



# MarLIN

## Marine Information Network

Information on the species and habitats around the coasts and sea of the British Isles

## Carrageen (*Chondrus crispus*)

MarLIN – Marine Life Information Network  
Biology and Sensitivity Key Information Review

Will Rayment & Paolo Pizzola

2008-05-22

A report from:

The Marine Life Information Network, Marine Biological Association of the United Kingdom.

**Please note.** This MarESA report is a dated version of the online review. Please refer to the website for the most up-to-date version [<https://www.marlin.ac.uk/species/detail/1444>]. All terms and the MarESA methodology are outlined on the website (<https://www.marlin.ac.uk>)

This review can be cited as:

Rayment, W.J. & Pizzola, P.F. 2008. *Chondrus crispus* Carrageen. In Tyler-Walters H. and Hiscock K. (eds) *Marine Life Information Network: Biology and Sensitivity Key Information Reviews*, [on-line]. Plymouth: Marine Biological Association of the United Kingdom.  
DOI <https://dx.doi.org/10.17031/marlin.sp.1444.1>



The information (TEXT ONLY) provided by the Marine Life Information Network (MarLIN) is licensed under a Creative Commons Attribution-Non-Commercial-Share Alike 2.0 UK: England & Wales License. Note that images and other media featured on this page are each governed by their own terms and conditions and they may or may not be available for reuse. Permissions beyond the scope of this license are available [here](#). Based on a work at [www.marlin.ac.uk](http://www.marlin.ac.uk)

(page left blank)



The seaweed *Chondrus crispus*.  
 Photographer: Nova Mieszkowska  
 Copyright: MarClim

See online review for  
 distribution map

Distribution data supplied by the Ocean  
 Biogeographic Information System (OBIS). To  
 interrogate UK data visit the NBN Atlas.

<b>Researched by</b>	Will Rayment & Paolo Pizzola	<b>Refereed by</b>	Dr Stefan Kraan
<b>Authority</b>	Stackhouse, 1797		
<b>Other common names</b>	-	<b>Synonyms</b>	-

## Summary

### 🔍 Description

*Chondrus crispus* is a small purplish-red seaweed (up to 22 cm long) found on rocky shores and in pools. The fronds grow dichotomously from a narrow, unbranched stipe and are flat and wide with rounded tips. This seaweed is highly variable in appearance depending on the level of wave exposure of the shore and has a tendency to turn green in strong sunlight. Underwater, the tips of the frond can be iridescent.

### 📍 Recorded distribution in Britain and Ireland

Widely distributed on rocky shores on all British and Irish coasts.

### 📍 Global distribution

See additional information.

### 🏠 Habitat

Abundant on rocks on the middle to lower rocky shore and in tide pools. It occurs sublittorally to 24 m. It can tolerate some reduction in salinity and can be found in estuaries.

## ↓ Depth range

mid eulittoral, exceptionally to 24 m

## 🔍 Identifying features

- Thallus with discoid holdfast and erect fronds arising in tufts.
- Un-branched stipe gradually expanding into fan-like blade.
- Fronds repeatedly dichotomous (up to 5 times) with rounded axils, usually expanding but occasionally tapering towards rounded apices.
- Female fruiting bodies (carposporangia) occur terminally in cystocarps that protrude strongly as concave-convex swellings 2 mm in diameter.
- Form highly variable depending on environment.

## 🏛️ Additional information

Also known as Irish moss. Together with *Mastocarpus stellatus*, *Chondrus crispus* is harvested commercially as carrageen to be used in the pharmaceutical and food industries. May be confused with *Mastocarpus stellatus*, although the latter species has a rounded stipe, channeled fronds and papillate reproductive bodies.

## ✓ Listed by

## 🔗 Further information sources

Search on:

   

## Biology review

### ☰ Taxonomy

Phylum	Rhodophyta	Red seaweeds
Class	Florideophyceae	
Order	Gigartinales	
Family	Gigartinaceae	
Genus	Chondrus	
Authority	Stackhouse, 1797	
Recent Synonyms	-	

### 🌿 Biology

Typical abundance	High density
Male size range	up to 22cm
Male size at maturity	12cm
Female size range	12cm
Female size at maturity	
Growth form	Turf
Growth rate	0.33mm/day
Body flexibility	High (greater than 45 degrees)
Mobility	
Characteristic feeding method	Autotroph
Diet/food source	
Typically feeds on	Not relevant
Sociability	
Environmental position	Epilithic
Dependency	Independent.
Supports	Substratum algal and faunal epiphytes (see additional information). No
Is the species harmful?	<i>Chondrus crispus</i> is commercially harvested for the extraction of the phycocolloid, carrageenan.

### 🏛️ Biology information

#### Size at maturity

Surprisingly little information was found concerning size at maturity. Pybus (1977) estimated that *Chondrus crispus* from Galway Bay, Ireland, reached maturity approximately 2 years after the initiation of the basal disc, at which stage, the fronds were approximately 12 cm in length.

#### Growth

Growth rates of *Chondrus crispus* vary widely according to environmental conditions. Pybus (1977) reported mean growth for *Chondrus crispus* from Galway Bay of 0.33 mm/day, with little seasonal variation in growth rate. A similar rate of 0.37 mm/day was reported for plants from Maine, USA

(Prince & Kingsbury, 1973). Sporelings grew at 0.02-0.08 mm/day in culture, and growth rate was governed principally by temperature (Tasende & Fraga, 1999). Peak growth occurred from May to November in eastern Canada (Juanes & McLachlan, 1992; Chopin *et al.*, 1999). Optimum growth of *Chondrus crispus* in culture occurred at 10-15°C (Fortes & Lüning, 1980), 15-17°C (Tasende & Fraga, 1999) and 20°C (Simpson & Shacklock, 1979). Kuebler & Dudgeon (1996) reported higher growth rates at 20°C vs. 5°C, in terms of length, biomass, surface area, dichotomy and branch production, for *Chondrus crispus* from the Gulf of Maine, USA. North Sea plants grown in culture were growth saturated at light intensities of 70  $\mu\text{E}/\text{m}^2/\text{s}$  and growth rate increased up to a 24 hour photoperiod (Fortes & Lüning, 1980). For cultured spores of *Chondrus crispus* from NW Spain, growth rate increased with salinity between 23 and 33 psu, declined above light intensities of 20  $\mu\text{mol}/\text{m}^2/\text{s}$  and below photoperiods of 16:8 (light: dark) (Tasende & Fraga, 1999).

### Supports which species

*Chondrus crispus* from Galway Bay, Ireland, was a host for algal epiphytes including *Ceramium nodulosum*, *Melobesia membranaceum*, *Lomentaria articulata*, *Membranoptera alata*, *Palmaria palmata*, and faunal epiphytes including *Alcyonidium hirsutum*, *Dynamena pumila*, *Electra pilosa*, *Grantia compressa*, *Patella pellucida* and *Spirorbis spirorbis* (as *Spirorbis borealis*) (Pybus, 1977). *Leathesia difformis* grew epiphytically on *Chondrus crispus* in Nova Scotia, Canada (Chapman & Goudey, 1983). In substratum choice experiments in the laboratory in New Hampshire, USA, the bryozoan *Alcyonidium polyoum* preferentially settled on *Chondrus crispus* and *Fucus distichus*, rather than other algae (Hurlbut, 1991). The epiphytes, *Ulva* sp. (studied as *Enteromorpha*) and *Ectocarpus* sp. grew epiphytically on *Chondrus crispus* in culture, and were in turn grazed by the crustaceans *Gammarus lawrencianus* and *Idotea baltica* (Shacklock & Doyle, 1983). *Idotea baltica* readily consumed *Chondrus crispus* when no other food was available, whereas *Gammarus lawrencianus* did not.

