding its perennial holdfast in June to September, and producing erect fronds from October onwards reaching a maximum in February to May (Maggs & Hommersand, 1993). Maggs & Hommersand (1993) reported that spermatangia of *Ceramium virgatum* (as *nodulosum*) are recorded in January, March-April, June and August-September; cystocarps in January-February and April-September; tetrasporangia in February-September. The advantage of being fertile through the winter, as in the case of *Ahnfeltia plicata*, *Furcellaria lumbricalis* and *Chondrus crispus*, is the availability of substrata for colonization as other annual species die back (Kain, 1975).

Corallina officinalis may be overgrown by epiphytes, especially during summer. This overgrowth regularly leads to high mortality of fronds due to light reduction (Wiedemann, pers. comm.). The ephemeral green seaweeds *Ulva intestinalis* and *Ulva lactuca* are likely to be more abundant in summer depending on grazing pressure. In summer, erect and encrusting corallines may be bleached (especially in shallow pools or near the surface or deep pools) and lose their pink pigment but in some species, e.g. *Phymatolithon* sp., this does not necessarily result in death of the plant and pigment may be re-synthesized (Little & Kitching, 1996).

Habitat structure and complexity

As already noted, no two rockpools exhibit exactly the same physio-chemical conditions and exhibit large spatial variation in community structure, even between adjacent pools at the same shore height (Ganning, 1971; Metaxas & Scheibling, 1993; Metaxas *et al.*, 1994). Habitat complexity will vary with macroalgal cover, the dominant macroalgal species, shore height, pool depth and topography. Deeper pools are likely to be more complex than shallower pools. This biotope resembles the mid and low tidal pools described by Goss-Custard *et al.* at Carrigathorna near Lough Ine, Ireland.

In deep pools the underlying rock is likely to be covered by erect and encrusting corallines. Large macroalgal species (e.g. kelps and fucooids) may dominate the surface of the pool. Their depth within the pool (vertical zonation) is limited by self-shading so that only corallines and red algae occur beneath them. The upper limit of some species of algae within the pool may be limited by the summer surface water temperatures e.g. *Bifurcaria bifurcaria* (Kooistra *et al.*, 1989), and or desiccation after evaporation (e.g. corallines). For example, Goss-Custard *et al.* (1979) noted that *Laminaria* spp. and *Halidrys siliquosa* formed a margin in deep mid shore pools of 0.5-0.6 m deep,

with *Laminaria hyperborea* below them, wherever the substratum was stable enough. The *Corallina officinalis* supported colonies of bryozoans, encrusting corallines and spirorbids and provided refuge for a wide variety of fauna including polychaetes, isopods, rissoid gastropods, amphipods, and *Hiatella arctica* (Goss-Custard *et al.*, 1979; and 'ecological relationships' above). The *Laminaria* spp. provide substratum for specialist grazers such as *Patella pellucida* and epiphytic bryozoans and algae (see 'ecological relationships' above). Goss-Custard *et al.* (1979) noted that the edge of pools that lost water slowly due to leakage during emersion was dominated by ephemeral green algae, e.g. *Ulva* spp. Grazing intensity due to littorinids may also affect the abundance of fleshy macroalgae, so that the pools may be dominated by less palatable red algae (e.g. *Chondrus crispus* and *Mastocarpus stellatus*). In deep pools the understorey is likely to be dominated by coralline turf and red algae. For example, Goss-Custard *et al.* (1979) reported that, in their deepest pool, the laminarians thinned below 0.5 m and the brown algae *Dictyota dichotoma*, *Desmarestia ligulata* appeared, together with *Dilsea carnosa*, *Delesseria sanguinea*, while *Chondrus crispus* and *Corallina officinalis* remained. Below 2m, the laminarians were absent and replaced by a mixed algal shrub of *Dictyota dichotoma*, *Phyllophora crispa*, *Nitophyllum punctatum* and *Cryptopleura ramosa* (Goss-Custard *et al.*, 1979)

Vertical surfaces within deep pools, and crevices or overhangs present, are likely to be dominated by encrusting fauna e.g. the sponges *Halichondria panicea* and *Hymeniacidon perleve*, tubeworms (*Spirobranchus* spp.) and anemones. For example, Goss-Custard *et al.* (1979) noted *Corynactis viridis* and *Sagartia elegans* on the sides of deep mid shore pools.

The presence of boulders and large stones at the bottom of the pools provides additional niches. The surface of larger stones and pebbles may support tubeworms, spirorbids and the holdfasts of kelps or *Chorda filum*, if stable enough and not too deep. The undersides support typical underboulder communities (see MLR.Fser.Fser.Bo; Gordon, 1972), likely to include encrusting sponges, bryozoans and tubeworms, small ascidians, the saddle oyster *Anomia ephippium*, and the porcelain crabs *Porcellana platycheles* and *Pisidia longicornis*. Underboulder habitats also provide refugia for crabs (e.g. *Carcinus maenas* and *Necora puber*) and fish.

The holdfasts of kelps and fucoids, and fronds of filamentous species and erect corallines provide refuges for small invertebrates (e.g. amphipods, isopods and small gastropods) or meiofauna (e.g. copepods) (see ecological relationships above). In addition, the shade of macroalgae provide refuges for shrimps (e.g. *Palaemon* spp.) and intertidal fish (e.g. blennies and gobies), while crevices provide additional refuges for crabs.

Rockpool species also display zonation patterns, similar to the emergent species. For example, brown algae and corallines are usually dominant in mid to low shore pools, while green algae tend to dominate high shore pools (Metaxas & Scheibling, 1993). Kooistra *et al.* (1989) noted vertical zonation within pools and found that macroalgal communities could be allocated to different depths within pools in the lower or higher parts of the shore. However, the communities studied in Brittany differed markedly from those found in this biotope. Similarly, zonation patterns have also been reported in flatworms, rotifers, oligochaetes, cladocans, copepods, ostracods, barnacles, amphipods, isopods, chironomid larvae and fish (see Metaxas & Scheibling, 1993). *Littorina littorea*, mussels, whelks, limpets and sea urchins tend to dominate in lower shore pools, while other littorinids dominate higher on the shore (Metaxas & Scheibling, 1993). Nevertheless, Metaxas *et al.* (1994) noted that horizontal spatial variability between pools within the same shore height appeared to be as great as variability along the intertidal gradient, and suggested that the physical setting of the pool may be of primary importance in determining the macroalgal abundance. Dethier (1984) examined the effect of natural disturbance rockpool communities in the coast of

Washington State. She noted that disturbance such as heat stress in summer and wave action in winter occurred regularly (ca 1.6 times per year per pool). The observed disturbances affected dominant species, so that no one dominant species could occupy all the pools within the tidal range at any one time. None of the tidal pool assemblages observed were stable over many generations and disturbances resulted in a mosaic of species assemblages within pools in any one region (Dethier, 1984).

Productivity

Although little information on rockpool productivity was found, rocky shore communities are highly productive and are an important source of food and nutrients for members of neighbouring terrestrial and marine ecosystems (Raffaelli & Hawkins, 1999; Hill *et al.*, 1998). Macroalgae exude considerable amounts of dissolved organic carbon which are absorbed readily by bacteria and may even be taken-up directly by some larger invertebrates. Only about 10% of the primary production is directly cropped by herbivores (Raffaelli & Hawkins, 1999). Dissolved organic carbon, algal fragments and microbial film organisms are continually removed by the sea. This may enter the food chain of local, subtidal ecosystems, or be exported further offshore. Rocky shores make a contribution to the food of many marine species through the production of planktonic larvae and propagules which contribute to pelagic food chains. Accumulations of algal debris are also likely in rockpools and such detrital material contributes to overall productivity.

Information specific to the community was not found but Workman (1983) gave an estimate of primary production by microalgal films on the lower shore in the British Isles to be in the region of 100 g C/m²/yr, much of which will be utilized directly by grazers, while primary productivity for fucoids on sheltered shores was estimated to be 1250 g C/m²/yr (Hawkins *et al.*, 1992) and for encrusting corallines to be 1000 g C/m²/yr (Dawes *et al.*, 1991; Raffaelli & Hawkins, 1999). Ganning & Wulff (1970) reported primary productivity values in terms of gross photosynthesis of between 2 and 3.5 O₂/m³/hr in brackish water rock pools dominated by green algae. Overall, deep rockpools with abundant macroalgae are likely to be highly productive mesocosms on the shore.

Recruitment processes

As with the emergent rock surfaces, variation and unpredictability in recruitment of species contributes to the variation in dominant species within rockpool communities and hence spatial variation between rockpools (Dethier, 1984). Recruitment processes of characteristic or dominant species are described here.

Flora

- Vadas *et al.* (1992) reviewed recruitment and mortality of early post settlement stages of benthic algae. They concluded that grazing, canopy and turf effects were the most important but that desiccation and water movement may be as important for the early stages. The review indicated that recruitment is highly variable and episodic and that mortality of algae at this period is high. Chance events during the early post settlement stages are therefore likely to play a large part in survival.
- *Laminaria hyperborea* and *Laminaria digitata* produce vast numbers of spores, however they need to settle and form gametophytes within about 1 mm of each other to ensure fertilization and therefore may suffer from dilution effects over distance. However, Chapman (1981) demonstrated that substantial recruitment of *Laminaria digitata* plants to areas barren of kelp plants was possible up to 600 m away from reproductive plants.

Saccharina latissima (studied as *Laminaria saccharina*), is short-lived (2-4 years), reaches maturity quickly and colonizes bare substratum rapidly (ca 6 months) (Kain, 1975; Kain, 1979; Birkett *et al.*, 1998b; see *MarLIN* review) and may be regarded as relatively opportunistic.

- Fucooids (e.g. *Fucus serratus* and *Fucus vesiculosus*) recruit readily to cleared areas, especially in the absence of grazers (Holt *et al.*, 1997). However, fucooid propagules tend to settle near to the parent plants, due to turbulent deposition by water flow. Within monospecific stands recruitment of conspecifics is most likely, and community recovery is likely to be rapid. However, in cleared areas, recruitment is likely to be rapid but recovery of the original community structure is likely to take some years (Holt *et al.*, 1997). Sousa *et al.* (1981) reported that experimental removal of sea urchins significantly increased recruitment in long-lived brown algae. In experimental plots cleared of algae and sea urchins in December, *Halidrys dioica* colonized the plots, in small numbers, within 3-4 months. Plots cleared in August received few, if any recruits, suggesting that recolonization was dependant on zygote availability and therefore the season. *Halidrys dioica* did not colonize plots grazed by urchins in their experiments (Sousa *et al.*, 1981). Wernberg *et al.* (2001) suggested that the lack of long range dispersal success in *Halidrys siliquosa* was responsible for its regional distribution in the north east Atlantic.
- Settlement of algal spores is partly dependant on their motility (if any) and adhesive properties together with preferences for topography (surface roughness), the chemical nature of the substratum and water movement (Norton 1992; Fletcher & Callow 1992). As with all red algae, the spores of *Chondrus crispus*, *Palmaria palmata* and *Ceramium virgatum* are non-flagellate and therefore dispersal is a wholly passive process (Fletcher & Callow, 1992). In general, due to the difficulties of re-entering the benthic boundary layer, it is likely that successful colonization is achieved under conditions of limited dispersal and/or minimum water current activity. Norton (1992) reported that although spores may travel long distances (e.g. *Ulva* sp. 35 km, *Phycodrys rubens* 5 km), the reach of the furthest propagule does not equal useful dispersal range, and most successful recruitment occurs within 10 m of the parent plants. It is expected, therefore, that recruitment of red algae, e.g. *Chondrus crispus*, *Palmaria palmata*, *Furcellaria lumbricalis*, *Mastocarpus stellatus* and the majority of other macroalgae in the biotope would occur from local populations on the surrounding emergent rock but that establishment and recovery of isolated populations would be patchy and sporadic. Scrosati *et al.* (1994) commented that viability of spores of *Chondrus crispus* was low (<30%) and suggested that reproduction by spores probably does not contribute much to maintenance of the intertidal population in Nova Scotia, compared to vegetative growth of gametophytes. However, macroalgae are highly fecund and widespread in the coastal zone so that recruitment may be still be rapid, especially in the rapid growing ephemeral species such as *Ulva* spp., which reproduce throughout the year with a peak in summer. Similarly, *Ceramium* species produce reproductive propagules throughout the year, while *Mastocarpus stellatus* produce propagules from February to December, and exhibit distinct reproductive papillae in summer (Dixon & Irvine, 1977; Burrows, 1991; Maggs & Hommersand, 1993).
- *Lithophyllum incrustans*, representing the encrusting corallines in the biotope, it has been calculated that 1 mm x 1mm of reproductive thallus produces 17.5 million bispores per year with average settlement of only 55 sporelings/year (Edyvean & Ford, 1984). Dispersal is likely to be in excess of 5 km and spores will settle and new colonies will arise rapidly on bare substratum, although the growth rate is slow (2-7 mm per annum - see Irvine & Chamberlain, 1994). The erect coralline *Corallina officinalis* has isomorphic sexual (gametophyte) and asexual (sporophyte) stages (see *MarLIN* review). Settlement and development of fronds is optimal on rough surfaces but settlement can occur on smooth

surfaces (Harlin & Lindbergh, 1977; Wiedeman pers comm.). *Corallina officinalis* settled on artificial substrata within 1 week of their placement in the intertidal in New England summer suggesting that recruitment is high (Harlin & Lindbergh, 1977).

Fauna

- Gastropods exhibit a variety of reproductive life cycles. The common limpets *Patella vulgata* and *Patella ulyssiponensis*, the top shell *Steromphala umbilicalis*, and *Littorina littorea* have pelagic larvae with a high dispersal potential, although recruitment and settlement is probably variable. However, *Littorina obtusata* lays its eggs on the fronds of fucooids from which hatch crawl-away miniature adults. Similarly, the dog whelk *Nucella lapillus* lays egg capsules on hard substrata in damp places on the shore, from which crawl-always emerge. Therefore, their dispersal potential is limited but probably designed to colonize an abundant food source. In addition, most gastropods are relatively mobile, so that a large proportion of recruitment of available niches would involve migration. *Nucella lapillus* is an exception, as they generally do not move far, averaging 100 mm /tidal cycle, or between 30 cm or 10 m per year when in the vicinity of an abundant food source (see MarLIN reviews for details; Fish & Fish, 1996).
- Many species of mobile epifauna have long lived pelagic larvae and/or are highly motile as adults. Gammarid amphipods brood their embryos and offspring but are highly mobile as adults and probably capable of colonizing new habitats from the surrounding area (e.g. see *Hyale prevostii* review for example). Similarly, isopods such as *Idotea* species brood their young. *Idotea* species are mobile and active swimmers and probably capable to recruiting to new habitats from the surrounding area by adult migration. Hicks (1985) noted that epiphytic harpacticoid copepods lack planktonic dispersive larval stages but are active swimmers, which is therefore the primary mechanism for dispersal and colonization of available habitats. Some species of harpacticoids are capable to moving between low and mid-water levels on the shore with the tide, while in others colonization rates decrease with increasing distance from resident population. Overall immigration and *in situ* reproduction were thought to maintain equilibrium populations exposed to local extinction, although there may be local spatial variation in abundance (see Hicks, 1985).
- Epiphytic and sessile fauna, such as sponges, hydroids, bryozoans and ascidians, have pelagic but short lived larvae with relatively short effective dispersal ranges, depending on the local hydrography. However, most epiphytic species are widespread and ubiquitous and would probably recruit rapidly from adjacent or nearby populations.

Time for community to reach maturity

Development of the community in this biotope, from bare or denuded rock, is likely to follow a similar successional pattern to emergent sheltered rocky shore communities. The loss of grazing species results in an initial proliferation of ephemeral green then fucooid algae, which then attracts mobile grazers, and encourages settlement of other grazers. Limpet grazing reduces the abundance of fucooids allowing barnacles to colonize the shore. After the *Torrey Canyon* oil spill in March 1967, recovery rates were dependant on local variation in recruitment and mortality so that sites varied in recovery rates, for example maximum cover of fucooids occurred within 1-3 years, barnacle abundance increased in 1-7 years, limpet number were still reduced after 6-8 years and species richness was regained in 2 to >10 years (Southward & Southward, 1978; Hawkins & Southward, 1992; Raffaelli & Hawkins, 1999). Where only the rockpool was affected, recruitment is potentially good, especially in motile species. However, variability in rockpool communities and their response to disturbance (recovery) has been attributed to

variation and seasonality in recruitment (Metaxas & Scheibling, 1993).

Dethier (1984) noted that few rockpool populations, even of dominant species, remained static over time, based on long-term observations over several years. On the coast of Washington State, partial disturbance (a reduction in abundance or cover) resulted in relatively rapid recovery of the community, for examples encrusting corallines recovered in over 2 months, erect corallines attained 87% of its original cover in 2 years. The red algae *Rhodomela* sp. exhibited 39% recovery from total loss after 2 years and *Cladophora* sp. exhibited 77% recovery after total loss. Dethier (1984) concluded that disturbance was a factor that developed a mosaic of different communities in rockpools within an area and that, at any point in time, rockpool communities were probably in different stages of recovery.

Additional information

None entered

Preferences & Distribution

Habitat preferences

Depth Range	Mid shore, Lower shore
Water clarity preferences	
Limiting Nutrients	No information found
Salinity preferences	Full (30-40 psu)
Physiographic preferences	Enclosed coast / Embayment, Open coast
Biological zone preferences	Lower eulittoral, Eulittoral
Substratum/habitat preferences	Bedrock
Tidal strength preferences	
Wave exposure preferences	Exposed, Moderately exposed, Sheltered
Other preferences	Deep rockpools

Additional Information

This biotope is characterized by macroalgal dominated, deep rockpools. The physical characteristics of the rockpool environment are described under 'Seasonal and longer term change' on the 'Ecology' page. Pyefinch (1943) and Goss-Custard *et al.* (1979) provide detailed species lists for the rockpools they studied in British and Irish waters.

Species composition

Species found especially in this biotope

Rare or scarce species associated with this biotope

-

Additional information

The MNCR database lists 667 species in 213 records of this biotope (JNCC, 1999), although not all species occur in all records of the biotope. Lewis (1964) noted that deep pools in the lower shore, especially in the southwest, are rich areas for collecting the rarer species of algae.

