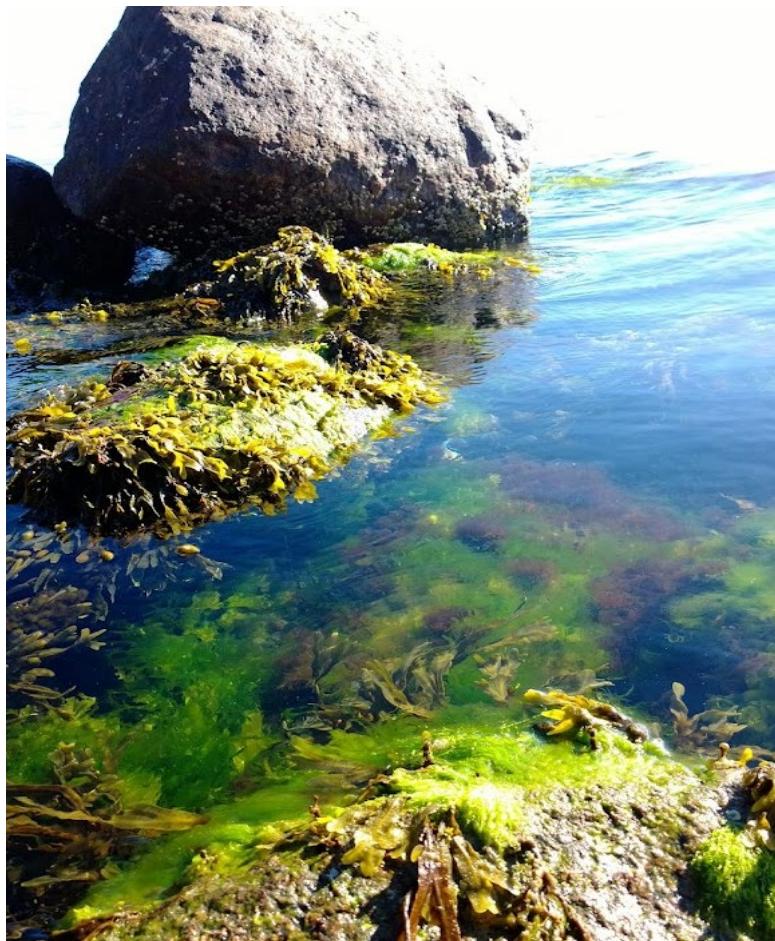


# Literature review of general responses of macroalgae to light, nutrient, salinity and temperature variations relevant to Danish waters

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Scientific briefing from DCE – Danish Centre for Environment and Energy

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# Data sheet

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# **1 Introduction**

This scientific briefing contains a literature review focused on how the literature can support the development of macroalgae indicators as indices of the ecological status of Danish marine waters. The review includes literature on general responses of macroalgae to light, nutrients and salinity and evaluates how eutrophication and temperature can act as pressures for marine macroalgae vegetation.

The briefing is made on the request from the Danish Environmental Protection Agency (Miljøstyrelsen) and is one of three concurrent scientific briefings concerning the development of macroalgae indicators applicable to environmental assessment of Danish coastal waters. The accompanying briefings are “Analysis of historical macroalgae data” and “Macroalgae indicators for assessing ecological status in the Baltic and North East Atlantic”.

# 1 Background

This briefing includes a broad literature review of general effects of light, nutrient, salinity and temperature on the composition and development of macroalgae communities and a narrower literature review of photosynthesis and nutrient uptake kinetics of macroalgae commonly found in Danish marine waters.

From monitoring data of shallow coastal and deep stone reefs in Danish marine waters from 1989-2019 and 1986-2019, respectively, the 10 most abundant species from both areas have been identified and included in the two reviews "Light demands and potential macroalgae distribution" and "Nutrient uptake and effect of species composition", where data/literature was available. Also other species were included if they were confirmed to being naturally occurring species in Danish waters. Therefore, abundant species, naturally occurring in Danish waters, are favoured in the analysis, but where data was available, also other Danish species are included in the review.