*Chondrus crispus* can sometimes be epiphytic on kelps (S. Kraan, pers. comm.).



### Habitat preferences

Physiographic preferences	Open coast, Strait / sound, Estuary, Enclosed coast / Embayment
Biological zone preferences	Lower eulittoral, Lower infralittoral, Mid eulittoral, Sublittoral fringe, Upper circalittoral, Upper infralittoral
Substratum / habitat preferences	Bedrock, Large to very large boulders, Rockpools, Small boulders
Tidal strength preferences	Moderately Strong 1 to 3 knots (0.5-1.5 m/sec.), Strong 3 to 6 knots (1.5-3 m/sec.), Very Weak (negligible), Weak < 1 knot (<0.5 m/sec.)
Wave exposure preferences	Exposed, Moderately exposed, Sheltered
Salinity preferences	Full (30-40 psu), Variable (18-40 psu)
Depth range	mid eulittoral, exceptionally to 24 m
Other preferences	No text entered
Migration Pattern	Non-migratory / resident

### Habitat Information

In Galway Bay, Ireland, *Chondrus crispus* occurs in relatively stable conditions. The annual variation in sea surface temperature was 10-16°C and in salinity was 32-35 psu (Pybus, 1977). However, the

species is capable of existing in much more variable environments. In New Hampshire, USA, *Chondrus crispus* formed its most extensive populations on the open coast on massive outcrops and boulders in the shallow subtidal (3 to 5 metres deep) (Mathieson & Burns, 1975). The annual variation in sea surface temperatures was -1 to 19°C. The species also occurred in an estuarine tidal rapid experiencing currents up to 5.5 knots and salinity fluctuations from 16-32 psu (Mathieson & Burns, 1975).

### Global distribution

Occurs in Iceland, the Faroes, the western Baltic Sea, from northern Russia to southern Spain, the Mediterranean, Portugal, the Azores and West Africa. In north America it occurs in Alaska and from Labrador in Canada to New Jersey in the USA. Also occurs in the Bering Sea (East Asia).

## Life history

### Adult characteristics

<b>Reproductive type</b>	Alternation of generations
<b>Reproductive frequency</b>	Annual protracted
<b>Fecundity (number of eggs)</b>	See additional information
<b>Generation time</b>	2-3 years
<b>Age at maturity</b>	2 years
<b>Season</b>	See additional information
<b>Life span</b>	See additional information

### Larval characteristics

<b>Larval/propagule type</b>	-
<b>Larval/juvenile development</b>	Spores (sexual / asexual)
<b>Duration of larval stage</b>	Not relevant
<b>Larval dispersal potential</b>	No information
<b>Larval settlement period</b>	

## Life history information

### Lifespan

The fronds of *Chondrus crispus* typically have a life of 2-3 years (Taylor, cited in Pringle & Mathieson, 1986) but may live up to 6 years in sheltered waters (Harvey & McLachlan, 1973). The holdfast is much longer lived (Taylor, cited in Pringle & Mathieson, 1986) and is capable of regenerating new fronds after disturbance (Mathieson & Burns, 1975; Dudgeon & Johnson, 1992).

### Fecundity

Fernandez & Menendez (1991) reported that reproductive capacity was similar for both gametophytes and tetrasporophytes in northern Spain, the estimated number of spores being  $8 \times 10^{10}/m^2/year$ . The greater number of fertile gametophytes was counterbalanced by the high numbers of tetrasporangial sori and tetraspores.

### Timing of reproduction

Dickinson (1963) reported that *Chondrus crispus* was fertile in the UK from autumn to spring, but that the exact timings varied according to local environment. Similarly, Pybus (1977) reported that

although carposporic plants were present throughout the year in Galway Bay, Ireland, maximum reproduction occurred in the winter and estimated that settling of spores occurred between January and May. In northern Spain, *Chondrus crispus* had reproductive capacity all year round but was greatest for gametophytes between November and March and for tetrasporophytes in April (Fernandez & Menendez, 1991). In Nova Scotia, Canada, cystocarps and tetrasporangia have been recorded on *Chondrus crispus* all year round with a reproductive peak from August to October (Scrosati *et al.*, 1994). However, spores failed to germinate below 5°C and so winter temperatures in Nova Scotia are unsuitable for spore germination. It was suggested therefore that simple counts of spore production do not adequately model reproductive potential (Scrosati *et al.*, 1994). Scrosati *et al.* (1994) also commented that viability of spores was low (<30%) and suggested that reproduction by spores probably does not contribute much to maintenance of the intertidal population of *Chondrus crispus* in Nova Scotia, compared to vegetative growth of gametophytes.



## Sensitivity review

This MarLIN sensitivity assessment has been superseded by the MarESA approach to sensitivity assessment. MarLIN assessments used an approach that has now been modified to reflect the most recent conservation imperatives and terminology and are due to be updated by 2016/17.

### A Physical Pressures

	Intolerance	Recoverability	Sensitivity	Confidence
<b>Substratum Loss</b>	High	High	Moderate	High
<p><i>Chondrus crispus</i> lives permanently attached to the substratum (Dixon &amp; Irvine, 1977) and therefore the entire population would be removed if the substratum were to be lost. Intolerance is therefore recorded as high. Recovery of <i>Chondrus crispus</i> was monitored after a rocky shore was totally denuded by ice scour in Nova Scotia, Canada (Minchinton <i>et al.</i>, 1997). Recovery to original biomass was achieved in 5 years (see additional information below). Recoverability is therefore recorded as high.</p>				
<b>Smothering</b>	Intermediate	High	Low	Low
<p><i>Chondrus crispus</i> is an erect species which grows up to 24 cm in height (Dixon &amp; Irvine, 1977) and therefore mature plants are unlikely to be affected by smothering with 5 cm of sediment. However, recently settled propagules, regenerating holdfasts and small developing plants would be buried by 5 cm of sediment and be unable to photosynthesize. For example, Vadas <i>et al.</i> (1992) stated that algal spores and propagules are adversely affected by a layer of sediment, which can exclude up to 98% of light. Intolerance has been assessed as intermediate to reflect some mortality. As some portion of the population is likely to remain for vegetative regrowth, recovery is likely to occur within 18 months (see additional information below) and recoverability is therefore assessed as high.</p>				
<b>Increase in suspended sediment</b>	Intermediate	High	Low	Low
<p><i>Chondrus crispus</i> is not likely to be affected directly by an increase in suspended sediment. However, increased suspended sediment will have knock on effects in terms of light attenuation (considered in 'turbidity') and siltation. As discussed above in 'smothering', increased rate of siltation may inhibit development of algal spores and propagules resulting in some mortality. Intolerance is therefore assessed as intermediate. As some portion of the population is likely to remain for vegetative regrowth, recovery is likely to occur within 18 months (see additional information below) and recoverability is therefore assessed as high.</p>				
<b>Decrease in suspended sediment</b>	Tolerant	Not relevant	Not sensitive	Low
<p><i>Chondrus crispus</i> is not likely to be affected directly by a decrease in suspended sediment and the consequent decrease in siltation. The effects of changes in light attenuation are discussed below in 'turbidity'.</p>				
<b>Desiccation</b>	Intermediate	High	Low	Moderate
<p><i>Chondrus crispus</i> is most abundant in the shallow subtidal and in rockpools in the intertidal (Mathieson &amp; Burns, 1971; Holt <i>et al.</i>, 1995). A study by Lubchenco (1980) on the coast of New England suggested that the upper limit of <i>Chondrus crispus</i> distribution is determined by desiccation. The species was found to extend into the mid-intertidal where it was found underneath a furoid canopy. Removal of this canopy lead to bleached, dried out and dead plants within two to three weeks (Lubchenco, 1980). Mathieson &amp; Burns (1971) measured the</p>				

photosynthetic rate of *Chondrus crispus* at varying degrees of desiccation and concluded that apparent photosynthesis always decreases with dehydration. For example, after loss of 65% of its water content, rate of photosynthesis in *Chondrus crispus* was 55% of the control rate. In comparison, photosynthetic rate of *Mastocarpus stellatus*, a closely related species which is typically found further up the shore, was at 95% of its control rate at the same level of dehydration. *Chondrus crispus* recovered from 65% water loss but could not tolerate 88% (Mathieson & Burns, 1971). Dudgeon *et al.* (1995) recorded that temperature affects the rate of desiccation in *Chondrus crispus*. 60% water loss occurred after 1.9 hours of emersion at 20°C, photosynthetic rate was reduced by 2/3 on reimmersion and took 24 hours to recover. The same level of water loss occurred after only 1.2 hours at 30°C, there was no net photosynthesis on reimmersion and after 24 hours photosynthesis was only at 59% of control levels. Desiccation also increased respiration rate (Dudgeon *et al.*, 1995).