Sensitivity review

Sensitivity characteristics of the habitat and relevant characteristic species

Deep or large rock pools within the lower eu littoral on wave exposed to moderately exposed shores characterized by *Fucus serratus*, *Laminaria digitata* and *Corallina officinalis*. Other brown seaweeds such as *Saccharina latissima* (syn. *Laminaria saccharina*) and *Halidrys siliquosa* may also occur. A wide variety of filamentous and foliose seaweeds occur beneath the brown algal canopy, for example red seaweeds *Palmaria palmata*, *Chondrus crispus*, *Mastocarpus stellatus*, *Ceramium nodulosum* and *Dumontia contorta*, and green seaweeds such as *Ulva* spp. and *Cladophora rupestris* can be present as well. Algal-free vertical and overhanging faces often support the sponge *Halichondria panicea* and anemones including *Actinia equina* and *Urticina feline* (Connor *et al.*, 2004).

In undertaking this assessment of sensitivity, account is taken of knowledge of the biology of all characterizing species in the biotope. For this sensitivity assessment *Fucus serratus*, *Laminaria digitata* and *Corallina officinalis* are the primary foci of research. However, loss of any one of these species would not in itself result in loss of a recognizable biotope. The understory red seaweed communities also define the biotope. Examples of important species groups are mentioned where appropriate.

Resilience and recovery rates of habitat

Fucus serratus is a dioecious, perennial brown macroalgae, characteristic of the eu littoral zone. Sexual reproduction starts in late spring/early summer and continues through summer and autumn, peaking in August-October. Eggs and sperm are released and fertilization occurs in the water column. Fertilized spores then develop into a gametes and fertilized eggs which then settle onto the substratum, however are generally restricted to within 1–2 m from the parent (Arrontes, 1993). Average annual expansion rates for *Fucus serratus* have been estimated at 0.3 to 0.6 km per year (Coyer *et al.*, 2006a; Brawley *et al.*, 2009). Dispersal is highly limited as the negatively buoyant eggs are fertilized almost immediately after release and dispersal by rafting reproductive individuals is unlikely (Coyer *et al.*, 2006a).

Schiel & Foster (2006) observed long-term demographic lags in recovery after important losses of fucoids. Loss of fucoids can cause systems shifts to a state dominated by low-lying turf or filamentous ephemeral algae (Airoldi *et al.*, 2008; Mangialajo *et al.*, 2008; Perkol-Finkel & Airoldi, 2010). Turf algae, especially corallines, are often highly resilient and positively associated with perturbed areas, and can recover and reach greater abundance compared to prior disturbance conditions (Bulleri *et al.*, 2002; Bertocci *et al.*, 2010). These turf algae can then prevent canopy recovery by inhibiting recruitment. Stagnol *et al.* (2013) observed *Patella vulgata* recruiting in bare patches of disturbed plots. Experimental studies have shown that limpets control the development of macroalgae by consuming microscopic phases (Jenkins *et al.*, 2005) or the adult stages (Davies *et al.*, 2007). The increase in *Patella vulgata* abundance could thus limit the recruitment and growth of *Fucus serratus* on the wave impact zone. Stagnol *et al.* (2013) found that opportunistic ephemeral green algae such as *Ulva* sp. responded positively to disturbance (removal

of the canopy). These green ephemeral algae are major competitors of *Fucus serratus* for space colonization and nutrient uptake. Blooms of ephemeral algae facilitated by disturbance may then slow the development of longer-lived perennial algae, especially fucoids.

Disturbance is a structuring factor in intertidal habitats. Perturbation events often remove organisms, increasing mortality, and also release resources such as space, nutrients and light that may enhance the appearance of new colonists (Connell *et al.*, 1997). As a result of these contrasting effects, post-disturbance communities are frequently different from initial communities in terms of composition and dominance of species. Overall, disturbance causes a shift towards a disturbance tolerant seaweed community (Little *et al.*, 2009). The changes in dominant species and community structure take some time to develop and, although some effects occur rapidly, many are manifested over a period of several years (Schiel & Lilley, 2011). For example, Hawkins & Southward (1992) found that, after the *Torrey Canyon* oil spill, it took between 10 and 15 years for the *Fucus sp.* to return to 'normal' levels of spatial and variation in cover on moderately exposed shores.

The dispersal of *Laminaria digitata*'s spores and subsequent successful recruitment has been recorded 600 m from reproductive individuals (Chapman, 1981). Local water movement plays an important role in the potential recovery of *Laminaria digitata* dominated biotopes, with larva dependant on currents to extend their dispersal range, although the majority of larvae settle within its local biotope (Brennan *et al.*, 2014). The growth rate of *Laminaria digitata* changes with the seasons. Growth is rapid from February to July, slower in August to January, and occurs diffusely in the lamina (blade; Kain, 1979). This diffuse growth may enhance its resistance to potential grazers. Sori (spores) are produced at temperatures lower than 18°C with a minimum of 10 weeks a year between 5-18°C needed to ensure spore formation (Bartsch, 2013). Thus temperature and by default season impacts the level of reproductive activity. In order to maximise survival rates of mature gametophytes, gametophyte development can be delayed by the algae until optimum conditions return and the gametophyte produces gametes (Hoek van den *et al.*, 1995), which suggests a degree of resistance to short-term changes in temperature which may be anthropogenic in origin. Another factor that is likely to affect recovery is the dominance of Invasive Non Indigenous Species (INIS). Species, such as *Sargassum muticum* and *Codium fragile* exploit gaps in kelp beds and can out-compete *Laminaria digitata*, so that high frequency, low impact disturbances may make the kelp stands more vulnerable to competition from these and other turf forming algae (Staehr *et al.*, 2000; Scheibling *et al.*, 2008; Connell & Russell 2010).

Engelen *et al.* (2011) showed that removal of 0.25m² areas of *Laminaria digitata* forest in the spring and autumn had different recovery rates, with autumn recovery more rapid than spring (taking a minimum of 12 months). Return to conditions prior to removal took 18-24 months, with competition for space by *Saccorhiza polyschides* impacting recovery rates in the first year of recolonization (Engelen *et al.*, 2011). Recolonization of concrete blocks by *Laminaria digitata* was investigated by Kain (1975) at Port Erin, Isle of Man. *Laminaria digitata* was considered re-established two years after removal, with the characteristic red foliose algae following one year later. Similarly, recovery after simulated harvesting of a standing crop of *Laminaria digitata* occurred within 18-20 months (Kain, 1979). While colonization of young *Laminaria*

sporophytes may occur one year after initial substratum clearance (Kain, 1979), the return of the biotope to its original mature condition is likely to lag behind this recolonization. These findings agree with previous studies which showed that when 60% of sporophytes (adult alga) were removed from a location, 18 months were required for the stand to rejuvenate (Perez, 1971), while in France, CIAM (Le Comité interprofessionnel des algues marines) proposed that, regardless of collection method, the restoration of stands of laminarians took up to 18 months post harvesting (Arzel, 1998). Some disparities between reported recovery rates do exist, with cleared plots in Helgoland taking 25 months, probably because plots were burned to ensure total removal of spores and germlings (Markham & Munda, 1980). Even after 25 months, although algal density had returned to pre-clearance levels, the *Laminaria digitata* alga were smaller than those on undisturbed plots, suggesting full recovery is longer than 25 months (Markham & Munda, 1980).

Recovery of *Corallina officinalis* will require either re-growth from surviving holdfast or basal crusts or recolonization by propagules. The crustose holdfast or base is perennial and grows apically (continuous growth at tips), similar to encrusting corallines such as *Lithothamnium* sp. The basal crust may grow continuously until stimulated to produce fronds (Littler & Kauker, 1984; Colhart & Johanssen, 1973). Littler & Kauker (1984) suggest that the crustose bases are an adaptation to resist grazing and desiccation whereas the fronds are adapted for higher primary productivity and reproduction. The basal crusts are tougher than the upright fronds (requiring a pressure of 94 g/mm² to penetrate, compared to 43 g/mm² respectively). Regeneration of the basal crusts provides a more rapid route to recovery than recolonization. Experiments in the intertidal in southern California found that areas scraped back to crusts recovered four times more rapidly than sterilised plots where the crusts were removed (Littler & Kauker, 1984). In culture *Corallina officinalis* fronds exhibited an average growth rate of 2.2 mm/month at 12 and 18°C. Growth rate was only 0.2 mm/month at 6°C and no growth was observed at 25°C (Colhart & Johanssen, 1973). Similarly, Blake & Maggs (2003) observed much higher growth rates of 2 mm/month over 6 months starting from September in *Corallina officinalis* grown in Strangford Lough (Northern Ireland) at 5 and 10m depth, these rates are similar to those observed by Andrade & Johansen (1980) in winter in New Hampshire. The evidence for growth rate suggests that to achieve a height of 10 cm the turf would be at least 4 years old; probably older as higher temperatures appear to slow growth. A lower level turf of, for example 5 cm, could theoretically be achieved within 2 years.

Where the bases are removed, recovery will depend on recolonization. Areas that are cleared during the reproductive period have the potential to be rapidly colonized. *Corallina officinalis* was shown to settle on artificial substances within 1 week of their placement in the intertidal in New England summer (Harlin & Lindbergh, 1977). However, settlement plates laid out in the autumn were not recolonized until the next spring. In the lower rocky intertidal in southern California dominated by *Corallina officinalis* with foliose over-storey algae present, Littler & Kauker (1984) experimentally cleared plots and followed the recovery for 12 months. Some areas were scraped allowing the basal crusts to remain whereas others were completely sterilised (removal of all material and surfaces then scorched with a blow torch to remove bases). In scraped plots up to 15% cover of *Corallina officinalis* fronds returned within 3 months after removal of fronds and all other epiflora/fauna (Littler & Kauker,

1984) while in sterilized plots (all basal crusts removed) appearance of articulated fronds occurred 6 months following clearance. At the end of the 12 month observation period *Corallina officinalis* cover had increased to approximately 18% in plots where basal crusts remained and to approximately 10% in sterilised plots. Similarly, Bamber & Irving (1993) reported that new plants grew back in scraped transects within 12 months, although the resistant crustose bases were probably not removed.

Once established turfs of *Corallina spp.* can persist for a long time, surveys of rocky intertidal ledges at Hinkley point, Somerset in England have found that the patches mapped in the 1980s (Bamber & Irving, 1993) had not changed position when resurveyed 18 years later (Burdon *et al.*, 2009). It has been speculated but not definitively demonstrated that turf-forming algae and canopy forming algae may represent alternate stable states on temperate rocky shores and a shift in balance to the alternate state may prevent recovery. Some potential mechanisms for inhibition of canopy forming species are space pre-emption by turfs that prevent recruitment of taller algae (Perkol-Finkel & Airoidi, 2010; Kennelly, 1987) due to the coverage of suitable rock surfaces and the presence of sediments within the turf (Airoidi, 2003). Clearance experiments on rocky, intertidal shores in Southern California (Sousa, 1979) found that *Ulva spp.* which have a longer reproductive season could colonize cleared areas preventing the establishment of perennial red algae. However grazing by crabs removed the green algae (Sousa, 1979), highlighting the potential importance of grazers, particularly littorinids, to the re-establishment of macroalgal dominated biotopes.

Resilience assessment. *Fucus serratus*, *Laminaria digitata* and *Corallina officinalis* are the main structural species within this biotope. *Fucus serratus* recovery will be variable, dependant on the scale of disturbance. If resistance is assessed as Low-None, recovery could be affected by inter-specific competition and or a short range recruitment from adjacent populations, and may therefore extend to >10 years (Low resilience). However, after small scale disturbance (medium resistance) *Fucus serratus* recruitment may take no more than 2 years. Similarly, the clearance experiments by Littler & Kauker (1984) suggest that recovery of a dense *Corallina officinalis* turf whether basal crusts remained or were totally removed would require more than 2 years (medium resilience). Evidence suggests indicated that complete recovery of *Laminaria digitata* and its associated epibiota can occur within 18-24 month after complete removal. Resilience is, therefore, dependent on the recovery of the *Fucus serratus* and *Corallina officinalis*, which may take from 2-10 years (**Medium resilience**).



Hydrological Pressures

	Resistance	Resilience	Sensitivity
Temperature increase (local)	Medium Q: High A: High C: High	Medium Q: High A: High C: High	Medium Q: High A: High C: High

Rockpools experience variation in temperature on a daily and seasonal basis. The range and extremes of temperature change increasing with shore height but also dependent on shading, aspect, topography and depth of the pool (Pyefinch, 1943; Ganning, 1971; Daniel & Boyden, 1975; Goss-Custard *et al.*, 1979; Morris & Taylor, 1983; Huggett & Griffiths, 1986; Metaxas & Scheibling, 1993). For example, reported

temperature ranges for mid to low shore pools include annual maxima and minima of 1-25°C and 2-22°C (Morris & Taylor, 1983), a diurnal range of 24°C (day) and 13°C (night) for a mid shore pool (Daniel & Boyden, 1975), and surface water temperature ranges of 14-19.25°C and 15.5-20.75°C in mid shore pools (Pyefinch, 1943). Temperature stratification within pools may result in higher surface temperatures and lower deep water temperatures in sunlight (Daniel & Boyden, 1977) or be reversed due to wind cooling, night or in winter (Naylor & Slinn, 1958; Ganning, 1971; Morris & Taylor, 1983). The temperature range will limit the distribution of sensitive species within the pools, especially normally sublittoral species, e.g. laminarians

The temperature tolerance of *Laminaria digitata* sporophyte growth and reproduction is between 0-18 °C, and for gametophytes 0-17 °C (Gayral & Cosson, 1973). The thermal optimum of *Laminaria digitata* is between 10-15°C. Temperature of 22-23°C is likely to cause cell damage and increase mortality (Sundene, 1964; Bolton & Lüning, 1982). A minimum of 10 weeks a year between 5-18°C is needed in order to ensure spore formation and hence reproduction (Bartsch, 2013), and is the most temperature sensitive stage of reproduction. However, above 15°C reproduction is severely reduced, reproductive ability is impaired to 20% at 18°C (Arzel, 1998).

Nielsen *et al.* (2014b) found no negative effects on growth rates of adult *Fucus serratus* to water temperatures of 2 °C (based on a laboratory experiment with specimen collected from Firth of Forth, Scotland) and Arrontes (1993) observed that *Fucus serratus* survived in laboratory experiments for 1 week at 25°C. Nielsen *et al.* (2014b) did, however, report that germlings were negatively affected by increased temperature indicating that early life stages are more vulnerable than mature algae to this pressure.

Several studies have observed adverse effects of *Fucus serratus* as a result to warm thermal stress in terms of growth, physiological performance and reproductive output in Spain and Portugal (Pearson *et al.*, 2009; Viejo *et al.*, 2011; Martínez *et al.*, 2012). Jueterbock *et al.* (2014) determined that these negative impacts can be explained by restricted within-population genetic diversity. South west Ireland and Brittany are hot-spots of genetic diversity (Coyer *et al.*, 2003; Hoarau *et al.*, 2007) and may thus be more resilient to changes in temperature. Phenotypic plasticity therefore plays an important role in determining the sensitivity of individual populations to changes in temperature.

Latham (2008) investigated the effects of temperature stress on *Corallina officinalis* through laboratory tests on samples collected in the Autumn in Devon, England from rock pools. Samples were kept at 15 °C for three days and then exposed to temperatures of 5, 15, 20, 25 and 30 °C (the normal range of temperature experienced was suggested to be between 5 and 15 °C). At 35 °C *Corallina spp.* were completely bleached after 3 days with a sample kept at 30 °C beginning to bleach. After 7 days (the end of the experiment) the sample kept at 30 °C was partially bleached. Samples kept at 5, 15, 20 and 25 °C showed little change in chemicals produced in reaction to thermal stress and no bleaching suggesting the temperatures in that range had not induced stress reactions.

Sensitivity assessment. *Fucus serratus* would not likely be affected at the benchmark level. In addition, the mid-shore pools probably experience a range of temperatures

wider than the benchmark level of change. However, some species may be affected. For example *Laminaria digitata* sporophyte growth may be affected by a 5 °C temperature increase combined with high UK summer temperatures. Within southern examples of the biotope a 2 °C increase for one year may impair *Laminaria digitata* spore production. Therefore, resistance has been assessed as 'Medium', and resilience as 'Medium'. Sensitivity has been assessed as 'Medium'.

Temperature decrease
(local)

High

Q: High A: High C: High

High

Q: High A: High C: High

Not sensitive

Q: High A: High C: High

Rockpools experience variation in temperature on a daily and seasonal basis. The range and extremes of temperature change increasing with shore height but also dependent on shading, aspect, topography and depth of the pool (Pyefinch, 1943; Ganning, 1971; Daniel & Boyden, 1975; Goss-Custard *et al.*, 1979; Morris & Taylor, 1983; Huggett & Griffiths, 1986; Metaxas & Scheibling, 1993). For example, reported temperature ranges for mid to low shore pools include annual maxima and minima of 1-25°C and 2-22°C (Morris & Taylor, 1983), a diurnal range of 24°C (day) and 13°C (night) for a mid shore pool (Daniel & Boyden, 1975), and surface water temperature ranges of 14-19.25°C and 15.5-20.75°C in mid shore pools (Pyefinch, 1943). Temperature stratification within pools may result in higher surface temperatures and lower deep water temperatures in sunlight (Daniel & Boyden, 1977) or be reversed due to wind cooling, night or in winter (Naylor & Slinn, 1958; Ganning, 1971; Morris & Taylor, 1983). The temperature range will limit the distribution of sensitive species within the pools, especially normally sublittoral species, e.g. laminarians

The temperature tolerance of *Laminaria digitata* sporophyte growth and reproduction is between 0-18 °C, and for gametophytes 0-17 °C (Gayral & Cosson, 1973). The thermal optimum of *Laminaria digitata* is between 10-15 °C (Arzel, 1998).

Lüning (1984) reported that *Fucus serratus* survived in the laboratory for a week a range temperature between 0°C and 25°C. Furthermore *Fucus serratus* has a boreal distribution, recorded from Svalbard where winter temperatures are 3 °C (Beszczynska-Möller & Dye, 2013) and is therefore unlikely to be unaffected at the benchmark level.

Lüning (1990) reported that *Corallina officinalis* from Helgoland survived exposure to 0 °C w for one week. New Zealand specimens were found to tolerate -4°C (Frazer *et al.*, 1988).

LR.FLR.Rkp.FK is distributed throughout the UK (Connor *et al.*, 2004). Northern to southern Sea Surface Temperature (SST) ranges from 8-16 °C in summer and 6-13 °C in winter (Beszczynska-Möller & Dye, 2013).