Literature searches were mainly conducted using Google Scholar with searches like:

"Light saturation benthic macroalgae"

"Light saturation Species sp"

"Light compensation point Species sp"

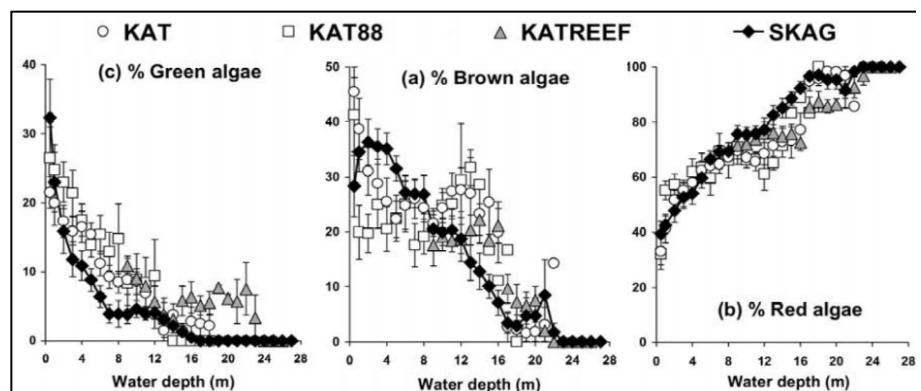
The literature searches were focused on the most abundant species in Danish waters.

The data was not filtered as physiological status or geographical origin of the species.

## 2 Light demands and potential macroalgae depth distribution

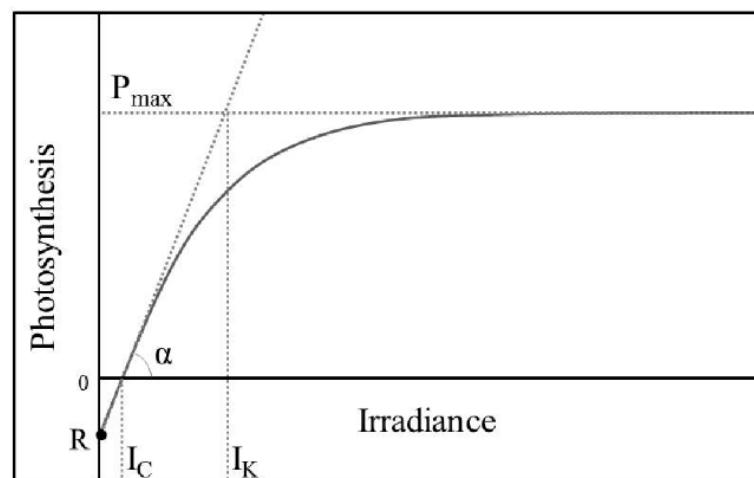
Marine macroalgae depend on light to grow, and their occurrence is, therefore, generally restricted to the euphotic zone. The distribution of green (Chlorophyta), brown (Phaeophyta) and red marine macroalgae (Rhodophyta) in Danish marine waters is regulated by factors such as light availability, salinity, temperature, nutrient availability, exposure and substrate characteristics within the euphotic zone. Light generally divides the distribution of macroalgae – thus, green algae occur closest to the surface followed by brown and red algae (Fig. 1). Red and brown algae extend deeper, partly due to their content of accessory pigments such as phycocyanin and fucoxanthin, enabling them to exploit the green/blue light that penetrates deepest into marine waters (Pedersén and Snoeijs, 2001), partly due to differences in grazing pressure on the algae groups (Boaventura et al., 2002; Duffy & Hay, 2000).

**Figure 1.** Depth distribution of brown (a), red (b) and green algae (c) in percent of total cover at various stations in the Kattegat (KAT, KAT88 and KATREEF) and Skagerrak region. Modified from Pedersén & Snoeijs (2001).



The photosynthetic capacities of a species/individual can be evaluated by subjecting it to a range of light densities from no light to high light conditions, which produces a relationship between light intensity and photosynthesis rate (PI-curve, Fig. 2). PI-curve parameters are typically measured on single leaves or thallus fragments that are placed with an optimal angle towards the light source.

**Figure 2.** Typical PI-curve with parameters: R (respiration),  $I_C$  (light compensation point),  $\alpha$  (light use efficiency),  $I_K$  (light saturation point) and  $P_{max}$  (maximal photosynthesis rate). Modified from Ewers (2013).