The benchmark level of desiccation is a shift of one biological zone up the shore. Although the resultant increase in desiccation is unlikely to cause mortality directly, photosynthetic rate would be reduced, compromising growth and reproduction. *Chondrus crispus* would be likely to be out-competed by higher shore species such as *Mastocarpus stellatus*, and some mortality would eventually result. Intolerance is therefore assessed as intermediate. As some portion of the population is likely to remain for vegetative regrowth, recovery is likely to occur within 18 months (see additional information below) and recoverability is therefore assessed as high.

**Increase in emergence regime**      Intermediate      High      Low      Moderate

A study by Lubchenco (1980) on the coast of New England suggested that the upper limit of *Chondrus crispus* distribution is determined by desiccation. The species was found to extend into the mid-intertidal where it was found underneath a fucoid canopy. Removal of this canopy lead to bleached, dried out and dead plants within two to three weeks (Lubchenco, 1980). An increase in emergence regime would increase the likelihood of desiccation and the effects are discussed in 'desiccation' above. An increase in emergence will also increase the exposure of *Chondrus crispus* to solar radiation. *Chondrus crispus* is growth saturated at light levels of 60-70  $\mu\text{E}/\text{m}^2/\text{s}$  and is not photoinhibited at 250  $\mu\text{E}/\text{m}^2/\text{s}$  (Bird *et al.*, 1979; Fortes & Lüning, 1980). However, Bischoff *et al.* (2000) reported that the photochemistry of *Chondrus crispus* is negatively affected by UV-B radiation, while Aguirre-von-Wobeser *et al.* (2000) concluded that photosynthetically active radiation (PAR) is responsible for most of the photoinhibition in the species. Bischoff *et al.* (2000) suggested that intolerance to UV-B may be a factor restricting *Chondrus crispus* to the subtidal and lower intertidal, whereas *Mastocarpus stellatus*, which is better adapted to UV radiation, competes better in the upper intertidal. An increase in emergence regime would result in desiccation and radiation stress and some mortality is likely. Intolerance is therefore assessed as intermediate. As some portion of the population is likely to remain for vegetative regrowth, recovery is likely to occur within 18 months (see additional information below) and recoverability is therefore assessed as high.

**Decrease in emergence regime**      Tolerant      Not relevant      Not sensitive      High

*Chondrus crispus* is most abundant in the shallow subtidal (Mathieson & Burns, 1971; Holt *et al.*, 1995) and is therefore unlikely to be affected by a decrease in emergence regime.

**Increase in water flow rate**      Intermediate      High      Low      Low

*Chondrus crispus* typically occurs in areas of 'moderately strong' or 'strong' water flow. In New Hampshire, USA, for example, the species is found in estuarine tidal rapids where currents reach 5.5 knots (Mathieson & Burns, 1975). Moderate water movement is beneficial to seaweeds as it carries a supply of nutrients and gases to the plants, removes waste products, and prevents settling of silt. However, if flow becomes too strong, plants may be damaged and

growth stunted. Additionally, an increase to 'very strong' flows may inhibit settlement of spores and may remove adults or germlings. It is expected that some mortality would result from an increase in water flow, so intolerance is assessed as intermediate. As some portion of the population is likely to remain for vegetative regrowth, recovery is likely to occur within 18 months (see additional information below) and recoverability is therefore assessed as high.

**Decrease in water flow rate**                      **Intermediate**    **High**                      **Low**                      **Low**

*Chondrus crispus* typically occurs in areas of 'moderately strong' or 'strong' water flow. The benchmark decrease in water flow would place the species in areas of 'very weak' water flow. Seaweeds in still water rapidly deplete the nutrients in the immediate vicinity (Kain & Norton, 1990) and are likely to be more vulnerable to depletion of essential dissolved gases and accumulation of waste products. Furthermore, decreased water flow would result in deposition of fine sediments and possible smothering of low growing forms, such as developing sporelings. Some mortality is likely to result and so intolerance is assessed as intermediate. As some portion of the population is likely to remain for vegetative regrowth, recovery is likely to occur within 18 months (see additional information below) and recoverability is therefore assessed as high.

**Increase in temperature**                      **Low**                      **Very high**                      **Very Low**                      **High**

*Chondrus crispus* has a wide geographical range, occurring in Europe from northern Russia to southern Spain (Dixon & Irvine, 1977). In New Hampshire, USA, *Chondrus crispus* grows abundantly in waters with an annual variation in surface temperature from -1 to +19°C (Mathieson & Burns, 1975). The species is therefore unlikely to be particularly intolerant of temperature changes in British and Irish waters (Holt *et al.*, 1995). A wealth of research has been published concerning the effects of varying temperature on growth of *Chondrus crispus*. The optimum temperature for growth has been reported as 10-15°C (Fortes & Lüning, 1980), 15°C (Bird *et al.*, 1979), 15-17°C (Tasende & Fraga, 1999) and 20°C (Simpson & Shacklock, 1979). Above the optimum temperature, growth rate is reported to decline (Bird *et al.*, 1979; Simpson & Shacklock, 1979). Compared to *Chondrus crispus* plants grown at 5°C, plants grown at 20°C had higher growth rates in terms of length, biomass, surface area, dichotomy and branch production. The differences resulted in growth of morphologically more complex thalli at higher temperatures with more efficient nutrient exchange and light harvesting (Kuebler & Dudgeon, 1996). *Chondrus crispus* plants acclimated to growth at 20°C (vs. 5°C) had higher levels of chlorophyll a and phycobilins, resulting in higher rates of light limited photosynthesis for a given photon flux density (Kuebler & Davison, 1995). Plants grown at 20°C were able to maintain constant rates of light saturated photosynthesis at 30°C for 9 hours. In contrast, in plants acclimated to 5°C, light saturated photosynthetic rates declined rapidly following exposure to 30°C (Kuebler & Davison, 1993). Prince & Kingsbury (1973) reported cessation of growth in *Chondrus crispus* cultures at 26°C, first mortality of spores at 21.1°C and total mortality of spores at 35-40°C, even if exposed for just 1 minute.

Considering that maximum sea surface temperatures around the British Isles rarely exceed 20°C (Hiscock, 1998), it is unlikely that *Chondrus crispus* would suffer mortality due to the benchmark increase in temperature. However, elevated temperatures would probably result in sub-optimal growth and hence intolerance is recorded as low. Growth should quickly return to normal when temperatures return to their original levels so recoverability is assessed as very high.