Sensitivity assessment. None of the characterizing species are likely to be affected by a temperature decrease at the benchmark level, and many are protected from temperature extremes and winter frost by the depth of the pool. Resistance has been assessed as 'High', resilience as 'High' and sensitivity as 'Not sensitive' at the benchmark level

Salinity increase (local)**Medium**

Q: Low A: NR C: NR

Medium

Q: High A: Medium C: High

Medium

Q: Low A: Low C: Low

High air temperatures cause surface evaporation, which can result in a steady salinity increase. However, Daniel & Boyden (1975) and Morris & Taylor (1983) reported little variability in salinity over one tidal cycle, and Ganning (1971) suggested that changes in salinity were of limited importance. Morris & Taylor (1983) reported an annual maximum salinity of 36.5 ppt in the pools studied on the west coast of Scotland. Goss-Custard *et al.* (1979) recorded salinities of 34.8 and 35.05 ppt in mid-shore pools. Therefore, the biotope is likely to be tolerant of small increases in salinity. High shore pools exhibit greater variation and higher extremes of salinity (Pyefinch, 1943; Ganning, 1971) and different communities but mid to low shore pools are unlikely to experience such extremes unless the emergence regime is increased (see relevant pressure) or they are exposed to hypersaline effluents.

Laminaria digitata has been found to tolerate 20-55 psu for a period of 5 days. At 60 psu photosynthetic rate declined to 66% of that at normal salinity (34 psu). Therefore indicating that *Laminaria digitata* can tolerate hyper-saline conditions of 55 psu, at least in the short-term. However, Birkett *et al.* (1998b) reported that *Laminaria digitata*, was a stenohaline species that typically required regular salinities of 30-34 psu to maintain optimum growth rates. Therefore, long-term reductions in salinity may result in the loss of kelp in the affected area and thus loss of the biotope (Birkett *et al.*, 1998b). Fucooids are able to compensate for changes in salinity by adjusting internal ion concentrations. However this will occur at a cost, reducing photosynthetic rate and hence affecting the growth rate of the seaweed. *Fucus serratus* is reported to have high growth rates from 20-30‰ (Bird *et al.*, 1979; Malm *et al.*, 2001). Kinne (1971b) cites maximal growth rates for *Corallina officinalis* between 33 and 38 psu in Texan lagoons.

Sensitivity assessment. The evidence suggests that *Laminaria digitata* can tolerate exposure to hypersaline conditions of $\geq 40\text{‰}$ for short periods of 5 days. The remaining characterizing species can be found in fully marine conditions, however the effects of long-term increases in salinity to $>40\text{psu}$ are unclear. Birkett *et al.* (1998) suggests that long-term increases in salinity may detriment *Laminaria digitata*, however the intertidal habit of both *Fucus serratus* and *Corallina officinalis* suggests these species would be tolerant of hypersaline conditions. Resistance has been assessed as 'Medium' because of the potentially negative effect this pressure could have on *Laminaria digitata*. Therefore, resilience is assessed as 'Medium' and the sensitivity of this biotope to an increase in salinity has been assessed as 'Medium'.

Salinity decrease (local)**Low**

Q: High A: High C: High

Medium

Q: High A: High C: High

Medium

Q: High A: High C: High

During periods of emersion, high rainfall will reduce pool salinity or create a surface layer of brackish/nearly freshwater for a period. The extremes of salinity experienced will depend on the depth of the pool, shore height and flushing rate, and season. For example, Morris & Taylor (1983) stated that a low salinity layer of 2-10 mm was normal but after one storm the low salinity layer increased in depth, eventually resulting in a homogeneous pool of brackish water. Morris & Taylor (1983) reported an annual salinity range in mid to low shore pools of 26-36.5 ppt.

Mid shore examples of this biotope may lack more sensitive species, such as *Laminaria digitata* and some sublittoral species. For example, Karsten (2007) tested the short-term salinity tolerance of *Laminaria digitata* from 5-60 psu by measuring the photosynthetic rates after 2 and 5 days of exposure. Highest photosynthetic performance was measured between 20-55psu. Hyposaline treatments from 20-10 psu were accompanied with a gradual decrease in photosynthetic performance. Demonstrating that *Laminaria digitata* could tolerate short-term exposure to 20 psu, below which declines in photosynthesis were measured. However, Birkett *et al.*, (1998b) reported that *Laminaria digitata* was a stenohaline species that typically required regular salinities of 30-34 psu to maintain optimum growth rates. Therefore, long-term reductions in salinity may result in the loss of the kelp in the affected area (Birkett *et al.*, 1998b).

Fucooids are able to compensate for changes in salinity by adjusting internal ion concentrations. However this will occur at a cost, reducing photosynthetic rate and hence affecting the growth rate of the seaweed. Growth rates for *Fucus serratus* are highest at a salinity of 20 psu with the critical limit for recruitment at 7 psu (Malm *et al.*, 2001). Sufficient salinity is essential for successful fertilization and germination in fucooids (Brawley, 1992b; Serrão *et al.*, 1999). Malm *et al.* (2001) found fucooid fertilization success was 87% at 9 psu but declined to 5% at 6 psu (Malm *et al.*, 2001). Reduced salinity does also affect dispersal by decreasing swimming performance of fucooid sperm (Serrão *et al.*, 1996). In the Baltic, *Corallina officinalis* is confined to deeper waters as surface salinity decreases (Kinne, 1971b) suggesting that full salinity is required in the long-term although short-term fluctuations may be tolerated. Kinne (1971b) cites maximal growth rates for *Corallina officinalis* between 33 and 38 psu in Texan lagoons, so that a decrease in salinity at the pressure benchmark would be predicted to lead to reduced growth.

Sensitivity assessment. A decrease in one MNCR salinity scale from 'Full Salinity' (30-40psu) to 'Reduced Salinity' (18-30 psu) may result in a decrease of *Laminaria digitata* and *Corallina officinalis* growth and therefore the biotope may diminish. Fucooids are unlikely to be affected. But a long-term reduction in salinity on the shore for a year is likely to result in a loss of the more sensitive species, inc. mobile amphipods, and some red algae, and an overall reduction in species richness. Resistance has been assessed as '**Low**' and resilience as '**Medium**'. Therefore, sensitivity of this biotope to a decrease in salinity has been assessed as '**Medium**'.

Water flow (tidal current) changes (local)

Not relevant (NR)
Q: NR A: NR C: NR

Not relevant (NR)
Q: NR A: NR C: NR

Not relevant (NR)
Q: NR A: NR C: NR

Water flow rate in this biotope is typically only that of the ebb and flood tide speed, which hardly affects intertidal habitats and is far exceeded by the strength of wave action. A change in water flow rate is therefore considered **Not relevant**.

Emergence regime changes

Medium
Q: Low A: NR C: NR

Medium
Q: High A: High C: High

Medium
Q: Low A: NR C: NR

LR.FLR.Rkp.FK is found within large rock pools, therefore water retention is likely to limit desiccation of the community. However, an increase in emergence may lead to

longer exposure to air temperatures with corresponding fluctuations in water temperature and changes in salinity following evaporation or dilution by rainfall (see seasonal and temporal change above). Mobile species within this biotope could relocate to preferred shore heights but an increase or decrease in abundance of predators and grazers may alter the structure of the assemblage.

Sensitivity assessment. Resilience has been assessed as 'Medium'. Resistance as 'Medium'. The sensitivity of this biotope to a change in emergence is considered as 'Medium'.

Wave exposure changes (local)	High Q: High A: High C: High	High Q: High A: Medium C: High	Not sensitive Q: High A: High C: High
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This rock pool biotope occurs in exposed to moderately exposed habitats. Rock pools provide a degree of shelter from wave action, especially deep pools, allowing more fragile sublittoral algae to survive. However, an increase in wave exposure from, for example moderately exposed to very exposed is likely change the community. Furoid abundance is characteristic of wave sheltered conditions, and on more wave exposed shores shallow rockpools are dominated by *Corallina officinalis* (Connor *et al.*, 2004). However, a change in wave exposure at the benchmark level would not be likely to have any significant affect.

Sensitivity assessment. Resistance has been assessed as 'High', resilience as 'High' and sensitivity as 'Not Sensitive' at the benchmark level.

Chemical Pressures

	Resistance	Resilience	Sensitivity
Transition elements & organo-metal contamination	Not Assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR

This pressure is **Not assessed** but evidence is presented where available.

Bryan (1984) suggested that the general order for heavy metal toxicity in seaweeds is: organic Hg > inorganic Hg > Cu > Ag > Zn > Cd > Pb. Cole *et al.* (1999) reported that Hg was very toxic to macrophytes. The sub-lethal effects of Hg (organic and inorganic) on the sporelings of *Plumaria elegans* were reported by Boney (1971). 100% growth inhibition was caused by 1 ppm Hg. Burdin & Bird (1994) reported that both gametophyte and tetrasporophyte forms of *Chondrus crispus* accumulated Cu, Cd, Ni, Zn, Mn and Pb when immersed in 0.5 mg/l solutions for 24 hours. No effects were reported however, and no relationship was detected between hydrocolloid characteristics and heavy metal accumulation.

It is generally accepted that adult fucooids are relatively tolerant of heavy metal pollution (Holt *et al.*, 1997). The effect of heavy metals on the growth rate of adult *Fucus serratus* plants has been studied by Strömngren (1979; 1980). Copper significantly reduces the growth rate of vegetative apices at 25 µg/l over 10 days (Strömngren, 1979). Zinc, lead, cadmium & mercury significantly reduce growth rate at

1400 µg/l, 810 µg/l, 450 µg/l and 5 µg/l respectively (Strömngren, 1980).

Zinc was found to inhibit growth in *Laminaria digitata* at a concentration of 100 µg/L and at 515 µg/L growth had almost completely ceased (Bryan, 1969). Axelsson & Axelsson (1987) investigated the effect of exposure to mercury (Hg), lead (Pb) and nickel (Ni) for 24 hours by measuring ion leakage to indicate plasma membrane damage. Inorganic and organic Hg concentrations of 1 mg/L resulted in the loss of ions equivalent to ion loss in seaweed that had been boiled for 5 minutes. *Laminaria digitata* was unaffected when subjected to Pb and Ni at concentrations up to 10 mg/L. Their results also indicated that the species is intolerant of the tin compounds butyl-Sn and phenyl-Sn.

Hydrocarbon & PAH contamination

Not Assessed (NA)

Q: NR A: NR C: NR

Not assessed (NA)

Q: NR A: NR C: NR

Not assessed (NA)

Q: NR A: NR C: NR

This pressure is **Not assessed** but evidence is presented where available.

Hydrocarbon contamination, e.g. from spills of fresh crude oil or petroleum products, may cause significant loss of component species in the biotope, through impacts on individual species viability or mortality, and resultant effects on the structure of the community. Rockpools are potentially vulnerable habitats, depending on depth, flushing rate and tidal height. Rockpool organisms may be protected, since oil will float on the pool surface. However, rockpool organisms will be exposed to the water soluble fraction of fresh oils, and a surface film of oil will prevent gaseous exchange and may reduce or exclude light. If exposed to oil the resident sediment is likely to adsorb oil and release it slowly, causing chronic long-term contamination and potentially prolonged recovery. The effects of oil contamination on marine organisms were reviewed by Suchanek (1993) and are summarized below.

Laminaria digitata is less susceptible to coating with oil than some other seaweeds because of its preference for exposed locations where wave action will rapidly dissipate oil. The effects of oil accumulation on the thalli are mitigated by the perennial growth of kelps. No significant effects of the Amoco Cadiz spill were observed for *Laminaria* populations and the World Prodigy spill of 922 tons of oil in Narragansett Bay had no discernible effects on *Laminaria digitata* (Peckol *et al.*, 1990). Mesocosm studies in Norwegian waters showed that chronic low level oil pollution (25 µg/L) reduced growth rates in *Laminaria digitata* but only in the second and third years of growth (Bokn, 1985).

Holt *et al.* 1995 reported that oil spills in the USA and from the 'Torrey Canyon' had little effect on kelp forest. Similarly, surveys of subtidal communities at a number sites between 1-22.5m below chart datum, including *Laminaria hyperborea* communities, showed no noticeable impacts of the Sea Empress oil spill and clean up (Rostron & Bunker, 1997)

Fucus vesiculosus shows limited intolerance to oil. After the Amoco Cadiz oil spill *Fucus vesiculosus* suffered very little (Floc'h & Diouris, 1980). Indeed, *Fucus vesiculosus* may increase significantly in abundance on a shore where grazing gastropods have been killed by oil, although very heavy fouling could reduce light available for photosynthesis and in Norway a heavy oil spill reduced fucoid cover.

Synthetic compound contamination	Not Assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR
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This pressure is **Not assessed** but evidence is presented where available

O'Brian & Dixon (1976) suggested that red algae were the most sensitive group of macrophytes to oil and dispersant contamination (Smith, 1968).

Radionuclide contamination	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	No evidence (NEv) Q: NR A: NR C: NR
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No Evidence

Introduction of other substances	Not Assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR
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This pressure is **Not assessed**

De-oxygenation	High Q: High A: High C: High	High Q: High A: High C: High	Not sensitive Q: High A: High C: High
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During emergence rockpools are closed systems and gaseous exchange occurs only over the air/water interface. In shallow pools the volume to surface area ratio is likely to be high, whereas in deep pools the ratio is likely to be low. In addition, the oxygen concentration is dependent on the community present. During the day, photosynthesis uses up CO₂ and produces O₂, in excess of respiration. However, at night respiration by flora and fauna deplete oxygen levels. As a result rockpool environments exhibit marked variation in oxygen levels. In summer, rockpools are likely to be supersaturated with oxygen during the day (Pyefinch, 1943). For example, the greatest range of oxygen saturation of 101.7% occurred in seaweed dominated, sediment floored pool, which reach over 190% saturation on some days (Pyefinch, 1943). Daniel & Boyden (1975) noted that a mid shore, seaweed dominated pool reached 194% saturation (ca 15 mg O₂/l) but that oxygenation was also marked in shaded pools. A pool with dense fauna exhibited a maximum saturation of 210% (Pyefinch, 1943). During photosynthesis algae absorb carbon dioxide and as concentrations fall, the pH rises. Morris & Taylor (1983) recorded pH values >9 in rockpools on the Isle of Cumbrae. At night, oxygen levels may fall below 100% saturation and pH will decrease as CO₂ levels increase. Morris & Taylor (1983) noted an annual maximum of oxygen concentration of 400-422 mm Hg (ca 23.4-24.7 mg/l) and an annual minimum of 18-38 mm Hg (ca 1-2.2 mg/l) in mid shore pools. Daniel & Boyden (1975) reported oxygen depletion at night, with mid to low shore pools reduced to 8-44% saturation. They noted that the crab *Carcinus maenas* leaves the pools at night, and that other species with the ability to air-breathe could also do so, e.g. limpets, littorinids, and the shanny *Lipophrys pholis*. They also observed that shrimps gathered at the edge of high shore pools at night, presumably to take advantage of the better oxygenated surface layer (Daniel & Boyden, 1975). Goss-Custard *et al.* (1979) noted that oxygen saturation levels decreased with depth in deep mid shore pools, while Morris & Taylor (1983) noted that oxygen saturation

varied with depth and proximity to algae, especially green algae such as *Cladophora spp.*

Sensitivity Assessment. On immersion, rockpool communities are exposed to potentially large, sudden fluctuations in oxygen concentrations depending on season and time of day (Morris & Taylor, 1983). Therefore, rockpool communities are likely to be exposed to variations equivalent to or greater than the benchmark level on a regular basis. Resistance has been assessed as 'High', Resilience as 'High'. Sensitivity has been assessed as 'Not sensitive' at the benchmark level.

Nutrient enrichment	Not relevant (NR)	Not relevant (NR)	Not sensitive
	Q: NR A: NR C: NR	Q: NR A: NR C: NR	Q: NR A: NR C: NR

Atalah & Crowe (2012) added nutrients to rockpools in controlled experiments. The rockpools were occupied by a range of algae including encrusting corallines, turfs of *Mastocarpus stellatus*, *Chondrus crispus* and *Corallina officinalis* and green and red filamentous algae. The invertebrates present were mostly *Patella ulyssiponensis*, the winkle *Littorina littorea* and the flat top shell *Gibbula umbilicalis*. Nitrogen and phosphorous enhancement was via the addition of fertilisers, as either 40 g/litre or 20 g/litre. The treatments were applied for seven month and experimental conditions were maintained every two weeks. A grazer and nutrient addition treatments was also applied where grazers were removed manually from pools and a 1 m strip bordering the pools. The experimental treatments do not directly relate to the pressure benchmark or this biotope specifically but indicate some general trends in sensitivity. In the pools the chronic addition of nutrients had no significant effect on the cover of crustose coralline algae or the red turfing algae. There was a significant interactive effect of grazing and nutrients however on the cover of crustose coralline algae. Pair-wise comparisons showed that cover of crustose coralline algae was significantly reduced where nutrients were added only under reduced grazing conditions, with an absolute decrease of 44% (± 8.0 S.E.) relative to the controls ($P < 0.05$). Grazers limit the effects of nutrient enrichment and in their absence significant changes in the structure of the algal assemblage may emerge following eutrophication.

The use of some kelp species in conjunction with fish aquaculture (buffering the effects of organic enrichment in the local area) suggests that many kelps (including *Laminaria digitata*) are tolerant to local increases in organic enrichment (Troell *et al.*, 2003). For example, abundant growth of *Laminaria hyperborea* has been found adjacent to untreated sewage outfalls in the Isle of Man. Handå *et al.* (2013) also reported *Saccharina latissima* sporophytes grew approx 1% faster per day when in close proximity to Norwegian Salmon farms, where elevated ammonium can be readily absorbed.

Husa *et al.* (2014) found that the macro-algal communities beyond the immediate proximity of fish farms in Hardangerfjord, Norway, seemed to be little affected by the deposition of organic matter from the salmon farming industry. Bellgrove *et al.* (2010) however determined that coralline turfs out-competed the furoid *Hormosira banksii* at a site associated with organic enrichment caused by a sewage outfall.

Sensitivity assessment There is contrasting evidence to suggest how this biotope

may be affected for this pressure. However this biotope is considered to be '**Not sensitive**' at the pressure benchmark, that assumes compliance with good status as defined by the WFD.

Organic enrichment	Medium	Medium	Medium
	Q: Low A: NR C: NR	Q: High A: High C: High	Q: Low A: Low C: Low

At the time of writing little information on the nutrient regime of rockpools was found. Rockpools are cut off from the sea for periods of time, depending on their shore height, and hence nutrients could potentially become limiting (e.g. nitrogen and phosphorous) within the period of emersion.

The use of some kelp species in conjunction with fish aquaculture (buffering the effects of organic enrichment in the local area) suggests that many kelps (including *Laminaria digitata*) are tolerant to local increases in organic enrichment (Troell *et al.*, 2003). For example, abundant growth of *Laminaria hyperborea* has been found adjacent to untreated sewage outfalls in the Isle of Man. Handå *et al.* (2013) also reported *Saccharina latissima* sporophytes grew approx 1% faster per day when in close proximity to Norwegian Salmon farms, where elevated ammonium can be readily absorbed.