From the PI-curve, key parameters such as the respiration rate ( $R$ ), light compensation point ( $I_c$ ), light use efficiency ( $\alpha$ ), light saturation point ( $I_k$ ) and maximal photosynthesis rate ( $P_{max}$ ) can be identified. In theory, the photosynthetic light parameters could explain the potential depth distribution and possibility of a species to compete in various light environments. The light compensation point ( $I_c$ ) reflects the ability to grow at low light conditions, and it can therefore be used to predict the theoretical depth distribution based on the light climate. The light saturation point,  $I_k$ , reflects the adaptation/acclimation to high or low light conditions and thereby the growth potential and sensitivity of a species to high light conditions.

Several factors can affect the photosynthetic performance of a species, such as the area of collection (Svahn et al., 2012; Nygård and Dring, 2008), temperature and salinity (Graiff et al., 2021; Kübler and Davison, 1993; Mathieson and Burns, 1971); Nygård and Dring, 2008), the season of collection (King and Schramm, 1976; Graiff et al., 2021) and the water depth of collection (Gómez et al., 1997). Thus, literature values are likely not to offer the potential to make general predictions of the photosynthetic parameters of a species and its performance in a specific setting. Another consideration is that  $I_c$  and  $I_k$  values of photosynthesis can be quite different to  $I_c$  and  $I_k$  values for growth. Both the  $I_c$  and  $I_k$  values for growth are typically lower than the  $I_c$  and  $I_k$  values for photosynthesis (Lobban and Wynne, 1981; Markager and Sand-Jensen, 1992), and therefore the direct translation of  $I_c$  values to minimum requirements for growth can lead to false conclusions.

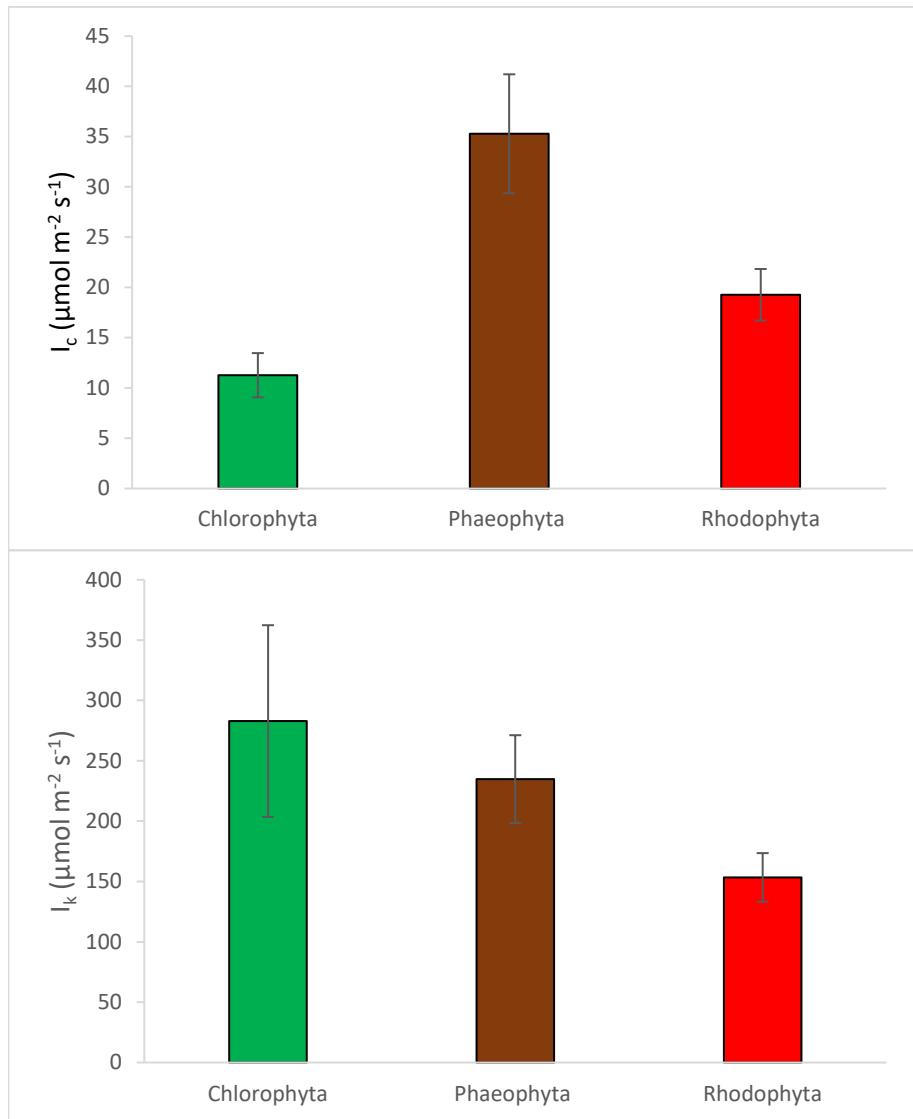
In 2002, Johansson & Snoeijs made a thorough investigation where photosynthesis parameters were obtained for 19 red algae species and 13 brown algae species from two locations in the Skagerrak and the Baltic Sea (Johansson and Snoeijs, 2002). In this study, a clear pattern was seen, where species with a maximum abundance at deeper depths had a lower  $I_c$  than species with a maximum abundance at shallower depths. Also, within the species they found a lower  $I_c$  for individuals growing in deep than for individuals growing in shallow water, demonstrating adaptation towards low or high light conditions as also shown in Gómez et al. (1997). The authors also divided the algae into functional form groups but did not find any significant differences between  $I_c$  and  $I_k$  values between these.