**Decrease in temperature**                      **Low**                      **Very high**                      **Very Low**                      **High**

*Chondrus crispus* has a wide geographical range, occurring in Europe from northern Russia to southern Spain (Dixon & Irvine, 1977). In New Hampshire, USA, *Chondrus crispus* grows

abundantly in waters with an annual variation in surface temperature from -1 to +19°C (Mathieson & Burns, 1975). The species is therefore unlikely to be particularly intolerant of temperature changes in British and Irish waters (Holt *et al.*, 1995). Dudgeon *et al.* (1990) investigated the effects of freezing on *Chondrus crispus*. Plants from Maine, USA, were frozen at -5°C for 3 hours a day for 30 days. Photosynthesis was reduced to 55% of control values, growth rates were reduced and fronds were eventually bleached and fragmented resulting in biomass losses. Additionally, fronds of *Chondrus crispus* which were frozen daily had higher photosynthetic rates following subsequent freezing events than unfrozen controls, indicating that the species is able to acclimate to freezing conditions (Dudgeon *et al.*, 1990). Pearson & Davison (1993) recorded that *Chondrus crispus* froze at -7.59°C when cooled slowly from 5°C and froze at -3.70°C when cooled rapidly. The authors suggested that photosynthetic inhibition in *Chondrus crispus* is probably due to cellular dehydration rather than low temperature.

Considering that surface water temperatures in Britain and Ireland rarely fall below 5°C (Hiscock, 1998), it is unlikely that *Chondrus crispus* would suffer mortality due to the benchmark decrease in temperature. However, reduced temperatures would probably result in suboptimal growth and hence intolerance is recorded as low. Growth should quickly return to normal when temperatures return to their original levels so recoverability is assessed as very high.

#### Increase in turbidity

Low

Very high

Very Low

Low

*Chondrus crispus* is growth saturated at light levels of 60-70  $\mu\text{E}/\text{m}^2/\text{s}$  and is not photoinhibited at 250  $\mu\text{E}/\text{m}^2/\text{s}$  (Bird *et al.*, 1979; Fortes & Lüning, 1980). Most algal species have higher saturation levels than *Chondrus crispus*, e.g. *Fucus serratus*, 100  $\mu\text{E}/\text{m}^2/\text{s}$  (Bird *et al.*, 1979). Similarly, *Chondrus crispus* was found to have the lowest light compensation point among a group of algae tested (Markager & Sand-Jensen, 1992). These findings suggest that *Chondrus crispus* is well adapted to living in low light conditions and is unlikely to be affected dramatically by an increase in turbidity. However, some red algal species have even lower light saturation levels (e.g. *Polyides rotundus* and *Furcellaria lumbricalis*) (Bird *et al.*, 1979). Therefore, if these species all share the same habitat in extremely sheltered conditions, the species that can survive lower light conditions are likely to proliferate at the expense of *Chondrus crispus*. Intolerance is therefore assessed as low. Growth and competitive ability are likely to return to normal soon after original turbidity is restored so recoverability is assessed as very high.

#### Decrease in turbidity

Tolerant\*

Not relevant

Not sensitive\*

Low

*Chondrus crispus* is growth saturated at light levels of 60-70  $\mu\text{E}/\text{m}^2/\text{s}$  and is not photoinhibited at 250  $\mu\text{E}/\text{m}^2/\text{s}$  (Bird *et al.*, 1979; Fortes & Lüning, 1980). Tasende & Fraga (1999), however, noted inhibition of growth above 20  $\mu\text{mol photons}/\text{m}^2/\text{s}$ . *Chondrus crispus* is, therefore, apparently tolerant of levels of irradiance above its optimum and would therefore be not sensitive to decreases in turbidity. Markager & Sand-Jensen (1992) suggested that there was no surplus of energy for macroalgae growing at their depth limits to balance grazing and mechanical losses. It is possible that a decrease in turbidity would allow *Chondrus crispus* to proliferate at greater depths and possibly expand its range.

#### Increase in wave exposure

Intermediate

High

Low

High

*Chondrus crispus* typically occurs in 'sheltered' and 'moderately exposed areas' (Dixon & Irvine, 1977). The benchmark increase in wave exposure would place the species in 'exposed' or 'very exposed' areas. Strong wave action is likely to cause some damage to fronds resulting in reduced photosynthesis and compromised growth. Furthermore, individuals may be damaged or dislodged by scouring from sand and gravel mobilized by increased wave action (Hiscock,

1983). Indeed, Dudgeon & Johnson (1992) noted wave induced disturbance of intertidal *Chondrus crispus* on shores of the Gulf of Maine during winter. 25-30% of cover of large *Chondrus crispus* thalli was lost in one winter. They also noted that *Chondrus crispus* suffered more heavily than *Mastocarpus stellatus* probably because the drag on the thallus was greater. Increased wave action is therefore likely to result in some mortality and so intolerance is assessed as intermediate. As some portion of the population is likely to remain for vegetative regrowth, recovery is likely to occur within 18 months (see additional information below) and recoverability is therefore assessed as high. Gutierrez & Fernandez (1992) described morphological variability of *Chondrus crispus* according to wave exposure and emersion. They identified 2 well defined morphotypes; filiform and planiform. The filiform morphotype had fewer dichotomies per unit length, a circular cross section, narrow fronds and was abundant in the low intertidal and at more exposed sites. The planiform morphotype had more dichotomies, was smaller, with a flattened cross section, broader fronds and was abundant higher up the shore and in more sheltered areas. An increase in wave exposure is likely to precipitate a shift towards a community of the filiform morphotype.

#### Decrease in wave exposure

Low

Very high

Very Low

Low

A decrease in wave exposure is unlikely to affect *Chondrus crispus* directly. The consequent effects of decreased wave action are likely to include increased deposition of fine material and increased risk of stagnation. Species more tolerant of these factors, e.g. *Polyides rotundus* and *Furcellaria lumbricalis*, are more likely to proliferate in these conditions, eventually at the expense of *Chondrus crispus*. However, over the course of a year, no mortality of *Chondrus crispus* is expected so intolerance is assessed as low. Growth and reproduction should quickly return to normal when wave exposure returns to typical levels so recoverability is assessed as very high. Gutierrez & Fernandez (1992) described morphological variability of *Chondrus crispus* according to wave exposure and emersion. They identified 2 well defined morphotypes; filiform and planiform. The filiform morphotype had fewer dichotomies per unit length, a circular cross section, narrow fronds and was abundant in the low intertidal and at more exposed sites. The planiform morphotype had more dichotomies, was smaller, with a flattened cross section, broader fronds and was abundant higher up the shore and in more sheltered areas. A decrease in wave exposure is likely to precipitate a shift towards a community of the planiform morphotype.

#### Noise

Tolerant

Not relevant

Not sensitive

High

Algae have no mechanisms for detection of sound and therefore would not be sensitive to disturbance by noise.

#### Visual Presence

Tolerant

Not relevant

Not sensitive

High

Algae have no visual acuity and therefore would not be affected by visual disturbance.

#### Abrasion & physical disturbance

Low

Very high

Very Low

Low

The erect thallus of *Chondrus crispus* is flexible (Dixon & Irvine, 1977) and would be expected to be relatively resistant to physical abrasion. Indeed, Worm & Chapman (1998) suggested that *Chondrus crispus* was highly resistant to intense physical and herbivore induced disturbance, ensuring competitive dominance on the lower shore. The benchmark level of abrasion, a scallop dredge but more likely lower shore sediment scour or ship grounding, would be expected to remove or damage some fronds, although the holdfasts are likely to escape unscathed. *Chondrus crispus* is capable of regenerating from its holdfasts (e.g. Dudgeon & Johnson, 1992) and so no mortality is expected. Growth and reproduction would be compromised however, so intolerance is assessed as low. Fronds may take up to 18 months to regrow (see additional information below), so recoverability is assessed as very high.

**Displacement****High****High****Moderate****Very low**

No information was found concerning displacement of *Chondrus crispus*. It seems unlikely that the holdfast could remain *in situ* for long enough on a rocky shore to reestablish a bond with the substratum. Intolerance is therefore assessed as high, though the decision is made with very low confidence. In the absence of holdfasts for regeneration, recovery is likely to take up to 5 years (see additional information below) so recoverability is recorded as high.