Corallina officinalis has been noted to increase in abundance and may form extensive turfs within the vicinity of sewage outfalls and at intermediately polluted sites (Bellgrove *et al.*, 2010; Littler & Murray, 1975; May, 1985; Brown *et al.*, 1990). *Corallina elongata* and the crusting coralline *Lithophyllum incrustans* were present at sites dominated by *Ulva spp.* in the Mediterranean exposed to high levels of organic pollution from domestic sewage (Arévalo *et al.*, 2007).

Husa *et al.* (2014) found that the macroalgal communities in close proximity to fish farms in Hardangerfjord, Norway, seemed to be little affected by the deposition of organic matter from the salmon farming industry. Bellgrove *et al.* (2010) however determined that coralline turfs out-competed the furoid *Hormosira banksii* at a site associated with organic enrichment caused by a sewage outfall.

Sensitivity assessment If the rockpool was enriched by effluent discharge *Laminaria digitata* is unlikely to be directly affected. However, coralline turfs may out-compete *Fucus serratus*. Resistance has therefore been assessed as '**Medium**', resilience as '**Medium**'. Sensitivity has been assessed as '**Medium**'.

A Physical Pressures

Physical loss (to land or freshwater habitat)	Resistance	Resilience	Sensitivity
	None	Very Low	High
	Q: High A: High C: High	Q: High A: High C: High	Q: High A: High C: High

All marine habitats and benthic species are considered to have a resistance of '**None**' to this pressure and to be unable to recover from a permanent loss of habitat (resilience is '**Very Low**'). Sensitivity within the direct spatial footprint of this pressure is therefore '**High**'. Although no specific evidence is described confidence in

this assessment is 'High', due to the incontrovertible nature of this pressure.

Physical change (to another seabed type)

None

Q: High A: High C: High

Very Low

Q: High A: High C: High

High

Q: High A: High C: High

A change in substratum type from bedrock to sedimentary is likely to have a similar effect as a 'physical loss (to land or freshwater habitat) because macroalgae require a stable substratum on which to settle.

Sensitivity assessment. This biotope is considered to have a resistance of 'None' to this pressure as sedimentary habitats are unsuitable for *Laminaria digitata* and the associated attached biological assemblage. Resilience is assessed as **Very low** (the pressure is a permanent change) and sensitivity is assessed as **High**. Although no specific evidence is described, confidence in this assessment is 'High', due to the incontrovertible nature of this pressure.

Physical change (to another sediment type)

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

'Not relevant' to bedrock biotopes.

Habitat structure changes - removal of substratum (extraction)

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant

Abrasion/disturbance of the surface of the substratum or seabed

Medium

Q: High A: High C: High

Medium

Q: High A: High C: High

Medium

Q: High A: High C: High

No studies of the effects of trampling on rock pools were found but studies of the effects on emergent algal communities are probably indicative (Tyler-Walters 2005, Tyler-Walters & Arnold, 2008). For example, moderate (50 steps per 0.09 square metre) or more trampling on intertidal articulated coralline algal turf in New Zealand reduced turf height by up to 50%, and the weight of sand trapped within the turf to about one third of controls. This resulted in declines in densities of the meiofaunal community within two days of trampling. Although the community returned to normal levels within 3 months of trampling events, it was suggested that the turf would take longer to recover its previous cover (Brown & Taylor, 1999). Similarly, Schiel & Taylor (1999) noted that trampling had a direct detrimental effect on fucoid algae and coralline turf species on the New Zealand rocky shore. Low trampling intensity (10 tramples) reduced fucoid cover by 25%, while high intensity (200 tramples) reduced fucoid cover by over 90%, although over 97% cover returned within 21 months after spring trampling; autumn treatments took longer to recover due to the delay in recruitment. Coralline bases were seen to peel from the rocks (Schiel & Taylor, 1999) due to increased desiccation caused by loss of the algal canopy. Brosnan & Cumrie (1994) demonstrated that foliose species (e.g. fucoids and *Mastocarpus papillatus*) were the most susceptible to trampling disturbance, while turf

forming species were more resistant. However, the algae and barnacles recovered in the year following the trampling (Brosnan & Cumrie, 1994). Similarly, Boalch *et al.* (1974) and Boalch & Jephson (1981) noted a reduction in fucoid cover (especially of *Ascophyllum nodosum*) at Wembury, Devon, when compared with the same transects surveyed 43 years previously. They suggested that the reduction in fucoid cover was due to the large number of visitors and school groups received by the site.

Sensitivity assessment. The depth of LR.FLR.Rkp.FK is likely to protect this biotope from heavy trampling. Therefore, resistance has been assessed as '**Medium**', resilience as '**Medium**', and sensitivity as '**Medium**'.

Penetration or disturbance of the substratum subsurface	Not relevant (NR)	Not relevant (NR)	Not relevant (NR)
	Q: NR A: NR C: NR	Q: NR A: NR C: NR	Q: NR A: NR C: NR

Not relevant

Changes in suspended solids (water clarity)	Low	Medium	Medium
	Q: Low A: NR C: NR	Q: High A: High C: High	Q: Low A: Low C: Low

The macroalgae in the biotope require light for photosynthesis, and decreases in light availability as a result of increased water turbidity may limit growth. The absence of *Laminaria digitata* in the Firth of Forth, Scotland was suggested to be caused by the outflow from a sewage treatment plant that increased the turbidity of the water and thus decreased photosynthetic activity, although the effect of turbidity was probably coupled with increased nutrient levels (Read *et al.*, 1983). Other *Laminaria* species show a decrease of 50% photosynthetic activity when turbidity increases by 0.1/m (light attenuation coefficient = 0.1-0.2/m; Staehr & Wernberg, 2009). In locations where water clarity is severely decreased, *Laminaria* species experience a significant decrease in growth from the shading of suspended matter and/or phytoplankton (Lyngby & Mortensen, 1996; Spilmont *et al.*, 2009).

Sensitivity Assessment. An increase in turbidity is likely to result in a decline photosynthetic ability, and abundance of macroalgae species. Laminarians at depth in the pool would probably be the worst affected, while red algae and encrusting corallines would probably come to dominate. The resultant scour within the pool (from suspended sediment) may well remove the fleshy red seaweeds, resulting in a change to Rkp.SwSed dominated by corallines, robust red seaweeds and fast growing Laminarians Therefore, resistance to this pressure is defined as '**Low**' and resilience to this pressure is defined as '**Medium**' at the benchmark level due to the scale of the impact. Hence, this biotope is regarded as having a sensitivity of '**Medium**'.

Smothering and siltation rate changes (light)	Medium	Medium	Medium
	Q: Low A: NR C: NR	Q: High A: High C: High	Q: Low A: Low C: Low

Seapy & Littler (1982) reported a decrease in macro-algal cover from 47.3 to 37.5% on a Californian rocky shore due to sediment deposition on the mid to lower shore following rain and flooding. *Corallina sp.* and *Pelvetia sp.* were the most affected macro-algal species, while associated red algae were only slightly affected by the

resultant scour. Daly & Mathieson (1977) examined intertidal zonation on a shore affected by sand scour, and noted that fucoids were reduced to small or young plants, while sand tolerant species such as *Ahnfeltia plicata* dominated on areas affected by sediment. Smothering by 5 cm of sediment is likely to increase scour and be detrimental to macro-algae, especially *Corallina officinalis* and fucoids, and the more fleshy red algae. While laminarians and red algae such as *Chondrus crispus* and *Ceramium spp.* are large enough not to be smothered completely by 5 cm of sediment, the resultant scour is likely to damage fronds but, in particular, remove juveniles, sporelings and other propagules. In addition, the rockpool environment is likely to be more vulnerable to smothering as sediment is likely to accumulate in, and be retained by the rockpool itself, effectively increasing the depth of the sediment layer in the pool. In wave exposed conditions the sediment may be removed but in sheltered areas it is likely to be retained for longer than indicated by the benchmark. In deep pools, the macro-algae are likely to reduce in depth penetration into the pool. The resultant scour may result in a change in the biotope to resemble RkP.SwSed.

Sensitivity assessment. Resistance has been assessed as 'Low', resilience as 'Medium'. Sensitivity has been assessed as 'Medium'.

Smothering and siltation rate changes (heavy) **Low**

Q: Low A: NR C: NR

Medium

Q: High A: High C: High

Medium

Q: Low A: Low C: Low

Seapy & Littler (1982) reported a decrease in macro-algal cover from 47.3 to 37.5% on a Californian rocky shore due to sediment deposition on the mid to lower shore following rain and flooding. *Corallina sp.* and *Pelvetia sp.* were the most affected macro-algal species, while associated red algae were only slightly affected by the resultant scour. Macro invertebrates declined in cover from 15.8% to 6.5%. Daly & Mathieson (1977) examined intertidal zonation on a shore affected by sand scour, and noted that fucoids were reduced to small or young plants, while sand tolerant species such as *Ahnfeltia plicata* dominated on areas affected by sediment. Smothering by 30cm of sediment is likely to increase scour and inundate macro-algae, especially *Corallina officinalis* and fucoids, and the more fleshy red algae. While laminarians are large enough not to be smothered completely by 30cm of sediment, the resultant scour is likely to damage fronds but, in particular, remove juveniles, sporelings and other propagules. In addition, the rockpool environment is likely to be more vulnerable to smothering as sediment is likely to accumulate in, and be retained by the rockpool itself, effectively increasing the depth of the sediment layer in the pool. In wave exposed conditions the sediment may be removed but in sheltered areas it is likely to be retained for longer than indicated by the benchmark. In deep pools, the macroalgae and associated invertebrates are likely to reduce in depth penetration into the pool while sediment tolerant algae increase. The resultant scour may result in a change in the biotope to RkP.SwSed.

Sensitivity assessment. Resistance has been assessed as 'Low', resilience as 'Medium'. Sensitivity has been assessed as 'Medium'.

Litter

Not Assessed (NA)

Q: NR A: NR C: NR

Not assessed (NA)

Q: NR A: NR C: NR

Not assessed (NA)

Q: NR A: NR C: NR

Not assessed. It is feasible that discarded fishing line or plastic netting, or similar discards could tangle on kelp fronds and potentially damage or remove individuals. but no evidence was found.

Electromagnetic changes	Not relevant (NR)	Not relevant (NR)	No evidence (NEv)
	Q: NR A: NR C: NR	Q: NR A: NR C: NR	Q: NR A: NR C: NR

No Evidence

Underwater noise changes	Not relevant (NR)	Not relevant (NR)	Not relevant (NR)
	Q: NR A: NR C: NR	Q: NR A: NR C: NR	Q: NR A: NR C: NR

Not relevant

Introduction of light or shading	Low	Medium	Medium
	Q: Low A: NR C: NR	Q: Low A: NR C: NR	Q: Low A: Low C: Low

There is no evidence to suggest that anthropogenic light sources would affect macro-algae. Shading of the biotope (e.g. by construction of a pontoon, pier etc) could adversely affect the biotope in areas where the water clarity is also low, and tip the balance to shade tolerant species, resulting in the loss of the biotope directly within the shaded area, or a reduction in laminarian abundance.

Sensitivity assessment. Resistance is probably 'Low', with a 'Medium' resilience and a sensitivity of 'Medium', albeit with 'low' confidence due to the lack of direct evidence.

Barrier to species movement	Not relevant (NR)	Not relevant (NR)	Not relevant (NR)
	Q: NR A: NR C: NR	Q: NR A: NR C: NR	Q: NR A: NR C: NR

Not relevant. This pressure is considered applicable to mobile species, e.g. fish and marine mammals rather than seabed habitats. Physical and hydrographic barriers may limit the dispersal of spores, but spore dispersal is not considered under the pressure definition and benchmark.

Death or injury by collision	Not relevant (NR)	Not relevant (NR)	Not relevant (NR)
	Q: NR A: NR C: NR	Q: NR A: NR C: NR	Q: NR A: NR C: NR

'Not relevant' to seabed habitats.

Visual disturbance	Not relevant (NR)	Not relevant (NR)	Not relevant (NR)
	Q: NR A: NR C: NR	Q: NR A: NR C: NR	Q: NR A: NR C: NR

Not relevant



Biological Pressures

Resistance

Resilience

Sensitivity

Genetic modification & translocation of indigenous species	Not relevant (NR)	Not relevant (NR)	No evidence (NEv)
	Q: NR A: NR C: NR	Q: NR A: NR C: NR	Q: NR A: NR C: NR

No evidence regarding the genetic modification or translocation of the characteristic species was found.

Introduction or spread of invasive non-indigenous species	None	Very Low	High
	Q: High A: High C: High	Q: High A: High C: High	Q: High A: High C: High

Sargassum muticum is a non-native macroalgae spreading around the coasts of Britain and Europe (Eno *et al.*, 1997) and is often found in low to mid shore rockpools in the intertidal in areas it has colonized. Although, no studies on its effects on rockpool species were found, studies of its effect on shallow sublittoral macroalgae suggest that it can out-compete fucoids and kelps. For example, Stæhr *et al.* (2000) reported that an increase in the abundance of *Sargassum muticum* in the Limfjorden (Denmark) from 1990 to 1997 was accompanied by a decrease in the abundance of thick, slow growing macroalgae such as *Saccharina latissima* (studied as *Laminaria saccharina*), *Codium fragile*, *Halidrys siliquosa*, *Fucus vesiculosus*, and *Fucus serratus*, together with other algae such as *Ceramium nodulosum* (as *rubrum*) and *Dictyota dichotoma*. In *Sargassum muticum* removal experiments on the coast of Washington State, Britton-Simmonds (2004) concluded that *Sargassum muticum* reduced the abundance of native canopy algae (especially kelps) by 75% and native understorey algae by 50% probably as a result of shading. However, Viejo (1999) noted that mobile epifauna (e.g. amphipods, isopods) successfully colonized *Sargassum muticum* which provided additional habitat. Overall, *Sargassum muticum* can successfully invade rockpools, and would probably out-compete resident fucoids and kelp species, and some red algae.

Sensitivity assessment. If *Sargassum muticum* was to become dominant in this biotope, then the biotope would be replaced by RkP.Sar Therefore, Resistance to the pressure is considered 'None', and resilience 'Very Low'. The sensitivity of this biotope to INIS is assessed as 'High'.

Introduction of microbial pathogens	Medium	High	Low
	Q: Medium A: High C: Medium	Q: Low A: NR C: NR	Q: Low A: Low C: Low

Laminarians may be infected by the microscopic brown alga *Streblonema aecidioides*. Infected algae show symptoms of Streblonema disease, i.e. alterations of the blade and stipe ranging from dark spots to heavy deformations and completely crippled thalli (Peters & Scaffelke, 1996). Infection can reduce growth rates of host algae. Other species present, eg. littorinids may carry bird or fish parasites in a proportion of the population, and suffer from reduced productive rates and poor condition as a result. However, the effect of the resident population is likely to be limited.

Sensitivity assessment. Resistance to the pressure is considered 'High', and resilience 'High'. The sensitivity of this biotope to introduction of microbial pathogens is assessed as 'Low'.

Removal of target species**Low**

Q: High A: High C: High

Medium

Q: High A: High C: High

Medium

Q: High A: High C: High

Corallina officinalis is collected for medical purposes; the fronds are dried and converted to hydroxyapatite and used as bone forming material (Ewers *et al.* 1987). *Laminaria digitata* is extracted for the production of alginates, which is used in the cosmetic, pharmaceutical and agri-food industries (Kervarec *et al.*, 1999; McHugh, 2003). *Laminaria digitata* is harvested with a 'Scoubidou' (a mechanically operated curved iron hook). This device is considered to be selective-only harvesting individuals older than 2 years (Arzel, 2002). France reportedly harvests 75,000t kelp, mainly consisting of *Laminaria digitata* annually (FAO, 2007). If *Laminaria digitata*, a characterizing species of this biotope is removed then the biotope is considered lost and a significant alteration to the biotope classification and character of the habitat is likely.

Canopy removal of *Laminaria digitata* has been shown to reduce shading, resulting in the bleaching of sub canopy algae (Hawkins & Harkin, 1985). Harvesting may also result in habitat fragmentation, a major threat to this biotope's ecosystem functioning (Valero *et al.*, 2011). In the UK harvesting of *Laminaria digitata* is currently restricted to manual removal and farming on small scales (netalgae, 2012).

In addition, several of the characterizing red algae species are subject to harvesting. *Chondrus crispus* is extracted commercially in Ireland, but the harvest has declined since its peak in the early 1960s (Pybus, 1977). Mathieson & Burns (1975) described the recovery of *Chondrus crispus* following experimental drag raking (see MarLIN review: Rayment & Pizzola, 2008) and concluded that control levels of biomass and population structure are probably re-established after 18 months of regrowth. *Palmaria palmata* is used as a vegetable substitute or animal fodder although harvesting on a commercial scale only takes place in Ireland and France (Guiry & Blunden, 1991). *Littorina littorea* is also subject to harvesting in the UK and limpets in France. Hand collection may reduce the population of *Littorina littorea* within rockpools and hence reduce grazing pressure which may actually benefit the algal component of the biotope, especially opportunistic green algae and epiphytes.

Overall, while rockpools in areas subject to commercial algal harvesting may be directly affected, most examples of the biotope are unlikely to be affected by commercial harvesting in the UK. In deep pools characterized by this biotope, only the margins of the pool are likely to be affected. However, due to the relative small size of the community, even small scale hand collecting may have a significant effect.

Sensitivity assessment. Resistance has been assessed as '**Low**', resilience as '**Medium**' and sensitivity as '**Medium**'

Removal of non-target species**Low**

Q: High A: Medium C: High

Medium

Q: High A: High C: High

Medium

Q: High A: High C: High

Laminaria digitata is extracted for the production of alginates, which is used in the cosmetic, pharmaceutical and agri-food industries (Kervarec *et al.*, 1999; McHugh, 2003). *Laminaria digitata* is harvested with a 'Scoubidou' (a mechanically operated curved iron hook). This device is considered to be selective-only harvesting

individuals older than 2 years (Arzel, 2002). France reportedly harvests 75,000t kelp, mainly consisting of *Laminaria digitata* annually (FAO, 2007). If *Laminaria digitata*, a characterizing species of this biotope is removed then the biotope is considered lost and a significant alteration to the biotope classification and character of the habitat is likely.

If *Laminaria digitata* were to be removed from this biotope, it is feasible *Fucus serratus*, another canopy forming species within this biotope, may also be accidentally removed. Incidental/accidental removal of the canopy forming/characteristic species of this biotope would result in a fundamental changed to this biotope. Furthermore removal of the canopy is likely to result in the mortality of the understory red seaweed community (Hawkins & Harkin, 1985) and hence the biotope would be lost.

Sensitivity assessment. Resistance has been assessed as '**Low**', resilience as '**Medium**' and sensitivity as '**Medium**'.