In Appendix 1,  $I_c$  and  $I_k$  values from both the investigation by Johansson & Snoeijs (2002) and other studies are listed for a range of macroalgae species endemic to coastlines and stone reefs in Danish marine waters. In Fig. 3, the values from Appendix 1 are divided into red, brown and green algae species.

When dividing the algae into classes, green algae have the lowest  $I_c$  values followed by red and brown algae, whereas green algae have the highest  $I_k$  followed by brown and red algae. Therefore, based solely on the  $I_c$  values, green algae should have the maximum distribution depth, which is generally not the case. As described above, green algae do not possess accessory pigment, and are therefore restricted to use the parts of the light available for chlorophyll a/b. As chlorophyll a/b only absorb minor parts of the green wavelengths that penetrate deepest into marine waters, the light available for photosynthesis is lower for green algae than for brown and red algae with increasing depth, but this might not be the sole explanation for the typical distribution of macroalgae groups at deep depths (Dring, 1981). As described by Sand-Jensen (1988), a typical shallow water species like *Ulva lactuca* has the physical capacity of photosynthesis to grow at great depths; therefore, other

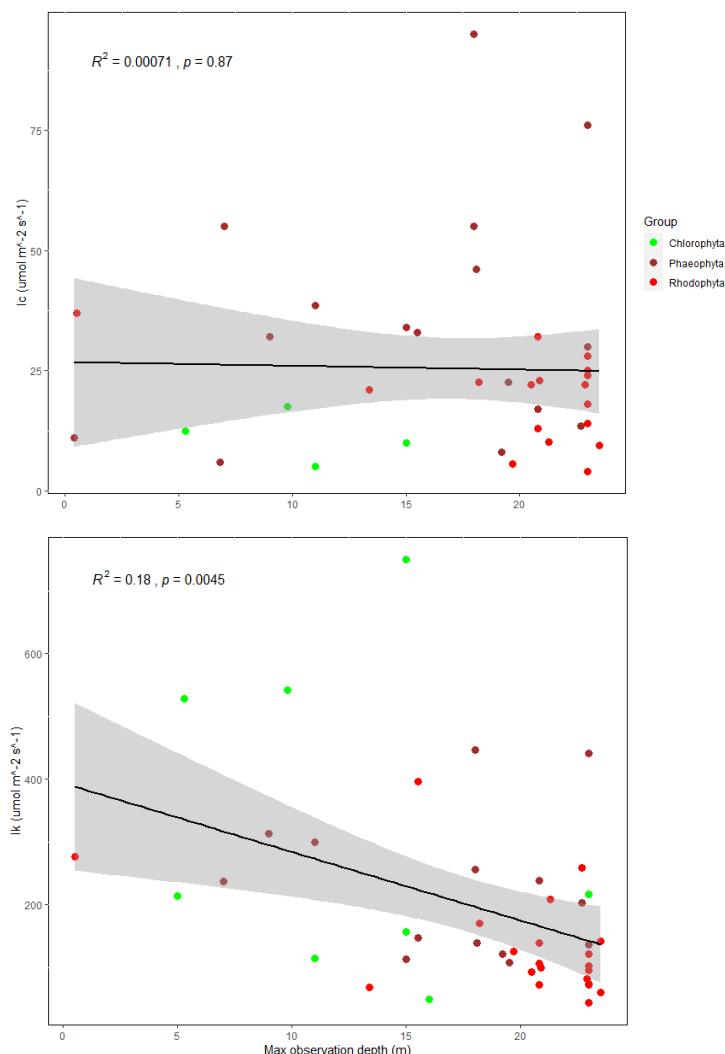
factors such as grazing preferences of herbivores may control the depth distribution of this species (Boaventura et al., 2002; Duffy & Hay, 2000). If losses due to grazing exceed growth rates at a given depth, a species will be unable to maintain a population despite a favourable  $I_c$ .