**⚗ Chemical Pressures**

Intolerance

Recoverability

Sensitivity

Confidence

**Synthetic compound contamination****High****High****Moderate****Low**

No evidence was found specifically relating to the intolerance of *Chondrus crispus* to synthetic chemicals. However, inferences may be drawn from the sensitivities of red algal species generally. O'Brien & Dixon (1976) suggested that red algae were the most sensitive group of algae to oil or dispersant contamination, possibly due to the susceptibility of phycoerythrins to destruction. They also report that red algae are effective indicators of detergent damage since they undergo colour changes when exposed to relatively low concentration of detergent. Smith (1968) reported that 10 ppm of the detergent BP 1002 killed the majority of specimens in 24hrs in toxicity tests, although *Chondrus crispus* was amongst the algal species least affected by the detergent used to clean up the *Torrey Canyon* oil spill. Laboratory studies of the effects of oil and dispersants on several red algal species concluded that they were all sensitive to oil/dispersant mixtures, with little difference between adults, sporelings, diploid or haploid life stages (Grandy, 1984, cited in Holt *et al.*, 1995). Cole *et al.* (1999) suggested that herbicides, such as simazine and atrazine, were very toxic to macrophytes. The evidence suggests that in general red algae are very sensitive to synthetic chemicals. Intolerance of *Chondrus crispus* is therefore recorded as high. Recoverability is recorded as high (see additional information below) although it may take up to 5 years as recovery will be largely dependent on recruitment of spores from distant unperturbed populations.

**Heavy metal contamination****Not relevant**

Little information was found concerning the intolerance of *Chondrus crispus* to heavy metals. Burdin & Bird (1994) reported that both gametophyte and tetrasporophyte forms 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. 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 an intertidal red algae, *Plumaria elegans*, were reported by Boney (1971). 100% growth inhibition was caused by 1 ppm Hg. In light of the lack of information found, an intolerance assessment has not been attempted.

**Hydrocarbon contamination****Low****Very high****Very Low****Moderate**

The long term effects on *Chondrus crispus* of continuous doses of the water accommodated fraction (WAF) of diesel oil were determined in experimental mesocosms (Bokn *et al.*, 1993). Mean hydrocarbon concentrations tested were 30.1 µg/l and 129.4 µg/l. After 2 years, there were no demonstrable differences in the abundance patterns of *Chondrus crispus*. Kaas (1980) (cited in Holt *et al.*, 1995) reported that the reproduction of adult *Chondrus crispus* plants on the French coast was normal following the *Amoco Cadiz* oil spill. However, it was suggested that the development of young stages to adult plants was slow, with biomass still reduced 2 years after the event. O'Brien & Dixon (1976) and Grandy (1984) (cited in Holt *et al.*, 1995)

comment on the high intolerance of red algae to oil/dispersant mixtures, but it is unclear which factor is responsible for the intolerance. In light of the studies by Kaas (1980) and Bokn *et al.* (1993), intolerance is assessed as low. Resumption of original growth rates is likely to be rapid when the hydrocarbons have dispersed so recoverability is assessed as very high, but will be dependent on persistence of the pollutants.

### Radionuclide contamination

Not relevant

A study in France found that *Chondrus crispus* was capable of absorbing a large number of artificial radioactive elements and that this had consequences considering the exploitation of this species as a harvestable resource (Cosson *et al.*, 1984). However, no information was found concerning the actual effects of radionuclide on *Chondrus crispus* and therefore insufficient information has been suggested.

### Changes in nutrient levels

Intermediate

High

Low

Low

In studies of *Chondrus crispus* from Prince Edward Island, Canada, Juanes & McLachlan (1992) concluded that primary production was limited by temperature during the autumn to spring period and by nitrogen availability when production was maximal in the summer. They suggested that growth of *Chondrus crispus* became nutrient limited at approximately 14°C. To a certain degree, therefore, an increase in the level of nutrients would be likely to enhance growth of *Chondrus crispus*. However, if nutrient enrichment is extended or prolonged, *Chondrus crispus* may be out-competed by faster growing or ephemeral species. Johansson *et al.* (1998) investigated the changes in the algal vegetation of the Swedish Skagerrak coast, an area heavily affected by eutrophication, between 1960 and 1997. Slow growing species, including *Chondrus crispus* declined in abundance, probably due to competition from faster growing red algal species such as *Phycodrys rubens* and *Delesseria sanguinea*. The study suggests that, although *Chondrus crispus* may be tolerant of eutrophication *per se* and may even benefit from it, populations may suffer as result of the reactions of other algal species. Intolerance is therefore assessed as intermediate. As some portion of the population is likely to remain for vegetative regrowth, recovery is likely to occur within 18 months (see additional information below) and recoverability is therefore assessed as high.

### Increase in salinity

Tolerant

Not relevant

Not sensitive

High

*Chondrus crispus* occurs in areas of 'full' salinity (e.g. Mathieson & Burns, 1975) and so increase in salinity is not likely to be a relevant factor. Mathieson & Burns (1971) recorded maximum photosynthesis of *Chondrus crispus* in culture at 24 psu, but rates were comparable at 8, 16 and 32 psu. Photosynthesis continued up to 60 psu. Bird *et al.* (1979) recorded growth of Canadian *Chondrus crispus* in culture between 10 and 50 psu, with a maximum at 30 psu. The species would therefore appear to be extremely tolerant of hypersaline conditions.

### Decrease in salinity

Low

Very high

Very Low

High

*Chondrus crispus* does occur in areas of 'low' salinity. For example, the species occurs in estuaries in New Hampshire, USA, where surface water salinity varies from 16-32 psu (Mathieson & Burns, 1975). Mathieson & Burns (1971) recorded maximum photosynthesis of *Chondrus crispus* in culture at 24 psu, but rates were comparable at 8, 16 and 32 psu. Tasende & Fraga (1999) cultured *Chondrus crispus* spores from north west Spain and concluded that growth was correlated with salinity between 23 and 33 psu. A reduction in salinity, therefore, is unlikely to result in mortality of *Chondrus crispus* but may suppress growth and so intolerance is assessed as low. Growth is likely to return to normal quickly when salinity increases to original levels, so recoverability is recorded as very high.

### Changes in oxygenation

Not relevant

The effects of reduced oxygenation on algae are not well studied. Plants require oxygen for respiration, but this may be provided by production of oxygen during periods of photosynthesis. Lack of oxygen may impair both respiration and photosynthesis (see review by Vidaver, 1972). A study of the effects of anoxia on another red alga, *Delesseria sanguinea*, revealed that specimens died after 24 hours at 15°C but that some survived at 5°C (Hammer, 1972). Insufficient information is available to make an intolerance assessment for *Chondrus crispus*.

## Biological Pressures

	Intolerance	Recoverability	Sensitivity	Confidence
<b>Introduction of microbial pathogens/parasites</b>	Intermediate	High	Low	Moderate

Craigie & Correa (1996) described 'green spot' disease in *Chondrus crispus*, caused by the interaction of several biotic agents including fungi, bacteria, algal endophytes and grazers, and resulting in tissue necrosis. Correa & McLachlan (1992) infected *Chondrus crispus* with the green algal endophytes *Acrochaete operculata* and *Acrochaete heteroclada*. Infections resulted in detrimental effects on host performance, including slower growth, reduced carrageenan yield, reduced generation capacity and tissue damage. Stanley (1992) described the fungus *Lautita danica* being parasitic on cystocarpic *Chondrus crispus* and Molina (1986) was the first to report *Petersenia pollagaster*, a fungal invasive pathogen of cultivated *Chondrus crispus*. Pathogenic infections have the potential to cause mortality in *Chondrus crispus* and so intolerance is assessed as intermediate. As some portion of the population is likely to remain for vegetative regrowth, recovery is likely to occur within 18 months (see additional information below) and recoverability is therefore assessed as high.