Bibliography

- Airoldi, L., 2003. The effects of sedimentation on rocky coast assemblages. *Oceanography and Marine Biology: An Annual Review*, **41**, 161-236
- Airoldi, L., Balata, D. & Beck, M.W., 2008. The Gray Zone: relationships between habitat loss and marine diversity and their applications in conservation. *Journal of Experimental Marine Biology and Ecology*, **366** (1), 8-15.
- Andrake, W. & Johansen, H.W., 1980. Alizarin red dye as a marker for measuring growth in *Corallina officinalis* L. (Corallinaceae, Rhodophyta). *Journal of Phycology*, **16** (4), 620-622.
- Ankley, G.T., Erickson, R.J., Sheedy, B.R., Kosian, P.A., Mattson, V.R. & Cox, J.S., 1997. Evaluation of models for predicting the phototoxic potency of polycyclic aromatic hydrocarbons. *Aquatic Toxicology*, **37**, 37-50.
- Apt, K.E., 1988. Etiology and development of hyperplasia induced by *Streblonema* sp. (Phaeophyta) on members of the *Laminariales* (Phaeophyta). *Journal of Phycology*, **24**, 28-34.
- Arrontes, J., 1993. Nature of the distributional boundary of *Fucus serratus* on the north shore of Spain. *Marine Ecology Progress Series*, **93**, 183-183.
- Arzel, P., 2000. Revue des causes de variations de l'abondance du champ de laminaires. *Interactions des facteurs environnementaux et impacts sur les organismes vivants*, Actes du colloque, Brest: An Aximandre: Lesneven, pp. 10-17.
- Arzel, P., 2002. La laminaire digitée. *Les nouvelles de l'Ifremer*, **33** (4).
- Arzel, P., 1998. *Les laminaires sur les côtes bretonnes. Évolution de l'exploitation et de la flottille de pêche, état actuel et perspectives*. Plouzané, France: Ifremer.
- Atalah, J. & Crowe, T.P. (2012). Nutrient enrichment and variation in community structure on rocky shores: The potential of molluscan assemblages for biomonitoring. *Estuarine, Coastal and Shelf Science* **99**: 162-170.
- Austin, A.P., 1960b. Observations on the growth, fruiting and longevity of *Furcellaria fastigiata* (L.) Lamouroux. *Hydrobiologia*, **15**, 193-207.
- Axelsson, B. & Axelsson, L., 1987. A rapid and reliable method to quantify environmental effects on *Laminaria* based on measurements of ion leakage. *Botanica Marina*, **30**, 55-61.
- Baardseth, E., 1956. The growth rings in *Alaria stipes*. In *Proceedings of the International Seaweed Symposium, 2, Trondheim* (eds T. Braarud & N.A. Sorensen) pp. 153-157. London: Pergamon Press.
- Bamber, R.N. & Irving, P.W., 1993. The *Corallina* run-offs of Bridgewater Bay. *Porcupine Newsletter*, **5**, 190-197.
- Bartsch, I., Vogt, J., Pehlke, C. & Hanelt, D., 2013. Prevailing sea surface temperatures inhibit summer reproduction of the kelp *Laminaria digitata* at Helgoland (North Sea). *Journal of Phycology*, **49** (6), 1061-1073.
- Bartsch, I., Wiencke, C., Bischof, K., Buchholz, C.M., Buck, B.H., Eggert, A., Feuerpfeil, P., Hanelt, D., Jacobsen, S. & Karez, R., 2008. The genus *Laminaria* sensu lato: recent insights and developments. *European Journal of Phycology*, **43** (1), 1-86.
- Bégin, C., Johnson, L.E. & Himmelman, J.H., 2004. Macroalgal canopies: distribution and diversity of associated invertebrates and effects on the recruitment and growth of mussels. *Marine Ecology Progress Series*, **271** (1), 121-132.
- Bekkby, T. & Moy, F.E., 2011. Developing spatial models of sugar kelp (*Saccharina latissima*) potential distribution under natural conditions and areas of its disappearance in Skagerrak. *Estuarine Coastal and Shelf Science*, **95** (4), 477-483.
- Bellgrove, A., McKenzie, P.F., McKenzie, J.L. & Sfiligoj, B.J., 2010. Restoration of the habitat-forming furoid alga *Hormosira banksii* at effluent-affected sites: competitive exclusion by coralline turfs. *Marine Ecology Progress Series*, **419**, 47-56.
- Bertness, M.D., Leonard, G.H., Levine, J.M., Schmidt, P.R. & Ingraham, A.O., 1999. Testing the relative contribution of positive and negative interactions in rocky intertidal communities. *Ecology*, **80** (8), 2711-27
- Bertocci, I., Arenas, F., Matias, M., Vaselli, S., Araújo, R., Abreu, H., Pereira, R., Vieira, R. & Sousa-Pinto, I., 2010. Canopy-forming species mediate the effects of disturbance on macroalgal assemblages on Portuguese rocky shores. *Marine Ecology Progress Series*, **414**, 107-116.
- Beszczynska-Möller, A., & Dye, S.R., 2013. ICES Report on Ocean Climate 2012. In *ICES Cooperative Research Report*, vol. 321 pp. 73.
- Billot, C., Engel, C.R., Rousvoal, S., Kloareg, B. & Valero, M., 2003. Current patterns, habitat discontinuities and population genetic structure: the case of the kelp *Laminaria digitata* in the English Channel. *Marine Ecology Progress Series*, **253** (111), 21.
- Bird, C.J., Saunders, G.W. & McLachlan, J., 1991. Biology of *Furcellaria lumbricalis* (Hudson) Lamouroux (Rhodophyta: Gigartinales), a commercial carrageenophyte. *Journal of Applied Phycology*, **3**, 61-82.
- Bird, N.L., Chen, L.C.-M. & McLachlan, J., 1979. Effects of temperature, light and salinity of growth in culture of *Chondrus crispus*, *Furcellaria lumbricalis*, *Gracilaria tikvahiae* (Gigartinales, Rhodophyta), and *Fucus serratus*

(Fucales, Phaeophyta). *Botanica Marina*, **22**, 521-527.

Birkett, D.A., Maggs, C.A., Dring, M.J. & Boaden, P.J.S., 1998b. Infralittoral reef biotopes with kelp species: an overview of dynamic and sensitivity characteristics for conservation management of marine SACs. *Natura 2000 report prepared by Scottish Association of Marine Science (SAMS) for the UK Marine SACs Project.*, Scottish Association for Marine Science. (UK Marine SACs Project, vol V.). Available from:

<http://www.ukmarinesac.org.uk/publications.htm>

Blake, C. & Maggs, C.A., 2003. Comparative growth rates and internal banding periodicity of maerl species (Corallinales, Rhodophyta) from northern Europe. *Phycologia*, **42** (6), 606-612.

Blight, A.J. & Thompson, R.C., 2008. Epibiont species richness varies between holdfasts of a northern and a southerly distributed kelp species. *Journal of the Marine Biological Association of the United Kingdom*, **88** (03), 469-475.

Boalch, G.T. & Jephson, N.A., 1981. A re-examination of the seaweeds on Colman's traverses at Wembury. *Proceedings of the International Seaweed Symposium*, **8**, 290-293.

Boalch, G.T., Holme, N.A., Jephson, N.A. & Sidwell, J.M.C., 1974. A resurvey of Colman's intertidal traverses at Wembury, South Devon. *Journal of the Marine Biological Association of the United Kingdom*, **5**, 551-553.

Bokn, T., 1985. Effects of diesel oil on commercial benthic algae in Norway. In *Proceedings of 1985 Oil Spill Conference*, (ed. American Petroleum Institute), pp. 491-496. Washington, D.C.: American Petroleum Institute.

Bolton, J.J. & Lüning, K.A.F., 1982. Optimal growth and maximal survival temperatures of Atlantic *Laminaria* species (Phaeophyta) in culture. *Marine Biology*, **66**, 89-94.

Boney, A.D., 1971. Sub-lethal effects of mercury on marine algae. *Marine Pollution Bulletin*, **2**, 69-71.

Bower, S.M., 1996. *Synopsis of Infectious Diseases and Parasites of Commercially Exploited Shellfish: Bald-sea-urchin Disease*. [On-line]. Fisheries and Oceans Canada. [cited 26/01/16]. Available from:

<http://www.dfo-mpo.gc.ca/science/aah-saa/diseases-maladies/bsudsu-eng.html>

Bowling, J.W., Leversee, G.J., Landrum, P.F. & Giesy, J.P., 1983. Acute mortality of anthracene-contaminated fish exposed to sunlight. *Aquatic Toxicology*, **3**, 79-90.

Brawley, S.H., 1992b. Mesoherbivores. In *Plant-animal interactions in the marine benthos* (ed. D.M John, S.J. Hawkins & J.H. Price), pp. 235-263. Oxford: Clarendon Press. [Systematics Association Special Volume, no. 46.]

Brawley, S.H., Coyer, J.A., Blakeslee, A.M., Hoarau, G., Johnson, L.E., Byers, J.E., Stam, W.T. & Olsen, J.L., 2009. Historical invasions of the intertidal zone of Atlantic North America associated with distinctive patterns of trade and emigration. *Proceedings of the National Academy of Sciences*, **106** (20), 8239-8244.

Brennan, G., Kregting, L., Beatty, G.E., Cole, C., Elsässer, B., Savidge, G. & Provan, J., 2014. Understanding macroalgal dispersal in a complex hydrodynamic environment: a combined population genetic and physical modelling approach. *Journal of The Royal Society Interface*, **11** (95), 20140197.

Britton-Simmons, K.H., 2004. Direct and indirect effects of the introduced alga *Sargassum muticum* on benthic, subtidal communities of Washington State, USA. *Marine Ecology Progress Series*, **277**, 61-78.

Brodie J., Williamson, C.J., Smale, D.A., Kamenos, N.A., Mieszkowska, N., Santos, R., Cunliffe, M., Steinke, M., Yesson, C. & Anderson, K.M., 2014. The future of the northeast Atlantic benthic flora in a high CO₂ world. *Ecology and Evolution*, **4** (13), 2787-2798.

Brosnan, D.M. & Crumrine, L.L., 1994. Effects of human trampling on marine rocky shore communities. *Journal of Experimental Marine Biology and Ecology*, **177**, 79-97.

Brown, P.J. & Taylor, R.B., 1999. Effects of trampling by humans on animals inhabiting coralline algal turf in the rocky intertidal. *Journal of Experimental Marine Biology and Ecology*, **235**, 45-53.

Brown, V., Davies, S. & Synnot, R., 1990. Long-term monitoring of the effects of treated sewage effluent on the intertidal macroalgal community near Cape Schanck, Victoria, Australia. *Botanica Marina*, **33** (1), 85-98.

Bryan, G.W., 1969. The absorption of zinc and other metals by the brown seaweed *Laminaria digitata*. *Journal of the Marine Biological Association of the United Kingdom*, **49**, 225-243.

Bryan, G.W., 1984. Pollution due to heavy metals and their compounds. In *Marine Ecology: A Comprehensive, Integrated Treatise on Life in the Oceans and Coastal Waters*, vol. 5. *Ocean Management*, part 3, (ed. O. Kinne), pp.1289-1431. New York: John Wiley & Sons.

Bulleri, F., Benedetti-Cecchi, L., Acunto, S., Cinelli, F. & Hawkins, S.J., 2002. The influence of canopy algae on vertical patterns of distribution of low-shore assemblages on rocky coasts in the northwest Mediterranean. *Journal of Experimental Marine Biology and Ecology*, **267** (1), 89-106.

Burdin, K.S. & Bird, K.T., 1994. Heavy metal accumulation by carrageenan and agar producing algae. *Botanica Marina*, **37**, 467-470.

Burdon, D., Dawes, O., Eades, R., Leighton, A., Musk, M. & Thompson, S. 2009. *BEEMS WP6 Intertidal Studies; Hinkley Survey-Report to Cefas*. Institute of Estuarine and Coastal Studies, University of Hull.

Burrows, E.M., 1991. *Seaweeds of the British Isles. Volume 2. Chlorophyta*. London: British Museum (Natural History).

- Burrows, M.T., Smale, D., O'Connor, N., Rein, H.V. & Moore, P., 2014. Marine Strategy Framework Directive Indicators for UK Kelp Habitats Part 1: Developing proposals for potential indicators. *Joint Nature Conservation Committee*, Peterborough. Report no. 525.
- Casas, G., Scrosati, R. & Piriz, M.L., 2004. The invasive kelp *Undaria pinnatifida* (Phaeophyceae, Laminariales) reduces native seaweed diversity in Nuevo Gulf (Patagonia, Argentina). *Biological Invasions*, **6** (4), 411-416.
- Chapman, A.R.O. & Johnson, C.R., 1990. Disturbance and organization of macroalgal assemblages in the Northwest Atlantic. *Hydrobiologia*, **192**, 77-121.
- Chapman, A.R.O., 1981. Stability of sea urchin dominated barren grounds following destructive grazing of kelp in St. Margaret's Bay, Eastern Canada. *Marine Biology*, **62**, 307-311.
- Chapman, A.R.O., 1990. Effects of grazing, canopy cover and substratum type on the abundances of common species of seaweeds inhabiting littoral fringe rock pools. *Botanica Marina*, **33**, 319-326.
- Chia, F.S. & Spaulding, J.G., 1972. Development and juvenile growth of the sea anemone *Tealia crassicornis*. *Biological Bulletin, Marine Biological Laboratory, Woods Hole*, **142**, 206-218.
- Christie, H., Fredriksen, S. & Rinde, E., 1998. Regrowth of kelp and colonization of epiphyte and fauna community after kelp trawling at the coast of Norway. *Hydrobiologia*, **375/376**, 49-58.
- Cole, S., Codling, I.D., Parr, W., Zabel, T., 1999. Guidelines for managing water quality impacts within UK European marine sites [On-line]. *UK Marine SACs Project*. [Cited 26/01/16]. Available from: http://www.ukmarinesac.org.uk/pdfs/water_quality.pdf
- Cole, S., Codling, I.D., Parr, W. & Zabel, T., 1999. Guidelines for managing water quality impacts within UK European Marine sites. *Natura 2000 report prepared for the UK Marine SACs Project*. 441 pp., Swindon: Water Research Council on behalf of EN, SNH, CCW, JNCC, SAMS and EHS. [UK Marine SACs Project.], <http://www.ukmarinesac.org.uk/>
- Colhart, B.J., & Johanssen, H.W., 1973. Growth rates of *Corallina officinalis* (Rhodophyta) at different temperatures. *Marine Biology*, **18**, 46-49.
- Connell, J.H., Hughes, T.P. & Wallace, C.C., 1997. A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. *Ecological Monographs*, **67** (4), 461-488.
- Connell, S.D. & Russell, B.D., 2010. The direct effects of increasing CO₂ and temperature on non-calcifying organisms: increasing the potential for phase shifts in kelp forests. *Proceedings of the Royal Society B-Biological Sciences*, **277** (1686), 1409-1415.
- Connor, D.W., Allen, J.H., Golding, N., Howell, K.L., Lieberknecht, L.M., Northen, K.O. & Reker, J.B., 2004. The Marine Habitat Classification for Britain and Ireland. Version 04.05. ISBN 1 861 07561 8. In JNCC (2015), *The Marine Habitat Classification for Britain and Ireland Version 15.03*. [2019-07-24]. Joint Nature Conservation Committee, Peterborough. Available from <https://mhc.jncc.gov.uk/>
- Cosse, A., Potin, P. & Leblanc, C., 2009. Patterns of gene expression induced by oligoguluronates reveal conserved and environment-specific molecular defence responses in the brown alga *Laminaria digitata*. *New Phytologist*, **182** (1), 239-250.
- Coyer, J., Hoarau, G., Skage, M., Stam, W. & Olsen, J., 2006a. Origin of *Fucus serratus* (Heterokontophyta; Fucales) populations in Iceland and the Faroes: a microsatellite-based assessment. *European Journal of Phycology*, **41** (2), 235-246.
- Coyer, J., Peters, A., Stam, W. & Olsen, J., 2003. Post-ice age recolonization and differentiation of *Fucus serratus* L. (Phaeophyceae; Fucales) populations in Northern Europe. *Molecular Ecology*, **12** (7), 1817-1829.
- Crisp, D.J. (ed.), 1964. The effects of the severe winter of 1962-63 on marine life in Britain. *Journal of Animal Ecology*, **33**, 165-210.
- Crump, R.G. & Emson, R.H., 1997. Observations on the effects of the *Sea Empress* pollution incident on the seastars of tide pools at West Angle, Pembrokeshire. *Sea Empress Environmental Evaluation Committee (SEEEC)*, 6 pp.
- Daly, M.A. & Mathieson, A.C., 1977. The effects of sand movement on intertidal seaweeds and selected invertebrates at Bound Rock, New Hampshire, USA. *Marine Biology*, **43**, 45-55.
- Daniel, M.J. & Boyden, C.R., 1975. Diurnal variations in physico-chemical conditions within intertidal rockpools. *Field Studies*, **4**, 161-176.
- Dauvin, J.C., Bellan, G., Bellan-Santini, D., Castric, A., Francour, P., Gentil, F., Girard, A., Gofas, S., Mahe, C., Noel, P., & Reviers, B. de., 1994. Typologie des ZNIEFF-Mer. Liste des parametres et des biocoenoses des cotes francaises metropolitaines. 2nd ed. *Secretariat Faune-Flore, Museum National d'Histoire Naturelle, Paris (Collection Patrimoines Naturels, Serie Patrimoine Ecologique, No. 12)*. Coll. Patrimoines Naturels, vol. 12, Secretariat Faune-Flore, Paris.
- Davies, A.J., Johnson, M.P. & Maggs, C.A., 2007. Limpet grazing and loss of *Ascophyllum nodosum* canopies on decadal time scales. *Marine Ecology Progress Series*, **339**, 131-141.
- Davies, C.E. & Moss, D., 1998. European Union Nature Information System (EUNIS) Habitat Classification. *Report to European Topic Centre on Nature Conservation from the Institute of Terrestrial Ecology, Monks Wood*,