**Figure 3.** Light compensation ( $I_c$ ) and light saturation ( $I_k$ ) values in  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for different species of macroalgae divided into green (Chlorophyta), brown (Phaeophyta) and red (Rhodophyta) algae.



In Fig. 4, the  $I_c$  and  $I_k$  values listed in Appendix 1 are related to the maximum observation depth of the respective species found through observations at coastal sites (1989-2019) and open-water stone reefs (1986-2019) in Danish waters.

**Figure 4.** A Spearman correlation matrix between  $I_c$  (light compensation point),  $I_k$  (light saturation point) in  $\mu\text{mol m}^{-2} \text{s}^{-1}$  and maximum observation depth of the species listed in Table 1, Appendix 1.  $R^2 = R^2$ -value of the correlation fit and  $p = p$ -value of significant difference from a straight line (no correlation).



The data set showed no correlation between  $I_c$  and the maximum observation depth for each species. This shows that the literature values of  $I_c$  cannot be directly correlated to an observed maximum distribution depth of a species. Lüning in Lobban & Wynne (1981) also compared literature values of  $I_c$  to maximum observation depth, but no clear relationship was found. However,  $I_k$  correlated significantly with the maximum observation depth, with species having a low  $I_k$  showing the deepest maximal observation depth (Fig. 4). Hence, literature values for the light saturation point seem to better reflect the depth of maximum occurrence of a species than  $I_c$ . As described by Lüning in Lobban and Wynne (1981) and later shown by Gomez et al. (2009), macroalgae that are typically abundant in the upper littoral zone have higher  $I_k$  values than macroalgae in the lower littoral/sublittoral zone, meaning that species growing closest to the surface are adapted towards high light intensities.

The clear pattern between maximum abundance depth and  $I_c/I_k$  described by Johansson and Snoeijs (2002) showed that when algae were collected at their maximal abundance depth, and photosynthesis rates were measured quickly thereafter,  $I_c$  related well to the ability of a species to compete at deeper depths. The results were substantiated by the fact that the photosynthetic parameters were obtained fast upon collection and therefore resembled well the acclimation of the species/individual to the specific light conditions that they were exposed to. However, the clear results may also reflect that  $I_c$  was related to the maximum *abundance* depth and not the maximum *observation* depth of

the species. As the maximum abundance depth reflects the depth where a species is most abundant, and not only present, it better reflects the niche towards which the physiology of a given species is optimised. Therefore, the maximum abundance depth of a given species might be the best parameter to relate to the photosynthetic parameters of a species and thereby for use as an indicator of the light climate at a given location.

When translating the photosynthetic parameters of an individual to the abundance of a species relative to depth, also when other excluding parameters such as, for instance, substrate characteristics and salinity levels are considered, it should be considered that, as mentioned earlier, PI-curve parameters are measured on single leaves or thallus fragments, placed at an optimal angle towards the light source. Typically, a species is distributed in nature in a diverse multi-species community, which will affect its light compensation point via plant density and plant structure (Binzer and Sand-Jensen, 2002a). Therefore, when considering the light availability and depth distribution of algae, it is more appropriate to consider the photosynthetic performance of whole plant communities instead of using measurements of thallus/leaf fragments (Binzer and Middelboe, 2005). Parameters such as  $I_c$  and  $I_k$  can differ significantly between single leaf measurements and single-species communities of the same species (Binzer and Middelboe, 2005; Middelboe and Binzer, 2004). Thus,  $I_c$  and  $I_k$  can be 3-8 times higher for plant communities than for single individuals because plant communities tend to saturate at much higher irradiances than single individuals (Binzer and Middelboe, 2005). PI-curve parameters for whole communities are also less sensitive than single individuals to seasonal variations (Middelboe et al., 2006). Therefore, photosynthetic measurements made on whole plant communities are more likely to reflect the potential productivity of macroalgae in a given area. The photosynthetic performance of a plant community is also related to species richness due to the higher absorption efficiency of a more diverse canopy structure (Middelboe and Binzer, 2004). It might be argue that in the case of sedentary/single individuals,  $I_c$  measured on a single individual could offer a reasonable background for predicting the potential depth distributions of a species. However, leaf orientation would still affect the leaf area index and thereby the light absorbed by the individual (Binzer and Middelboe, 2005; Kriedeman et al., 1964).