<b>Introduction of non-native species</b>	Not relevant			
---	--------------	--	--	--

No information was found concerning the effect of alien species on *Chondrus crispus*. *Sargassum muticum* has proliferated since its introduction to British coasts but has different habitat preferences to *Chondrus crispus*.

<b>Extraction of this species</b>	Intermediate	High	Low	High
-----------------------------------	--------------	------	-----	------

*Chondrus crispus* is extracted commercially in Ireland, but the harvest has declined since its peak in the early 1960s (Pybus, 1977). The effect of harvesting has been best studied in Canada. Prior to 1980, the seaweed beds of Prince Edward Island were dominated by *Chondrus crispus* and the species was heavily exploited. Recently, there has been a marked increase in abundance of another red seaweed, *Furcellaria lumbicalis*, which is avoided by the commercial harvest, and an associated decline in abundance of *Chondrus crispus* (Sharp *et al.*, 1993). The authors suggested that harvesting has brought about the shift in community structure. Sharp *et al.* (1986) reported that the first drag rake harvest of the season, on a Nova Scotian *Chondrus crispus* bed, removed 11% of the fronds and 40% of the biomass. Efficiency declined as the harvesting season progressed. Chopin *et al.* (1988) noted that non-drag raked beds of *Chondrus crispus* in the Gulf of St Lawrence showed greater year round carposporangial reproductive capacity than a drag raked bed. In the short term therefore, harvesting of *Chondrus crispus* may remove biomass and impair reproductive capacity, while in the long term, it has the potential to alter community structure and change the dominant species. Intolerance is therefore assessed as intermediate. Mathieson & Burns (1975) described the recovery of *Chondrus crispus* following experimental drag raking (see additional information below) and concluded that control levels of biomass and population structure are probably re-established after 18 months of regrowth. Recoverability is therefore assessed as



high.

### Extraction of other species

Not relevant

No information was found concerning the effects of extracting other species on *Chondrus crispus*.

### Additional information

The life history characteristics of *Chondrus crispus* give the species strong powers of recoverability. It has an extended reproductive period (e.g. Pybus, 1977; Fernandez & Menendez, 1991; Scrosati *et al.*, 1994) and produces large numbers of spores (Fernandez & Menendez, 1991). Although growth of sporelings is not rapid in comparison to other macroalgae, maturity is probably reached approximately 2 years after initiation of the basal disc (Pybus, 1977) and the fronds may persist for up to 6 years (Harvey & McLachlan, 1973). The spores of red algae are non-motile (Norton, 1992) and therefore entirely reliant on the hydrographic regime for dispersal. Norton (1992) reviewed dispersal by macroalgae and concluded that dispersal potential is highly variable. Spores of *Ulva* sp. (studied as *Enteromorpha*) have been reported to travel 35 km, *Phycodrys rubens* 5 km and *Sargassum muticum* up to 1 km. However, the point is made that reach of the furthest propagule and useful dispersal range are not the same thing and recruitment usually occurs on a much more local scale, typically within 10 m of the parent plant. Hence, it is expected that *Chondrus crispus* would normally only recruit from local populations and that recovery of remote populations would be much more protracted.

Recovery of a population of *Chondrus crispus* following a perturbation is likely to be largely dependent on whether holdfasts remain, from which new thalli can regenerate (Holt *et al.*, 1995). Following experimental harvesting by drag raking in New Hampshire, USA, populations recovered to 1/3 of their original biomass after 6 months and totally recovered after 12 months (Mathieson & Burns, 1975). Raking is designed to remove the large fronds but leave the small upright shoots and holdfasts. The authors suggested that control levels of biomass and reproductive capacity are probably reestablished after 18 months of regrowth. It was noted however, that time to recovery was much extended if harvesting occurred in the winter, rather than the spring or summer (Mathieson & Burns, 1975).

Minchinton *et al.* (1997) documented the recovery of *Chondrus crispus* after a rocky shore in Nova Scotia, Canada, was totally denuded by an ice scouring event. Initial recolonization was dominated by diatoms and ephemeral macroalgae, followed by fucoids and then perennial red seaweeds. After 2 years, *Chondrus crispus* had reestablished approximately 50% cover on the lower shore and after 5 years it was the dominant macroalga at this height, with approximately 100% cover. The authors pointed out that although *Chondrus crispus* was a poor colonizer, it was the best competitor.

Therefore, recovery by *Chondrus crispus* will be relatively rapid (approximately 18 months) in situations where intolerance to a factor is intermediate and some holdfasts remain for regeneration of fronds. In situations of high intolerance, where the entire population of *Chondrus crispus* is removed, recovery will be limited by recruitment from a remote population and would be likely to take up to 5 years.

## Importance review

### Policy/legislation

- no data -

### ★ Status

National (GB)  
importance

-

Global red list  
(IUCN) category

-

### Non-native

Native

-

Origin

-

Date Arrived

-

### Importance information

*Chondrus crispus* is harvested commercially in Ireland, Spain, France, Portugal and North America for the extraction of carrageenan (Guiry & Blunden, 1991). In Ireland, the seaweed industry has experienced a decline since its peak in the early 1960s (Pybus, 1977). Harvesting in the north west Atlantic is centred on the Gulfs of Maine and St Lawrence where the species is dominant (Pringle & Mathieson, 1986). The annual catch peaked in 1974 at approximately 50,000 t and has since declined, due in part to decreased demand because of competition from other sources of commercial carrageenophyte production (Pringle & Mathieson, 1986). In Ireland, harvesting has generally remained sustainable through pickers developing an intuitive feel for the annual cycle of local stocks and certain practices which involve pulling only the bushy top half of the frond off leaving the base and holdfast behind (Morrissey *et al.*, 2001). With favourable conditions, yield can be as much as 150 kg (wet weight) per spring tide (Morrissey *et al.*, 2001).

The gelling and thickening properties of carrageenan are used widely in the food, pharmaceutical and cosmetics industries (see review by Guiry & Blunden, 1991). Applications include making ice cream and air fresheners, beer clarification and treatment for diarrhoea (see Morrissey *et al.*, 2001 for detailed list).