- Cambridgeshire. [Final draft with further revisions to marine habitats.], Brussels: European Environment Agency.
- Dawes, C.J., McCoy, E.D. & Heck, K.L., 1991. The tropical western Atlantic including the Caribbean Sea. In *Intertidal and Littoral Ecosystems*, (ed. A.C. Mathieson & P.H. Nienhuis), pp. 215-234. Amsterdam: Elsevier. [Ecosystems of the World no. 24].
- Dayton, P.K. & Tegner, M.J., 1984. Catastrophic storms, El-Nino, and patch stability in a southern-california kelp community. *Science*, **224** (4646), 283-285.
- Dayton, P.K., Tegner, M.J., Parnell, P.E. & Edwards, P.B., 1992. Temporal and spatial patterns of disturbance and recovery in a kelp forest community. *Ecological Monographs*, **62**, 421-445.
- Dethier, M.N., 1984. Disturbance and recovery in intertidal pools: maintenance of mosaic patterns. *Ecological Monographs*, **54**, 99-118.
- Devinny, J. & Volse, L., 1978. Effects of sediments on the development of *Macrocystis pyrifera* gametophytes. *Marine Biology*, **48** (4), 343-348.
- Devlin, M.J., Barry, J., Mills, D.K., Gowen, R.J., Foden, J., Sivyver, D. & Tett, P., 2008. Relationships between suspended particulate material, light attenuation and Secchi depth in UK marine waters. *Estuarine, Coastal and Shelf Science*, **79** (3), 429-439.
- Dickinson, C.I., 1963. *British seaweeds*. London & Frome: Butler & Tanner Ltd.
- Dieck, T.I., 1992. North Pacific and North Atlantic digitate *Laminaria* species (Phaeophyta): hybridization experiments and temperature responses. *Phycologia*, **31**, 147-163.
- Dieck, T.I., 1993. Temperature tolerance and survival in darkness of kelp gametophytes (Laminariales: Phaeophyta) - ecological and biogeographical implications. *Marine Ecology Progress Series*, **100**, 253-264.
- Dinesen G., 1999. *Modiolus modiolus* and the associated fauna. In Bruntse, G., Lein, T.E., Nielsen, R. (eds), *Marine benthic algae and invertebrate communities from the shallow waters of the Faroe Islands: a base line study*. Kaldbak Marine Biological Laboratory, pp. 66-71.
- Dixon, P.S. & Irvine, L.M., 1977. *Seaweeds of the British Isles. Volume 1 Rhodophyta. Part 1 Introduction, Nemaliales, Gigartinales*. London: British Museum (Natural History) London.
- Dring, M.J. & Brown, F.A., 1982. Photosynthesis of intertidal brown algae during and after periods of emersion: a renewed search for physiological causes of zonation. *Marine Ecology Progress Series*, **8**, 301-308.
- Ebere, A.G. & Akintonwa, A., 1992. Acute toxicity of pesticides to *Gobius* sp., *Palaemonetes africanus*, and *Desmocar is trispinosa*. *Bulletin of Environmental Contamination and Toxicology*, **49**, 588-592.
- Eckman, J.E., 1983. Hydrodynamic processes affecting benthic recruitment 1. *Limnology and Oceanography*, **28** (2), 241-257.
- Edwards, A., 1980. Ecological studies of the kelp *Laminaria hyperborea* and its associated fauna in south-west Ireland. *Ophelia*, **9**, 47-60.
- Edyvean, R.G.J. & Ford, H., 1984b. Population biology of the crustose red alga *Lithophyllum incrustans* Phil. 3. The effects of local environmental variables. *Biological Journal of the Linnean Society*, **23**, 365-374.
- Ellertsdottir, E. & Peters, A.F., 1997. High prevalence of infection by endophytic brown algae in populations of *Laminaria* spp. (Phaeophyceae). *Marine Ecology Progress Series*, **146**, 135-143.
- Elnor, R.W. & Vadas, R.L., 1990. Inference in ecology: the sea urchin phenomenon in the northwest Atlantic. *American Naturalist*, **136**, 108-125.
- Elsäßer, B., Fariñas-Franco, J.M., Wilson, C.D., Kregting, L. & Roberts, D., 2013. Identifying optimal sites for natural recovery and restoration of impacted biogenic habitats in a special area of conservation using hydrodynamic and habitat suitability modelling. *Journal of Sea Research*, **77**, 11-21.
- Engelen, A.H., Leveque, L., Destombe, C. & Valer, M., 2011. Spatial and temporal patterns of recovery of low intertidal *Laminaria digitata* after experimental spring and autumn removal. *Cahiers De Biologie Marine*, **52** (4), 441-453.
- Eno, N.C., Clark, R.A. & Sanderson, W.G. (ed.) 1997. *Non-native marine species in British waters: a review and directory*. Peterborough: Joint Nature Conservation Committee.
- Erwin, D.G., Picton, B.E., Connor, D.W., Howson, C.M., Gilleece, P. & Bagues, M.J., 1990. Inshore Marine Life of Northern Ireland. *Report of a survey carried out by the diving team of the Botany and Zoology Department of the Ulster Museum in fulfilment of a contract with Conservation Branch of the Department of the Environment (N.I.)*, Ulster Museum, Belfast: HMSO.
- Fairweather, P.G., 1987. Experiments on the interaction between predation and the availability of different prey on rocky shores. *Journal of Experimental Marine Biology and Ecology*, **154**, 29-75.
- FAO, 2007. *Aquaculture production: values 1984-2005. FISHSTAT Plus - Universal software for fishery statistical time series [online or CD-ROM]*. Fishery Information, Data and Statistics Unit. Food and Agriculture Organization of the United Nations, Rome, Italy.
- Farrell, P. & Fletcher, R., 2006. An investigation of dispersal of the introduced brown alga *Undaria pinnatifida* (Harvey) Suringar and its competition with some species on the man-made structures of Torquay Marina

- (Devon, UK). *Journal of Experimental Marine Biology and Ecology*, **334** (2), 236-243.
- Feare, C.J., 1970b. Aspects of the ecology of an exposed shore population of dogwhelks *Nucella lapillus*. *Oecologia*, **5**, 1-18.
- Fish, J.D. & Fish, S., 1996. *A student's guide to the seashore*. Cambridge: Cambridge University Press.
- Fletcher, R.L. & Callow, M.E., 1992. The settlement, attachment and establishment of marine algal spores. *British Phycological Journal*, **27**, 303-329.
- Fletcher, R.L., 1996. The occurrence of 'green tides' - a review. In *Marine Benthic Vegetation. Recent changes and the Effects of Eutrophication* (ed. W. Schramm & P.H. Nienhuis). Berlin Heidelberg: Springer-Verlag. [Ecological Studies, vol. 123].
- Floc'h, J. H. & Diouris, M., 1980. Initial effects of Amoco Cadiz oil on intertidal algae. *Ambio*, **9**, 284-286.
- Folk, R.L., 1954. The distinction between grain size and mineral composition in sedimentary-rock nomenclature. **62**, *The Journal of Geology*, 344-359.
- Frazer, A.W.J., Brown, M.T. & Bannister, P., 1988. The frost resistance of some littoral and sub-littoral algae from southern New Zealand. *Botanica Marina*, **31**, 461-464.
- Fredriksen, S., Sjøtun, K., Lein, T.E. & Rueness, J., 1995. Spore dispersal in *Laminaria hyperborea* (Laminariales, Phaeophyceae). *Sarsia*, **80** (1), 47-53.
- Frieder, C., Nam, S., Martz, T. & Levin, L., 2012. High temporal and spatial variability of dissolved oxygen and pH in a nearshore California kelp forest. *Biogeosciences*, **9** (10), 3917-3930.
- Gainey, L.F., 1994. Volume regulation in three species of marine mussels. *Journal of Experimental Marine Biology and Ecology*, **181** (2), 201-211.
- Ganning, B & Wulff, F., 1970. Measurements of community metabolism in some Baltic brackish water rockpools by means of diel oxygen curves. *Oikos*, **21**, 292-298.
- Ganning, B., 1971. Studies on chemical, physical and biological conditions in Swedish rockpool ecosystems. *Ophelia*, **9**, 51-105.
- Gayral, P. & Cosson, J., 1973. Exposé synoptique des données biologiques sur la laminaire digitée *Laminaria digitata*. *Synopsis FAO sur les pêches*, no. **89**.
- Gerard, V.A., 1987. Hydrodynamic streamlining of *Laminaria saccharina* Lamour. in response to mechanical stress. *Journal of Experimental Marine Biology and Ecology*, **107**, 237-244.
- Gerard, V.A., 1988. Ecotypic differentiation in light-related traits of the kelp *Laminaria saccharina*. *Marine Biology*, **97**, 25-36.
- GESAMP (IMO/FAO/UNESCO/WMO/WHO/IAEA/UN/UNEP Joint Group of Experts on the Scientific Aspects of Marine Pollution), 1993. Impact of oil and related chemicals and wastes on the marine environment. GESAMP Report and Studies, no. 50., London: International Maritime Organization.
- Gevaert, F., Davoult, D., Creach, A., Kling, R., Janquin, M.-A., Seuront, L. & Lemoine, Y., 2001. Carbon and nitrogen content of *Laminaria saccharina* in the eastern English Channel: Biometrics and seasonal variations. *Journal of the Marine Biological Association of the United Kingdom*, **81**, 727-734.
- Gomez, J.L.C. & Miguez-Rodriguez, L.J., 1999. Effects of oil pollution on skeleton and tissues of *Echinus esculentus* L. 1758 (Echinodermata, Echinoidea) in a population of A Coruna Bay, Galicia, Spain. In *Echinoderm Research 1998. Proceedings of the Fifth European Conference on Echinoderms, Milan, 7-12 September 1998*, (ed. M.D.C. Carnevali & F. Bonasoro) pp. 439-447. Rotterdam: A.A. Balkema.
- Gordillo, F.J.L., Dring, M.J. & Savidge, G., 2002. Nitrate and phosphate uptake characteristics of three species of brown algae cultured at low salinity. *Marine Ecology Progress Series*, **234**, 111-116.
- Gordon, D.P., 1972. Biological relationships of an intertidal bryozoan population. *Journal of Natural History*, **6**, 503-514.
- Gorgula, S.K. & Connell, S.D., 2004. Expansive covers of turf-forming algae on human-dominated coast: the relative effects of increasing nutrient and sediment loads. *Marine Biology*, **145** (3), 613-619.
- Gorman, D., Bajjouk, T., Populus, J., Vasquez, M. & Ehrhold, A., 2013. Modeling kelp forest distribution and biomass along temperate rocky coastlines. *Marine Biology*, **160** (2), 309-325.
- Goss-Custard, S., Jones, J., Kitching, J.A. & Norton, T.A., 1979. Tide pools of Carrigathorna and Barloge Creek. *Philosophical Transactions of the Royal Society. Series B: Biological Sciences*, **287**, 1-44.
- Grandy, N., 1984. *The effects of oil and dispersants on subtidal red algae*. Ph.D. Thesis. University of Liverpool.
- Guiry, M.D. & Blunden, G., 1991. *Seaweed Resources in Europe: Uses and Potential*. Chichester: John Wiley & Sons.
- Gunnill, F., 1985. Population fluctuations of seven macroalgae in southern California during 1981-1983 including effects of severe storms and an El Niño. *Journal of Experimental Marine Biology and Ecology*, **85**, 149-164.
- Hammer, L., 1972. Anaerobiosis in marine algae and marine phanerogams. In *Proceedings of the Seventh International Seaweed Symposium, Sapporo, Japan, August 8-12, 1971* (ed. K. Nisizawa, S. Arasaki, Chihara, M., Hirose, H., Nakamura V., Tsuchiya, Y.), pp. 414-419. Tokyo: Tokyo University Press.

- Handå, A., Forbord, S., Wang, X., Broch, O.J., Dahle, S.W., Storseth, T.R., Reitan, K.I., Olsen, Y. & Skjermo, J., 2013. Seasonal and depth-dependent growth of cultivated kelp (*Saccharina latissima*) in close proximity to salmon (*Salmo salar*) aquaculture in Norway. *Aquaculture*, **414**, 191-201.
- Harder, D.L., Hurd, C.L. & Speck, T., 2006. Comparison of mechanical properties of four large, wave-exposed seaweeds. *American Journal of Botany*, **93** (10), 1426-1432.
- Harkin, E., 1981. Fluctuations in epiphyte biomass following *Laminaria hyperborea* canopy removal. In *Proceedings of the Xth International Seaweed Symposium, Gøteborg, 11-15 August 1980* (ed. T. Levring), pp.303-308. Berlin: Walter de Gruyter.
- Harlin, M.M., & Lindbergh, J.M., 1977. Selection of substrata by seaweed: optimal surface relief. *Marine Biology*, **40**, 33-40.
- Hawkins, S.J. & Harkin, E., 1985. Preliminary canopy removal experiments in algal dominated communities low on the shore and in the shallow subtidal on the Isle of Man. *Botanica Marina*, **28**, 223-30.
- Hawkins, S.J. & Southward, A.J., 1992. The *Torrey Canyon* oil spill: recovery of rocky shore communities. In *Restoring the Nations Marine Environment*, (ed. G.W. Thorpe), Chapter 13, pp. 583-631. Maryland, USA: Maryland Sea Grant College.
- Hawkins, S.J., Hartnoll, R.G., Kain, J.M. & Norton, T.A., 1992. Plant-animal interactions on hard substrata in the north-east Atlantic. In *Plant-animal interactions in the marine benthos* (ed. D.M. John, S.J. Hawkins & J.H. Price), pp. 1-32. Oxford: Clarendon Press. [Systematics Association Special Volume, no. 46.]
- Hayward, P.J. 1988. *Animals on seaweed*. Richmond, Surrey: Richmond Publishing Co. Ltd. [Naturalists Handbooks 9].
- Heiser, S., Hall-Spencer, J.M. & Hiscock, K., 2014. Assessing the extent of establishment of *Undaria pinnatifida* in Plymouth Sound Special Area of Conservation, UK. *Marine Biodiversity Records*, **7**, e93.
- Hicks, G.R.F., 1985. Meiofauna associated with rocky shore algae. In *The Ecology of Rocky Coasts: essays presented to J.R. Lewis, D.Sc.*, (ed. P.G. Moore & R. Seed, ed.), pp. 36-56. London: Hodder & Stoughton Ltd.
- Hill, S., Burrows, S.J. & Hawkins, S.J., 1998. *Intertidal Reef Biotopes (Volume VI). An overview of dynamics and sensitivity characteristics for conservation management of marine Special Areas of Conservation*. Oban: Scottish Association for Marine Science (UK Marine SACs Project), Scottish Association for Marine Science (UK Marine SACs Project).
- Hiscock, K. & Mitchell, R., 1980. *The Description and Classification of Sublittoral Epibenthic Ecosystems*. In *The Shore Environment, Vol. 2, Ecosystems*, (ed. J.H. Price, D.E.G. Irvine, & W.F. Farnham), 323-370. London and New York: Academic Press. [Systematics Association Special Volume no. 17(b)].
- Hoarau, G., Coyer, J., Veldsink, J., Stam, W. & Olsen, J., 2007. Glacial refugia and recolonization pathways in the brown seaweed *Fucus serratus*. *Molecular Ecology*, **16** (17), 3606-3616.
- Hoare, R. & Hiscock, K., 1974. An ecological survey of the rocky coast adjacent to the effluent of a bromine extraction plant. *Estuarine and Coastal Marine Science*, **2** (4), 329-348.
- Holt, T.J., Hartnoll, R.G. & Hawkins, S.J., 1997. The sensitivity and vulnerability to man-induced change of selected communities: intertidal brown algal shrubs, *Zostera* beds and *Sabellaria spinulosa* reefs. *English Nature, Peterborough, English Nature Research Report No. 234*.
- Holt, T.J., Jones, D.R., Hawkins, S.J. & Hartnoll, R.G., 1995. The sensitivity of marine communities to man induced change - a scoping report. *Countryside Council for Wales, Bangor, Contract Science Report*, no. 65.
- Hong, J. & Reish, D.J., 1987. Acute toxicity of cadmium to eight species of marine amphipod and isopod crustaceans from southern California. *Bulletin of Environmental Contamination and Toxicology*, **39**, 884-888.
- Hopkin, R. & Kain, J.M., 1978. The effects of some pollutants on the survival, growth and respiration of *Laminaria hyperborea*. *Estuarine and Coastal Marine Science*, **7**, 531-553.
- Huggett, J. & Griffiths, C.L., 1986. Some relationships between elevation, physico-chemical variables and biota of intertidal rockpools. *Marine Ecology Progress Series*, **29**, 198-197.
- Husa, V., Kutti, T., Ervik, A., Sjøtun, K., Hansen, P.K. & Aure, J., 2014. Regional impact from fin-fish farming in an intensive production area (Hardangerfjord, Norway). *Marine Biology Research*, **10** (3), 241-252.
- Irvine, L. M. & Chamberlain, Y. M., 1994. *Seaweeds of the British Isles*, vol. 1. *Rhodophyta*, Part 2B *Corallinales*, *Hildenbrandiales*. London: Her Majesty's Stationery Office.
- Jenkins, S., Coleman, R., Della Santina, P., Hawkins, S., Burrows, M. & Hartnoll, R., 2005. Regional scale differences in the determinism of grazing effects in the rocky intertidal. *Marine Ecology Progress Series*, **287**, 77-86.
- JNCC, 2015. The Marine Habitat Classification for Britain and Ireland Version 15.03. (20/05/2015). Available from <https://mhc.jncc.gov.uk/>
- JNCC, 2015. The Marine Habitat Classification for Britain and Ireland Version 15.03. (20/05/2015). Available from <https://mhc.jncc.gov.uk/>
- JNCC (Joint Nature Conservation Committee), 1999. *Marine Environment Resource Mapping And Information*

Database (MERMAID): Marine Nature Conservation Review Survey Database. [on-line]

<http://www.jncc.gov.uk/mermaid>

Jones, C.G., Lawton, J.H. & Shackak, M., 1994. Organisms as ecosystem engineers. *Oikos*, **69**, 373-386.

Jones, D.J., 1971. Ecological studies on macro-invertebrate communities associated with polluted kelp forest in the North Sea. *Helgolander Wissenschaftliche Meeresuntersuchungen*, **22**, 417-431.

Jones, L.A., Hiscock, K. & Connor, D.W., 2000. Marine habitat reviews. A summary of ecological requirements and sensitivity characteristics for the conservation and management of marine SACs. *Joint Nature Conservation Committee, Peterborough. (UK Marine SACs Project report.)*. Available from:

<http://www.ukmarinesac.org.uk/pdfs/marine-habitats-review.pdf>

Jones, N.S. & Kain, J.M., 1967. Subtidal algal recolonisation following removal of *Echinus*. *Helgolander Wissenschaftliche Meeresuntersuchungen*, **15**, 460-466.

Jueterbock, A., Kollias, S., Smolina, I., Fernandes, J.M., Coyer, J.A., Olsen, J.L. & Hoarau, G., 2014. Thermal stress resistance of the brown alga *Fucus serratus* along the North-Atlantic coast: Acclimatization potential to climate change. *Marine Genomics*, **13**, 27-36.

Kain, J.M., 1964. Aspects of the biology of *Laminaria hyperborea* III. Survival and growth of gametophytes. *Journal of the Marine Biological Association of the United Kingdom*, **44** (2), 415-433.

Kain, J.M. & Svendsen, P., 1969. A note on the behaviour of *Patina pellucida* in Britain and Norway. *Sarsia*, **38**, 25-30.

Kain, J.M., 1967. Populations of *Laminaria hyperborea* at various latitudes. *Helgolander Wissenschaftliche Meeresuntersuchungen*, **15**, 489-499.

Kain, J.M., 1971a. Synopsis of biological data on *Laminaria hyperborea*. *FAO Fisheries Synopsis*, no. 87.

Kain, J.M., 1975a. Algal recolonization of some cleared subtidal areas. *Journal of Ecology*, **63**, 739-765.

Kain, J.M., 1979. A view of the genus *Laminaria*. *Oceanography and Marine Biology: an Annual Review*, **17**, 101-161.

Kain, J.M., 1987. Photoperiod and temperature as triggers in the seasonality of *Delesseria sanguinea*. *Helgolander Meeresuntersuchungen*, **41**, 355-370.

Kain, J.M., & Norton, T.A., 1990. Marine Ecology. In *Biology of the Red Algae*, (ed. K.M. Cole & Sheath, R.G.). Cambridge: Cambridge University Press.

Kain, J.M., Drew, E.A. & Jupp, B.P., 1975. Light and the ecology of *Laminaria hyperborea* II. In *Proceedings of the Sixteenth Symposium of the British Ecological Society, 26-28 March 1974. Light as an Ecological Factor: II* (ed. G.C. Evans, R. Bainbridge & O. Rackham), pp. 63-92. Oxford: Blackwell Scientific Publications.

Karsten, U., 2007. Research note: salinity tolerance of Arctic kelps from Spitsbergen. *Phycological Research*, **55** (4), 257-262.

Kautsky, H., 1992. The impact of pulp-mill effluents on phytobenthic communities in the Baltic Sea. *Ambio*, **21**, 308-313.

Kelly, M.S., 2000. The reproductive cycle of the sea urchin *Psammechinus miliaris* (Echinodermata: Echinoidea) in a Scottish sea loch. *Journal of the Marine Biological Association of the United Kingdom*, **80**, 909-919.

Kervarec, F., Arzel, P. & Guyader, O., 1999. Fisher Behaviour and Economic Interactions Between Fisheries: Examining Seaweed and Scallop Fisheries of the Brest District (Western Brittany, France). *The XIth Annual Conference of the European Association of Fisheries Economists. 6th-10th April 1999, Dublin*, pp.

Kinne, O. (ed.), 1972. *Marine Ecology: A Comprehensive, Integrated Treatise on Life in Oceans and Coastal Waters*, Vol.1, *Environmental Factors*, part 3. New York: John Wiley & Sons.

Kinne, O. (ed.), 1980. *Diseases of marine animals*. vol. 1. *General aspects. Protozoa to Gastropoda*. Chichester: John Wiley & Sons.

Kinne, O., 1971b. Salinity - invertebrates. In *Marine Ecology: A Comprehensive, Integrated Treatise on Life in Oceans and Coastal Waters. Vol. 1 Environmental Factors*, Part 2, pp. 821-995. London: John Wiley & Sons.

Kinne, O., 1977. International Helgoland Symposium "Ecosystem research": summary, conclusions and closing. *Helgoländer Wissenschaftliche Meeresuntersuchungen*, **30**(1-4), 709-727.

Kitching, J., 1941. Studies in sublittoral ecology III. *Laminaria* forest on the west coast of Scotland; a study of zonation in relation to wave action and illumination. *The Biological Bulletin*, **80** (3), 324-337

Knight, M. & Parke, M., 1950. A biological study of *Fucus vesiculosus* L. and *Fucus serratus* L. *Journal of the Marine Biological Association of the United Kingdom*, **29**, 439-514.

Kooistra, W.H.C.F., Joosten, A.M.T. & van den Hoek, C., 1989. Zonation patterns in intertidal pools and their possible causes: a multivariate approach. *Botanica Marina*, **32**, 9-26.

Kregting, L., Blight, A., Elsäßer, B. & Savidge, G., 2013. The influence of water motion on the growth rate of the kelp *Laminaria hyperborea*. *Journal of Experimental Marine Biology and Ecology*, **448**, 337-345.

Krumhansl, K.A. & Scheibling, R.E., 2011. Detrital production in Nova Scotian kelp beds: patterns and processes. *Marine Ecological Progress Series*, **421**, 67-82.

- Krumhansl, K.A. & Scheibling, R.E., 2012. Detrital subsidy from subtidal kelp beds is altered by the invasive green alga *Codium fragile* ssp *fragile*. *Marine Ecology Progress Series*, **456**, 73-85.
- Krumhansl, K.A., 2012. *Detrital production in kelp beds*. degree of Doctor of Philosophy, Department of Biology, Dalhousie University, Halifax, Nova Scotia.
- Krumhansl, K.A., Lee, J.M. & Scheibling, R.E., 2011. Grazing damage and encrustation by an invasive bryozoan reduce the ability of kelps to withstand breakage by waves. *Journal of Experimental Marine Biology and Ecology*, **407** (1), 12-18.
- Kruuk, H., Wansink, D. & Moorhouse, A., 1990. Feeding patches and diving success of otters, *Lutra lutra*, in Shetland. *Oikos*, **57**, 68-72.
- Lang, C. & Mann, K., 1976. Changes in sea urchin populations after the destruction of kelp beds. *Marine Biology*, **36** (4), 321-326.
- Latham, H., 2008. Temperature stress-induced bleaching of the coralline alga *Corallina officinalis*: a role for the enzyme bromoperoxidase. *Bioscience Horizons*, 1-10
- Lee, R.E., 1971. Systemic viral material in the cells of the freshwater alga *Sirodotia tenuissima* (Holden) Skuja. *Journal of Cell Science*, **8**, 623-631.
- Lein, T.E, Sjøtun, K. & Wakili, S., 1991. Mass - occurrence of a brown filamentous endophyte in the lamina of the kelp *Laminaria hyperborea* (Gunnerus) Foslie along the south western coast of Norway *Sarsia*, **76**, 187-193.
- Leinaas, H.P. & Christie, H., 1996. Effects of removing sea urchins (*Strongylocentrotus droebachiensis*): stability of the barren state and succession of kelp forest recovery in the east Atlantic. *Oecologia*, **105**(4), 524-536.
- Lewis, J.R., 1964. *The Ecology of Rocky Shores*. London: English Universities Press.
- Little, C. & Kitching, J.A., 1996. *The Biology of Rocky Shores*. Oxford: Oxford University Press.
- Little, C., Williams, G.A. & Trowbridge, C.D., 2009. *The biology of rocky shores*: Oxford University Press New York.
- Littler, M. & Murray, S., 1975. Impact of sewage on the distribution, abundance and community structure of rocky intertidal macro-organisms. *Marine Biology*, **30** (4), 277-291.
- Littler, M.M., & Kauker, B.J., 1984. Heterotrichy and survival strategies in the red alga *Corallina officinalis* L. *Botanica Marina*, **27**, 37-44.
- Lobban, C.S. & Harrison, P.J., 1997. *Seaweed ecology and physiology*. Cambridge: Cambridge University Press.
- Long, D., 2006. BGS detailed explanation of seabed sediment modified Folk classification. Available from: http://www.emodnet-seabedhabitats.eu/PDF/GMHM3_Detailed_explanation_of_seabed_sediment_classification.pdf
- Lorentsen, S.-H., Sjøtun, K. & Grémillet, D., 2010. Multi-trophic consequences of kelp harvest. *Biological Conservation*, **143** (9), 2054-2062.
- Lubchenco, J., 1978. Plant species diversity in a marine intertidal community, importance of herbivore food preference and algal competitive abilities. *American Naturalist*, **112**, 23-39.
- Lüning, K., 1990. *Seaweeds: their environment, biogeography, and ecophysiology*: John Wiley & Sons.
- Lüning, K. & Dring, M.J., 1975. Reproduction, growth and photosynthesis of gametophytes of *Laminaria saccharina* grown in blue and red light. *Marine Biology*, **29**, 195-200.
- Lüning, K., 1984. Temperature tolerance and biogeography of seaweeds: the marine algal flora of Helgoland (North Sea) as an example. *Helgolander Meeresuntersuchungen*, **38**, 305-317.
- Lyngby, J.E. & Mortensen, S.M., 1996. Effects of dredging activities on growth of *Laminaria saccharina*. *Marine Ecology, Pubblicazioni della Stazione Zoologica di Napoli I*, **17**, 345-354.
- Maggs, C.A. & Hommersand, M.H., 1993. *Seaweeds of the British Isles: Volume 1 Rhodophycota Part 3A Ceramiales*. London: Natural History Museum, Her Majesty's Stationary Office.
- Maggs, C.A. & Pueschel, C.M., 1989. Morphology and development of *Ahnfeltia plicata* (Rhodophyta) : proposal of Ahnfeltiales ord. nov. *Journal of Phycology*, **25**, 333-351.
- Malm, T., Kautsky, L. & Engkvist, R., 2001. Reproduction, recruitment and geographical distribution of *Fucus serratus* L. in the Baltic Sea. *Botanica Marina*, **44** (2), 101-108.
- Mangialajo, L., Chiantore, M. & Cattaneo-Vietti, R., 2008. Loss of furoid algae along a gradient of urbanisation, and structure of benthic assemblages. *Marine Ecology Progress Series*, **358**, 63.
- Mann, K.H., 1982. Kelp, sea urchins, and predators: a review of strong interactions in rocky subtidal systems of eastern Canada, 1970-1980. *Netherlands Journal of Sea Research*, **16**, 414-423.
- Markham, J.W. & Munda, I.M., 1980. Algal recolonisation in the rocky eulittoral at Helgoland, Germany. *Aquatic Botany*, **9**, 33-71.
- MarLIN, 2015. MarLIN (Marine Life Network). (13-10-2015). <http://www.marlin.ac.uk>
- Martinez, B., Pato, L.S. & Rico, J.M., 2012. Nutrient uptake and growth responses of three intertidal macroalgae with perennial, opportunistic and summer-annual strategies. *Aquatic Botany*, **96** (1), 14-22.

- Mathieson, A.C. & Burns, R.L., 1971. Ecological studies of economic red algae. 1. Photosynthesis and respiration of *Chondrus crispus* (Stackhouse) and *Gigartina stellata* (Stackhouse) Batters. *Journal of Experimental Marine Biology and Ecology*, **7**, 197-206.
- May, V., 1985. Observations on algal floras close to two sewerage outlets. *Cunninghamia*, **1**, 385-394.
- McHugh, D.J., 2003. *A guide to the seaweed industry*: Food and Agriculture Organization of the United Nations Rome.
- Metaxas, A. & Scheibling, R.E., 1993. Community structure and organization of tidepools. *Marine Ecology Progress Series*, **98**, 187-198.
- Metaxas, A., Hunt, H.L., & Scheibling, R.E., 1994. Spatial and temporal variability of macrobenthic communities in tidepools on a rocky shore in Nova Scotia, Canada. *Marine Ecology Progress Series*, **105**, 89-103.
- Miller III, H.L., Neale, P.J. & Dunton, K.H., 2009. Biological weighting functions for UV inhibition of photosynthesis in the kelp *Laminaria hyperborea* (Phaeophyceae) 1. *Journal of Phycology*, **45** (3), 571-584.
- Minchinton, T.E., Schiebling, R.E. & Hunt, H.L., 1997. Recovery of an intertidal assemblage following a rare occurrence of scouring by sea ice in Nova Scotia, Canada. *Botanica Marina*, **40**, 139-148.
- Moore, J., Taylor, P. & Hiscock, K., 1995. Rocky shore monitoring programme. *Proceedings of the Royal Society of Edinburgh*, **103B**, 181-200.
- Moore, P.G., 1973a. The kelp fauna of north east Britain I. Function of the physical environment. *Journal of Experimental Marine Biology and Ecology*, **13**, 97-125.
- Moore, P.G., 1973b. The kelp fauna of north east Britain. II. Multivariate classification: turbidity as an ecological factor. *Journal of Experimental Marine Biology and Ecology*, **13**, 127-163.
- Moore, P.G., 1978. Turbidity and kelp holdfast Amphipoda. I. Wales and S.W. England. *Journal of Experimental Marine Biology and Ecology*, **32**, 53-96.
- Moore, P.G., 1985. Levels of heterogeneity and the amphipod fauna of kelp holdfasts. In *The Ecology of Rocky Coasts: essays presented to J.R. Lewis, D.Sc.* (ed. P.G. Moore & R. Seed), 274-289. London: Hodder & Stoughton Ltd.
- Morrell, S.L. & Farnham, W.F., 1982. Some effects of substratum on *Sargassum muticum*. *British Phycological Journal*, **17** (2), 236-237.
- Morris, S. & Taylor, A.C. 1983. Diurnal and seasonal variations in physico-chemical conditions within intertidal rock pools. *Estuarine, Coastal and Shelf Science*, **17**, 339-355.
- Moss, B. & Shearer, A., 1973. The effect of light and temperature upon the germination and growth of *Halidrys siliquosa* (L.) Lyngb. (Phaeophyceae, Fucales). *Phycologia*, **12**, 63-68.
- Moss, B.L., 1982. The control of epiphytes by *Halidrys siliquosa* (L.) Lyngb. (Phaeophyta; Cystoceiraceae). *Phycologia*, **21**, 185-198.
- Mueller, D., 1979. Sublethal and lethal effects of copper, cadmium and lead to organisms representative for the intertidal flats at the outer Elbe Estuary. *Archiv fur hydrobiologie*, supplement **43** (2-3), 289-346.
- Naylor, E. & Slinn, D.J., 1958. Observations on the ecology of some brackish water organisms in pools at Scarlett Point, Isle of Man. *Journal of Animal Ecology*, **27**, 15-25.
- Naylor, E. & Slinn, D.J., 1958. Observations on the ecology of some brackish water organisms in pools at Scarlett Point, Isle of Man. *Journal of Animal Ecology*, **27**, 15-25.
- NBN, 2015. National Biodiversity Network 2015(20/05/2015). <https://data.nbn.org.uk/>
- Nichols, D., 1981. The Cornish Sea-urchin Fishery. *Cornish Studies*, **9**, 5-18.
- Nielsen, S.L., Nielsen, H.D. & Pedersen, M.F., 2014. Juvenile life stages of the brown alga *Fucus serratus* L. are more sensitive to combined stress from high copper concentration and temperature than adults. *Marine Biology*, **161** (8), 1895-1904.
- Nimura, K., Mizuta, H. & Yamamoto, H., 2002. Critical contents of nitrogen and phosphorus for sorus formation in four *Laminaria* species. *Botanica Marina*, **45**, 184-188.
- Norderhaug, K., 2004. Use of red algae as hosts by kelp-associated amphipods. *Marine Biology*, **144** (2), 225-230.
- Norderhaug, K.M. & Christie, H.C., 2009. Sea urchin grazing and kelp re-vegetation in the NE Atlantic. *Marine Biology Research*, **5** (6), 515-528.
- Norderhaug, K.M., Christie, H. & Fredriksen, S., 2007. Is habitat size an important factor for faunal abundances on kelp (*Laminaria hyperborea*)? *Journal of Sea Research*, **58** (2), 120-124.
- Nordheim, van, H., Andersen, O.N. & Thissen, J., 1996. Red lists of Biotopes, Flora and Fauna of the Trilateral Wadden Sea area, 1995. *Helgolander Meeresuntersuchungen*, **50** (Suppl.), 1-136.
- North, W.J. & Schaefer, M., 1964. An investigation of the effects of discharged wastes on kelp. *Resource Agency of California, State Water Quality Control Board, Publication*, **26**.
- Norton, T.A., 1978. The factors influencing the distribution of *Saccorhiza polyschides* in the region of Lough Ine. *Journal of the Marine Biological Association of the United Kingdom*, **58**, 527-536.