## Bibliography

- Aguirre-von-Wobeser, E., Figueroa, F.L. & Cabello-Pasini, A., 2000. Effect of UV radiation on photoinhibition of marine macrophytes in culture systems. *Journal of Applied Phycology*, **12**, 159-168.
- 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.
- Bischof, K., Kraebs, G., Hanelt, D. & Wiencke, C., 2000. Photosynthetic characteristics and mycosporine-like amino acids under UV radiation: a competitive advantage of *Mastocarpus stellatus* over *Chondrus crispus* at the Helgoland shoreline? *Helgoland Marine Research*, **54**, 47-52.
- Bokn, T.L., Moy, F.E. & Murray, S.N., 1993. Long-term effects of the water-accommodated fraction (WAF) of diesel oil on rocky shore populations maintained in experimental mesocosms. *Botanica Marina*, **36**, 313-319.
- Boney, A.D., 1971. Sub-lethal effects of mercury on marine algae. *Marine Pollution Bulletin*, **2**, 69-71.
- 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.
- Burdin, K.S. & Bird, K.T., 1994. Heavy metal accumulation by carrageenan and agar producing algae. *Botanica Marina*, **37**, 467-470.
- Chapman, A.R.O. & Goudey, C.L., 1983. Demographic study of the macrothallus of *Leathesia difformis* (Phaeophyta) in Nova Scotia. *Canadian Journal of Botany*, **61**, 319-323.
- Chopin, T. & Wagey, B.T., 1999. Factorial study of the effects of phosphorus and nitrogen enrichments on nutrient and carrageenan content in *Chondrus crispus* (Rhododphyceae) and on residual nutrient concentration in seawater. *Botanica Marina*, **42**, 23-31.
- Chopin, T., Pringle, J.D. & Semple, R.E., 1988. Reproductive capacity of dragraked and non-dragraked Irish moss (*Chondrus crispus* Stackhouse) beds in the southern Gulf of St Lawrence. *Canadian Journal of Fisheries and Aquatic Sciences*, **45**, 758-766.
- Chopin, T., Sharp, G., Belyea, E., Semple, R. & Jones, D., 1999. Open water aquaculture of the red alga *Chondrus crispus* in Prince Edward Island, Canada. *Hydrobiologia*, **398/399**, 417-425.
- 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/>
- Correa, J.A. & McLachlan, J.L., 1992. Endophytic algae of *Chondrus crispus* (Rhodophyta). 4. Effects on the host following infections by *Acrochaete operculata* and *A. heteroclada* (Chlorophyta). *Marine Ecology Progress Series*, **81**, 73-87.
- Cosson, J., Lepy, M.C., Patry, M.C. & Saur, H., 1984. Etude sur les radioelements emetteurs presents dans les algues des cotes du Calvados (France) pendant les annees, 1980 - 1982. *Botanica marina*, **27**, 301-308.
- Craigie, J.S. & Correa, J.A., 1996. Etiology of infectious diseases in cultivated *Chondrus crispus* (Gigartinales, Rhodophyta). *Hydrobiologia*, **326-327**, 97-104.
- Dickinson, C.I., 1963. *British seaweeds*. London & Frome: Butler & Tanner Ltd.
- 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.
- Dudgeon, S.R. & Johnson, A.S., 1992. Thick vs. thin: thallus morphology and tissue mechanics influence differential drag and dislodgement of two co-dominant seaweeds. *Journal of Experimental Marine Biology and Ecology*, **165**, 23-43.
- Dudgeon, S.R., Davison, I.R. & Vadas, R.L., 1990. Freezing tolerance in the intertidal red algae *Chondrus crispus* and *Mastocarpus stellatus*: relative importance of acclimation and adaptation. *Marine Biology*, **106**, 427-436.
- Dudgeon, S.R., Kuebler, J.E., Vadas, R.L. & Davison, I.R., 1995. Physiological responses to environmental variation in intertidal red algae: does thallus morphology matter? *Marine Ecology Progress Series*, **117**, 193-206.
- Fernandez, C. & Menendez, M.P., 1991. Ecology of *Chondrus crispus* on the northern coast of Spain. 2. Reproduction. *Botanica Marina*, **34**, 303-310.
- Fish, J.D. & Fish, S., 1996. *A student's guide to the seashore*. Cambridge: Cambridge University Press.
- Fortes, M.D. & Lüning, K., 1980. Growth rates of North Sea macroalgae in relation to temperature, irradiance and photoperiod. *Helgolander Meeresuntersuchungen*, **34**, 15-29.
- Gudgeon, S.R., Davison, I.R. & Vadas, R.L., 1990. Freezing tolerance in the intertidal red algae *Chondrus crispus* and *Mastocarpus stellatus*: relative importance of acclimation and adaptation. *Marine Biology*, **106**, 427-436.
- Guiry, M.D. & Blunden, G., 1991. *Seaweed Resources in Europe: Uses and Potential*. Chichester: John Wiley & Sons.
- Guiry, M.D. & Nic Dhonncha, E., 2002. AlgaeBase. World Wide Web electronic publication <http://www.algaebase.org>,
- Gutierrez, L.M. & Fernandez, C., 1992. Water motion and morphology in *Chondrus crispus* (Rhodophyta). *Journal of Phycology*, **28**, 156-162.
- 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.
- Hardy, F.G. & Guiry, M.D., 2003. *A check-list and atlas of the seaweeds of Britain and Ireland*. London: British Phycological Society
- Harvey, M.J. & McLachlan, J., 1973. *Chondrus crispus*. *Proceedings of the Transactions of the Nova Scotian Institute of Science*, **27** (Suppl.1), 1-155.
- Hiscock, K., 1983. Water movement. In *Sublittoral ecology. The ecology of shallow sublittoral benthos* (ed. R. Earll & D.G. Erwin), pp. 58-96. Oxford: Clarendon Press.
- Hiscock, K., ed. 1998. *Marine Nature Conservation Review. Benthic marine ecosystems of Great Britain and the north-east Atlantic*. Peterborough, Joint Nature Conservation Committee.
- Hiscock, S., 1986b. *A field key to the British Red Seaweeds*. Taunton: Field Studies Council. [Occasional Publication No.13]
- 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.
- Hurlbut, C.J., 1991. Larval substratum selection and post-settlement mortality as determinants of the distribution of two bryozoans. *Journal of Experimental Marine Biology and Ecology*, **147**, 103-119.
- Johansson, G., Eriksson, B.K., Pedersen, M. & Snoeijis, P., 1998. Long term changes of macroalgal vegetation in the Skagerrak area. *Hydrobiologia*, **385**, 121-138.
- Juanes, J.A. & McLachlan, J.L., 1992. Productivity of *Chondrus crispus* Stackhouse (Rhodophyta, Gigartinales) in sublittoral Prince Edward Island. 2. Influence of temperature and nitrogen reserves. *Botanica Marina*, **35**, 399-405.
- 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.
- Kuebler, J.E. & Davison, I.R., 1993. High temperature tolerance of photosynthesis in the red alga *Chondrus crispus*. *Marine Biology*, **117**, 327-335.
- Kuebler, J.E. & Davison, I.R., 1995. Thermal acclimation of light use characteristics of *Chondrus crispus* (Rhodophyta). *Journal of Mycology*, **30**, 189-196.
- Kuebler, J.E. & Dudgeon, S.R., 1996. Temperature dependent change in the complexity of form of *Chondrus crispus* fronds. *Journal of Experimental Marine Biology and Ecology*, **207**, 15-24.
- Lubchenco, J., 1980. Algal zonation in the New England rocky intertidal community: an experimental analysis. *Ecology*, **61**, 333-344.
- Mann, K.H., 1972. Ecological energetics of the seaweed zone in a marine bay on the Atlantic coast of Canada. I. Zonation and biomass of seaweeds. *Marine Biology*, **12**, 1-10.
- Markager, S. & Sand-Jensen, K., 1992. Light requirements and depth zonation of marine macroalgae. *Marine Ecology Progress Series*, **88**, 83-92.
- 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.
- Mathieson, A.C. & Burns, R.L., 1975. Ecological studies of economic red algae. 5. Growth and reproduction of natural and harvested populations of *Chondrus crispus* Stackhouse in New Hampshire. *Journal of Experimental Marine Biology and Ecology*, **17**, 137-156.
- 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.
- Molina, F.I., 1986. *Petersenia pollagaster* (Oomycetes): an invasive fungal pathogen of *Chondrus crispus* (Rhodophyceae). In *The Biology of Marine Fungi* (ed. S.T. Moss), 165-175.
- Morrissey, J., Kraan, S. & Guiry, M.D., 2001. *A guide to commercially important seaweeds on the Irish coast*. Bord Iascaigh Mhara: Dun Laoghaire.
- Norton, T.A., 1992. Dispersal by macroalgae. *British Phycological Journal*, **27**, 293-301.
- O'Brien, P.J. & Dixon, P.S., 1976. Effects of oils and oil components on algae: a review. *British Phycological Journal*, **11**, 115-142.
- Pearson, G.A. & Davison, I.R., 1993. Freezing rate and duration determine the physiological response of intertidal fucoids to freezing. *Marine Biology*, **115**, 353-362.
- Prince, J.S. & Kingsbury, J.M., 1973. The ecology of *Chondrus crispus* at Plymouth, Massachusetts. 3. Effect of elevated temperature on growth and survival. *Biology Bulletin*, **145**, 580-588.
- Pringle, J.D. & Mathieson, A.C., 1986. *Chondrus crispus* Stackhouse. *Case Studies of Seven Commercial Seaweed Resources*, **281**, 49-122, FAO Fisheries Technical Paper.
- 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.
- Scrosati, R., Garbary, D.J. & McLachlan, J., 1994. Reproductive ecology of *Chondrus crispus* (Rhodophyta, Gigartinales) from Nova Scotia, Canada. *Botanica Marina*, **37**, 293-300.
- Shacklock, P.F. & Doyle, R.W., 1983. Control of epiphytes in seaweed cultures using grazers. *Aquaculture*, **31**, 141-151.