- Norton, T.A., 1992. Dispersal by macroalgae. *British Phycological Journal*, **27**, 293-301.
- Norton, T.A., Hiscock, K. & Kitching, J.A., 1977. The Ecology of Lough Ine XX. The *Laminaria* forest at Carrigathorna. *Journal of Ecology*, **65**, 919-941.
- O'Brien, P.J. & Dixon, P.S., 1976. Effects of oils and oil components on algae: a review. *British Phycological Journal*, **11**, 115-142.
- Oertzen, J.-A., Wulf, D. & Bruegmann, L., 1988. Ecotoxicological effects of two mercury compounds on *Neomysis integer* (Leach) and *Pomatoschistus microps* (Kroyer). *Kieler Meeresforschungen Sonderheft*, **6**, 414-123.
- Parker, T., Johnson, C. & Chapman, A.R.O., 1993. Gammarid amphipods and littorinid snails have significant but different effects on algal succession in littoral fringe tidepools. *Ophelia*, **38**, 69-88.
- Pearson, G.A., Lago-Leston, A. & Mota, C., 2009. Frayed at the edges: selective pressure and adaptive response to abiotic stressors are mismatched in low diversity edge populations. *Journal of Ecology*, **97** (3), 450-462.
- Peckol, P., Levings, S.C. & Garrity, S.D., 1990. Kelp response following the *World Prodigy* oil spill. *Marine Pollution Bulletin*, **21**, 473-476.
- Pedersen, M.F., Nejrup, L.B., Fredriksen, S., Christie, H. & Norderhaug, K.M., 2012. Effects of wave exposure on population structure, demography, biomass and productivity of the kelp *Laminaria hyperborea*. *Marine Ecology Progress Series*, **451**, 45-60.
- Penfold, R., Hughson, S., & Boyle, N., 1996. *The potential for a sea urchin fishery in Shetland*. <http://www.nafc.ac.uk/publish/note5/note5.htm>, 2000-04-14
- Pérez, R., 1971. Écologie, croissance et régénération, teneurs en acide alginique de *Laminaria digitata* sur les cotes de la Manche. *Revue des Travaux de l'Institut des Pêches Maritimes*, **35**, 287-346.
- Pérez, R., 1971. Écologie, croissance et régénération, teneurs en acide alginique de *Laminaria digitata* sur les cotes de la Manche. *Revue des Travaux de l'Institut des Pêches Maritimes*, **35**, 287-346.
- Perkol-Finkel, S. & Airoidi, L., 2010. Loss and recovery potential of marine habitats: an experimental study of factors maintaining resilience in subtidal algal forests at the Adriatic Sea. *PLoS One*, **5** (5), e10791.
- Peters, A.F. & Schaffelke, B., 1996. *Streblonema* (Ectocarpales, Phaeophyceae) infection in the kelp *Laminaria saccharina* in the western Baltic. *Hydrobiologia*, **326/327**, 111-116.
- Philippart, C.J., Anadón, R., Danovaro, R., Dippner, J.W., Drinkwater, K.F., Hawkins, S.J., Oguz, T., O'Sullivan, G. & Reid, P.C., 2011. Impacts of climate change on European marine ecosystems: observations, expectations and indicators. *Journal of Experimental Marine Biology and Ecology*, **400** (1), 52-69.
- Pybus, C., 1977. The ecology of *Chondrus crispus* and *Gigartina stellata* (Rhodophyta) in Galway Bay. *Journal of the Marine Biological Association of the United Kingdom*, **57**, 609-628.
- Pyefinch, K. A., 1943. The intertidal ecology of Bardsey Island, North Wales, with special reference to the recolonization of rock surfaces, and the rock pool environment. *Journal of Animal Ecology*, **12**, 82-108.
- Raffaelli, D. & Hawkins, S., 1999. *Intertidal Ecology* 2nd edn.. London: Kluwer Academic Publishers.
- Read, P.A., Anderson, K.J., Matthews, J.E., Watson, P.G., Halliday, M.C. & Shiells, G.M., 1983. Effects of pollution on the benthos of the Firth of Forth. *Marine Pollution Bulletin*, **14**, 12-16.
- Reed, D.C., Rassweiler, A. & Arkema, K.K., 2008. Biomass rather than growth rate determines variation in net primary production by giant kelp. *Ecology and evolution*, **89**, 2493-2505
- Rinde, E. & Sjøtun, K., 2005. Demographic variation in the kelp *Laminaria hyperborea* along a latitudinal gradient. *Marine Biology*, **146** (6), 1051-1062.
- Roleda, M.Y. & Dethleff, D., 2011. Storm-generated sediment deposition on rocky shores: Simulating burial effects on the physiology and morphology of *Saccharina latissima* sporophytes. *Marine Biology Research*, **7** (3), 213-223.
- Rostron, D.M. & Bunker, F. St P.D., 1997. An assessment of sublittoral epibenthic communities and species following the *Sea Empress* oil spill. A report to the Countryside Council for Wales from Marine Seen & Sub-Sea Survey., Countryside Council for Wales, Bangor, CCW *Sea Empress Contact Science*, no. 177.
- Rueness, J., 1989. *Sargassum muticum* and other introduced Japanese macroalgae: biological pollution of European coasts. *Marine Pollution Bulletin*, **20** (4), 173-176.
- Sawabe, T., Makino, H., Tatsumi, M., Nakano, K., Tajima, K., Iqbal, M.M., Yumoto, I., Ezura, Y. & Christen, R., 1998. *Pseudoalteromonas bacteriolytica* sp. nov., a marine bacterium that is the causative agent of red spot disease of *Laminaria japonica*. *International Journal of Systematic Bacteriology*, **48** (3), 769-774.
- Scanlan, C.M. & Wilkinson, M., 1987. The use of seaweeds in biocide toxicity testing. Part 1. The sensitivity of different stages in the life-history of *Fucus* and of other algae, to certain biocides. *Marine Environmental Research*, **21**, 11-29.
- Scheibling, R.E. & Gagnon, P., 2006. Competitive interactions between the invasive green alga *Codium fragile* ssp *tomentosoides* and native canopy-forming seaweeds in Nova Scotia (Canada). *Marine Ecology Progress Series*, **325**, 1-14.

- Scheibling, R.E., Hennigar, A.W. & Balch, T., 1999. Destructive grazing, epiphytism, and disease: the dynamics of sea urchin-kelp interactions in Nova Scotia. *Canadian Journal of Fisheries and Aquatic Sciences*, **56** (12), 2300-2314.
- Schiel, D.R. & Foster, M.S., 1986. The structure of subtidal algal stands in temperate waters. *Oceanography and Marine Biology: an Annual Review*, **24**, 265-307.
- Schiel, D.R. & Lilley, S.A., 2011. Impacts and negative feedbacks in community recovery over eight years following removal of habitat-forming macroalgae. *Journal of Experimental Marine Biology and Ecology*, **407** (1), 108-115.
- Schiel, D.R. & Taylor, D.I., 1999. Effects of trampling on a rocky intertidal algal assemblage in southern New Zealand. *Journal of Experimental Marine Biology and Ecology*, **235**, 213-235.
- Schmidt, A.L. & Scheibling, R.E., 2006. A comparison of epifauna and epiphytes on native kelps (*Laminaria* species) and an invasive alga (*Codium fragile* ssp *tomentosoides*) in Nova Scotia, Canada. *Botanica Marina*, **49** (4), 315-330.
- Scrosati, R., Garbary, D.J. & McLachlan, J., 1994. Reproductive ecology of *Chondrus crispus* (Rhodophyta, Gigartinales) from Nova Scotia, Canada. *Botanica Marina*, **37**, 293-300.
- Seapy, R.R. & Littler, M.M., 1982. Population and Species Diversity Fluctuations in a Rocky Intertidal Community Relative to Severe Aerial Exposure and Sediment Burial. *Marine Biology*, **71**, 87-96.
- Sebens, K.P., 1985. Community ecology of vertical rock walls in the Gulf of Maine: small-scale processes and alternative community states. In *The Ecology of Rocky Coasts: essays presented to J.R. Lewis, D.Sc.* (ed. P.G. Moore & R. Seed), pp. 346-371. London: Hodder & Stoughton Ltd.
- Sebens, K.P., 1986. Spatial relationships among encrusting marine organisms in the New England subtidal zone. *Ecological Monographs*, **56**, 73-96.
- Serrão, E.A., Brawley, S.H., Hedman, J., Kautsky, L. & Samuelsson, G., 1999. Reproductive success of *Fucus vesiculosus* (Phaeophyceae) in the Baltic Sea. *Journal of Phycology*, **35** (2), 254-269.
- Sheppard, C.R.C., Bellamy, D.J. & Sheppard, A.L.S., 1980. Study of the fauna inhabiting the holdfasts of *Laminaria hyperborea* (Gunn.) Fosl. along some environmental and geographical gradients. *Marine Environmental Research*, **4**, 25-51.
- Sivertsen, K., 1997. Geographic and environmental factors affecting the distribution of kelp beds and barren grounds and changes in biota associated with kelp reduction at sites along the Norwegian coast. *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 2872-2887.
- Sjøtun, K., Christie, H. & Helge Fosså, J., 2006. The combined effect of canopy shading and sea urchin grazing on recruitment in kelp forest (*Laminaria hyperborea*). *Marine Biology Research*, **2** (1), 24-32.
- Sjøtun, K. & Schoschina, E.V., 2002. Gametophytic development of *Laminaria* spp. (Laminariales, Phaeophyta) at low temperatures. *Phycologia*, **41**, 147-152.
- Sjøtun, K., 1993. Seasonal lamina growth in two age groups of *Laminaria saccharina* (L.) Lamour. in Western Norway. *Botanica Marina*, **36**, 433-441.
- Smale, D.A. & Wernberg, T., 2013. Extreme climatic event drives range contraction of a habitat-forming species. *Proceedings of the Royal Society B-Biological Sciences*, **280** (1754).
- Smale, D.A., Burrows, M.T., Moore, P., O'Connor, N. & Hawkins, S.J., 2013. Threats and knowledge gaps for ecosystem services provided by kelp forests: a northeast Atlantic perspective. *Ecology and evolution*, **3** (11), 4016-4038.
- Smale, D.A., Wernberg, T., Yunnice, A.L. & Vance, T., 2014. The rise of *Laminaria ochroleuca* in the Western English Channel (UK) and comparisons with its competitor and assemblage dominant *Laminaria hyperborea*. *Marine ecology*.
- Smith, B.D., 1985. Recovery following experimental harvesting of *Laminaria longicuris* and *Laminaria digitata* in Southwestern Nova Scotia. *Helgolander Meeresuntersuchungen*, **39**(1), 83-101.
- Smith, J.E. (ed.), 1968. 'Torrey Canyon'. *Pollution and marine life*. Cambridge: Cambridge University Press.
- Solé-Cava, A.M., Thorpe, J.P. & Todd, C.D., 1994. High genetic similarity between geographically distant populations in a sea anemone with low dispersal capabilities. *Journal of the Marine Biological Association of the United Kingdom*, **74**, 895-902.
- Somerfield, P.J. & Warwick, R.M., 1999. Appraisal of environmental impact and recovery using *Laminaria* holdfast faunas. *Sea Empress, Environmental Evaluation Committee., Countryside Council for Wales, Bangor, CCW Sea Empress Contract Science, Report no. 321*.
- Sousa, W.P., 1979. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. *Ecological Monographs*, **49** (3), 227-254.
- Sousa, W.P., Schroeter, S.C. & Daines, S.D., 1981. Latitudinal variation in intertidal algal community structure: the influence of grazing and vegetative propagation. *Oecologia*, **48**, 297-307.
- Southward, A.J. & Southward, E.C., 1978. Recolonisation of rocky shores in Cornwall after use of toxic

- dispersants to clean up the *Torrey Canyon* spill. *Journal of the Fisheries Research Board of Canada*, **35**, 682-706.
- Spilmont, N., Denis, L., Artigas, L.F., Caloin, F., Courcot, L., Creach, A., Desroy, N., Gevaert, F., Hacquebart, P., Hubas, C., Janquin, M.-A., Lemoine, Y., Luczak, C., Migne, A., Rauch, M. & Davoult, D., 2009. Impact of the *Phaeocystis globosa* spring bloom on the intertidal benthic compartment in the eastern English Channel: A synthesis. *Marine Pollution Bulletin*, **58** (1), 55-63.
- Stæhr, P.A. & Wernberg, T., 2009. Physiological responses of *Ecklonia radiata* (Laminariales) to a latitudinal gradient in ocean temperature. *Journal of Phycology*, **45**, 91-99.
- Stæhr, P.A., Pedersen, M.F., Thomsen, M.S., Wernberg, T. & Krause-Jensen, D., 2000. Invasion of *Sargassum muticum* in Limfjorden (Denmark) and its possible impact on the indigenous macroalgal community. *Marine Ecology Progress Series*, **207**, 79-88.
- Stagnol, D., Renaud, M. & Davoult, D., 2013. Effects of commercial harvesting of intertidal macroalgae on ecosystem biodiversity and functioning. *Estuarine, Coastal and Shelf Science*, **130**, 99-110.
- Steneck, R.S., Graham, M.H., Bourque, B.J., Corbett, D., Erlandson, J.M., Estes, J.A. & Tegner, M.J., 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environmental conservation*, **29** (04), 436-459.
- Steneck, R.S., Vavrinc, J. & Leland, A.V., 2004. Accelerating trophic-level dysfunction in kelp forest ecosystems of the western North Atlantic. *Ecosystems*, **7** (4), 323-332.
- Strömngren, T., 1979b. The effect of zinc on the increase in length of five species of intertidal Fucales. *Journal of Experimental Marine Biology and Ecology*, **40**, 95-102.
- Strömngren, T., 1980a. The effect of dissolved copper on the increase in length of four species of intertidal fucooid algae. *Marine Environmental Research*, **3**, 5-13.
- Strömngren, T., 1980b. The effect of lead, cadmium and mercury on the increase in length of five intertidal Fucales. *Journal of Experimental Marine Biology and Ecology*, **43**, 107-119.
- Stæhr, P.A., Pedersen, M.F., Thomsen, M.S., Wernberg, T. & Krause-Jensen, D., 2000. Invasion of *Sargassum muticum* in Limfjorden (Denmark) and its possible impact of the indigenous macroalgal community. *Marine Ecology Progress Series*, **207**, 79-88.
- Suchanek, T.H., 1993. Oil impacts on marine invertebrate populations and communities. *American Zoologist*, **33**, 510-523.
- Sundene, O., 1964. The ecology of *Laminaria digitata* in Norway in view of transplant experiments. *Nytt Magasin for Botanik*, **11**, 83-107.
- Svendsen, P. & Kain, J.M., 1971. The taxonomic status, distribution, and morphology of *Laminaria cucullata* sensu Jorde and Klavestad. *Sarsia*, **46** (1), 1-22.
- Thompson, G.A. & Schiel, D.R., 2012. Resistance and facilitation by native algal communities in the invasion success of *Undaria pinnatifida*. *Marine Ecology, Progress Series*, **468**, 95-105.
- Thompson, R.S. & Burrows, E.M., 1984. The toxicity of copper, zinc and mercury to the brown macroalga *Laminaria saccharina*. In *Ecotoxicological testing for the marine environment* (ed. G. Persoone, E. Jaspers, & C. Claus), Vol. 2, pp. 259-269. Ghent: Laboratory for biological research in aquatic pollution, State University of Ghent.
- Tillin, H.M., Hull, S.C. & Tyler-Walters, H., 2010. Development of a sensitivity matrix (pressures-MCZ/MPA features). *Report to the Department of the Environment, Food and Rural Affairs from ABPmer, Southampton and the Marine Life Information Network (MarLIN) Plymouth: Marine Biological Association of the UK.*, Defra Contract no. MB0102 Task 3A, Report no. 22., London, 145 pp.
- Troell, M., Halling, C., Neori, A., Chopin, T., Buschmann, A., Kautsky, N. & Yarish, C., 2003. Integrated mariculture: asking the right questions. *Aquaculture*, **226** (1), 69-90.
- Vadas, R.L. & Elnor, R.W., 1992. *Plant-animal interactions in the north-west Atlantic*. In *Plant-animal interactions in the marine benthos*, (ed. D.M. John, S.J. Hawkins & J.H. Price), 33-60. Oxford: Clarendon Press. [Systematics Association Special Volume, no. 46].
- Vadas, R.L., Johnson, S. & Norton, T.A., 1992. Recruitment and mortality of early post-settlement stages of benthic algae. *British Phycological Journal*, **27**, 331-351.
- Valero, M., Destombe, C., Mauger, S., Ribout, C., Engel, C.R., Daguin-Thiebaut, C. & Tellier, F., 2011. Using genetic tools for sustainable management of kelps: a literature review and the example of *Laminaria digitata*. *CBM-Cahiers de Biologie Marine*, **52**(4), 467.
- Van den Hoek, C., 1982. The distribution of benthic marine algae in relation to the temperature regulation of their life histories. *Biological Journal of the Linnean Society*, **18**, 81-144.
- Van den Hoek, C., Mann, D.G. & Jahns, H.M., 1995. *Algae: an introduction to phycology*: Cambridge University Press.
- Veà, J. & Ask, E., 2011. Creating a sustainable commercial harvest of *Laminaria hyperborea*, in Norway. *Journal of applied Phycology*, **23**(3), 489-494.
- Viejo, R.M., 1999. Mobile epifauna inhabiting the invasive *Sargassum muticum* and two local seaweeds in northern Spain. *Aquatic Botany*, **64**, 131-149.

- Viejo, R.M., Martínez, B., Arrontes, J., Astudillo, C. & Hernández, L., 2011. Reproductive patterns in central and marginal populations of a large brown seaweed: drastic changes at the southern range limit. *Ecography*, **34** (1), 75-84.
- Vost, L.M., 1983. The influence of *Echinus esculentus* grazing on subtidal algal communities. *British Phycological Journal*, **18**, 211.
- Wang, G., Shuai, L., Li, Y., Lin, W., Zhao, X. & Duan, D., 2008. Phylogenetic analysis of epiphytic marine bacteria on Hole-Rotten diseased sporophytes of *Laminaria japonica*. *Journal of applied phycology*, **20** (4), 403-409.
- Wernberg, T. & Thomsen, S., 2005. Miniview: What affects the forces required to break or dislodge macroalgae? *European Journal of Phycology*, **40** (2), 139-148.
- Wernberg, T., Smale, D.A., Tuya, F., Thomsen, M.S., Langlois, T.J., de Bettignies, T., Bennett, S. & Rousseaux, C.S., 2013. An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nature Climate Change*, **3** (1), 78-82.
- Wernberg, T., Thomsen, M.S., Staehr, P.A. & Pedersen, M.F., 2001. Comparative phenology of *Sargassum muticum* and *Halidrys siliquosa* (Phaeophyceae: Fucales) in Limfjorden, Denmark. *Botanica Marina*, **44**, 31-39.
- Werner, A. & Kraan, S., 2004. Review of the potential mechanisation of kelp harvesting in Ireland. *Marine Environment and Health Series*, (No. 17).
- Whittick, A., 1983. Spatial and temporal distributions of dominant epiphytes on the stipes of *Laminaria hyperborea* (Gunn.) Fosl. (Phaeophyta: Laminariales) in S.E. Scotland. *Journal of Experimental Marine Biology and Ecology*, **73**, 1-10.
- WHO (World Health Organization), 1989. Mercury - Environmental Aspects. *Environmental Health Criteria No. 86*. Geneva: World Health Organization., Geneva: World Health Organization.
- WHO (World Health Organization), 1991. Mercury - inorganic - Environmental Aspects. *Environmental Health Criteria No. 118*. Geneva: World Health Organization., Geneva: World Health Organization.
- Widdows, J., Livingstone, D.R., Lowe, D., Moore, M.N., Moore, S., Pipe, R. & Salkeld, P.N., 1981. Biological effects monitoring in the region of Sullom Voe, Shetland, September 1981. *Shetland Oil Terminal Environmental Advisory Group (SOTEAG), University of Aberdeen, 1982*.
- Williams, G.A. & Seed, R., 1992. Interactions between macrofaunal epiphytes and their host algae. In *Plant-animal interactions in the marine benthos* (ed. D.M John, S.J. Hawkins & J.H. Price), pp. 189-211. Oxford: Clarendon Press. [Systematics Association Special Volume, no. 46.]
- Wolfe, J.M. & Harlin, M.M., 1988a. Tidepools in Southern Rhode Island, U.S.A. I. Distribution and seasonality of algae. *Botanica Marina*, **31**, 525-536.
- Wolfe, J.M. & Harlin, M.M., 1988b. Tidepools in Southern Rhode Island, U.S.A. II. Species diversity and similarity analysis of macroalgal communities. *Botanica Marina*, **31**, 537-546.
- Workman, C., 1983. Comparisons of energy partitioning in contrasting age-structured populations of the limpet *Patella vulgata* L. *Journal of Experimental Marine Biology and Ecology*, **68**, 81-103.
- Wotton, D.M., O'Brien, C., Stuart, M.D. & Fergus, D.J., 2004. Eradication success down under: heat treatment of a sunken trawler to kill the invasive seaweed *Undaria pinnatifida*. *Marine Pollution Bulletin*, **49** (9), 844-849.
- Yarish, C., Penniman, C.A. & Egan, B., 1990. Growth and reproductive responses of *Laminaria longicuris* (Laminariales, Phaeophyta) to nutrient enrichment. *Hydrobiologia*, **204**, 505-511.