- Sharp, G.J., Tetu, C., Semple, R. & Jones, D., 1993. Recent changes in the seaweed community of western Prince Edward Island: implications for the seaweed industry. *Hydrobiologia*, **260-261**, 291-296.
- Sharp, G.J., Tremblay, D.M. & Roddick, D.L., 1986. Vulnerability of the southwestern Nova Scotia *Chondrus crispus* resource to handraking. *Botanica Marina*, **29**, 449-453.
- Simpson, F.J. & Shacklock, P.F., 1979. The cultivation of *Chondrus crispus*. Effect of temperature on growth and carageenan production. *Botanica Marina*, **22**, 295-298.
- Smith, J.E. (ed.), 1968. 'Torrey Canyon'. *Pollution and marine life*. Cambridge: Cambridge University Press.
- Stanley, S.J., 1992. Observations on the seasonal occurrence of marine endophytic and parasitic fungi. *Canadian Journal of Botany*, **70**, 2089-2096.
- Tasende, M.G. & Fraga, M.I., 1999. The growth of *Chondrus crispus* Stackhouse (Rhodophyta, Gigartinales) in laboratory culture. *Ophelia*, **51**, 203-213.
- 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.
- Vidaver, W., 1972. Dissolved gases - plants. In *Marine Ecology. Volume 1. Environmental factors (3)*, (ed. O. Kinne), 1471-1490. Wiley-Interscience, London.
- Worm, B. & Chapman, A.R.O., 1998. Relative effects of elevated grazing pressure and competition from a red algal turf on two post settlement stages of *Fucus evanescens*. *Journal of Experimental Marine Biology and Ecology*, **220**, 247-268.

## Datasets

- Bristol Regional Environmental Records Centre, 2017. BRERC species records recorded over 15 years ago. Occurrence dataset: <https://doi.org/10.15468/h1In5p> accessed via GBIF.org on 2018-09-25.
- Centre for Environmental Data and Recording, 2018. IBIS Project Data. Occurrence dataset: <https://www.nmni.com/CEDaR/CEDaR-Centre-for-Environmental-Data-and-Recording.aspx> accessed via NBNAtlas.org on 2018-09-25.
- Centre for Environmental Data and Recording, 2018. Ulster Museum Marine Surveys of Northern Ireland Coastal Waters. Occurrence dataset <https://www.nmni.com/CEDaR/CEDaR-Centre-for-Environmental-Data-and-Recording.aspx> accessed via NBNAtlas.org on 2018-09-25.
- Cofnod – North Wales Environmental Information Service, 2018. Miscellaneous records held on the Cofnod database. Occurrence dataset: <https://doi.org/10.15468/hcgqsi> accessed via GBIF.org on 2018-09-25.
- Environmental Records Information Centre North East, 2018. ERIC NE Combined dataset to 2017. Occurrence dataset: <http://www.ericnortheast.org.uk/home.html> accessed via NBNAtlas.org on 2018-09-38
- Fenwick, 2018. Aphotomarine. Occurrence dataset <http://www.aphotomarine.com/index.html> Accessed via NBNAtlas.org on 2018-10-01
- Fife Nature Records Centre, 2018. St Andrews BioBlitz 2014. Occurrence dataset: <https://doi.org/10.15468/erweal> accessed via GBIF.org on 2018-09-27.
- Fife Nature Records Centre, 2018. St Andrews BioBlitz 2015. Occurrence dataset: <https://doi.org/10.15468/xtrbvj> accessed via GBIF.org on 2018-09-27.
- Fife Nature Records Centre, 2018. St Andrews BioBlitz 2016. Occurrence dataset: <https://doi.org/10.15468/146yiz> accessed via GBIF.org on 2018-09-27.
- Kent Wildlife Trust, 2018. Biological survey of the intertidal chalk reefs between Folkestone Warren and Kingsdown, Kent 2009-2011. Occurrence dataset: <https://www.kentwildlifetrust.org.uk/> accessed via NBNAtlas.org on 2018-10-01.
- Kent Wildlife Trust, 2018. Kent Wildlife Trust Shoresearch Intertidal Survey 2004 onwards. Occurrence dataset: <https://www.kentwildlifetrust.org.uk/> accessed via NBNAtlas.org on 2018-10-01.
- Lancashire Environment Record Network, 2018. LERN Records. Occurrence dataset: <https://doi.org/10.15468/esxc9a> accessed via GBIF.org on 2018-10-01.
- Manx Biological Recording Partnership, 2017. Isle of Man wildlife records from 01/01/2000 to 13/02/2017. Occurrence dataset: <https://doi.org/10.15468/mopwow> accessed via GBIF.org on 2018-10-01.
- Manx Biological Recording Partnership, 2018. Isle of Man historical wildlife records 1990 to 1994. Occurrence dataset: <https://doi.org/10.15468/aru16v> accessed via GBIF.org on 2018-10-01.
- Manx Biological Recording Partnership, 2018. Isle of Man historical wildlife records 1995 to 1999. Occurrence dataset: <https://doi.org/10.15468/lo2tge> accessed via GBIF.org on 2018-10-01.
- National Trust, 2017. National Trust Species Records. Occurrence dataset: <https://doi.org/10.15468/opc6g1> accessed via GBIF.org on 2018-10-01.
- NBN (National Biodiversity Network) Atlas. Available from: <https://www.nbnatlas.org>.
- OBIS (Ocean Biogeographic Information System), 2019. Global map of species distribution using gridded data. Available from: Ocean Biogeographic Information System. [www.iobis.org](http://www.iobis.org). Accessed: 2019-03-21

Outer Hebrides Biological Recording, 2018. Non-vascular Plants, Outer Hebrides. Occurrence dataset:

<https://doi.org/10.15468/goidos> accessed via GBIF.org on 2018-10-01.

Royal Botanic Garden Edinburgh, 2018. Royal Botanic Garden Edinburgh Herbarium (E). Occurrence dataset:

<https://doi.org/10.15468/ypoair> accessed via GBIF.org on 2018-10-02.

South East Wales Biodiversity Records Centre, 2018. SEWBReC Algae and allied species (South East Wales). Occurrence dataset:

<https://doi.org/10.15468/55albd> accessed via GBIF.org on 2018-10-02.

South East Wales Biodiversity Records Centre, 2018. Dr Mary Gillham Archive Project. Occurrence

dataset: <http://www.sewbrec.org.uk/> accessed via NBNAtlas.org on 2018-10-02

The Wildlife Information Centre, 2018. TWIC Biodiversity Field Trip Data (1995-present). Occurrence dataset:

<https://doi.org/10.15468/ljc0ke> accessed via GBIF.org on 2018-10-02.

Yorkshire Wildlife Trust, 2018. Yorkshire Wildlife Trust Shoresearch. Occurrence dataset: <https://doi.org/10.15468/1nw3ch>

accessed via GBIF.org on 2018-10-02.