In conclusion, literature values of photosynthetic  $I_c$  and  $I_k$  obtained from measurements of plant fragments cannot be directly translated to the depth distribution of a species. Measurements of  $I_c$  and  $I_k$  can be related to the maximum abundance depth of a species if the measurements are related directly to the habitat/depth of origin, but extrapolations should be made with caution as many factors affect the potential distribution of a species and interact with the photosynthetic parameters. The growth response in a natural habitat is affected by plant density, leaf orientation, community structure and confounding effects of, for example, temperature, salinity and various adaptations as well as by factors such as grazing and discrepancies between  $I_c$  and  $I_k$  values for photosynthesis and growth. However, plant community responses to light are more robust, and, therefore, when conclusions are drawn as to light variations between sites based on macroalgae distribution patterns, cumulative cover would be a more reliable parameter than abundance data of individual species. The potential use of cumulative cover as a macroalgae indicator is described in Dahl and Carstensen (2019).

### 3 Nutrient uptake and effect of species composition

Algae with a thin sheet-like thallus generally exhibit fast opportunistic growth and are called "r"-strategists as opposed to algae with a thick and tough thallus that generally exhibit slow growth and are called "K"-strategists (Littler, 1980). The maximal growth rate of macroalgae generally follows the allometric scaling of organisms as species or individuals with a high surface area to volume ratio (SA/V-ratio) have higher maximal growth rates than species with a low SA/V-ratio (Nielsen and Sand-Jensen, 1990). There is a proportional relationship between the SA/V-ratio of a species and its nutrient uptake rate, and species with a high SA/V-ratio generally have the highest nutrient uptake rates (Rosenberg and Ramus, 1984; Alwyn and Rees, 2003; Wallentinus, 1984). Therefore, r-strategists with a high SA/V-ratio are expected to dominate in marine areas with high nutrient availability.

Another approach to divide algae into functional groups was provided by Steneck & Dethier (1994), who allocated algae to groups from 1 to 7 (the "Steneck" number) depending on their functional characteristics. This system has been adapted in the work with macroalgae indicators in Denmark, where algae in functional groups 1-3 are classified as "opportunists" (O) and algae in functional groups 3.5-7 as "late-successionals" (P) (Carstensen, 2017).

The ability of a species to respond to different nutrient levels can be depicted by plotting uptake rate ( $V$ ) against nutrient concentration ( $S$ ), which yields a rectangular hyperbola called the Michealis-Menten equation (Harrison and Hurd, 2001). From this equation, the initial slope of the curve ( $\alpha$ ;  $V_{max}/K_m$ ), the half saturation constant ( $K_m$ ) and the maximum nutrient uptake rate ( $V_{max}$ ) can be obtained. In a Michealis-Menten plot, the  $K_m$ -value shows the affinity of a species for a given nutrient, and therefore the  $K_m$ -value is often related to the ability of a species to take up nutrients at low concentrations. However, as the  $K_m$ -value is dependent on  $V_{max}$ , it is argued that the ratio between these ( $V_{max}:k_m$  i.e.  $\alpha$ ) should be used to evaluate the efficiency of a species in taking up nutrients at low nutrient levels, i.e. its ability to compete in a nutrient-poor environment (Harrison and Hurd, 2001; Wallentinus, 1984; Raven and Taylor, 2003). A high  $V_{max}:k_m$ -ratio therefore generally reflects an efficient uptake of nutrients at low ambient nutrient levels (Wallentinus, 1984). A wide range of factors such as temperature, light, water motion, carbon dioxide availability, salinity and tissue nutrient composition can affect nutrient uptake kinetics, and therefore literature values of nutrient uptake kinetics can be expected to be highly dependent on the conditions under which they are measured (Roleda & Hurd, 2019).

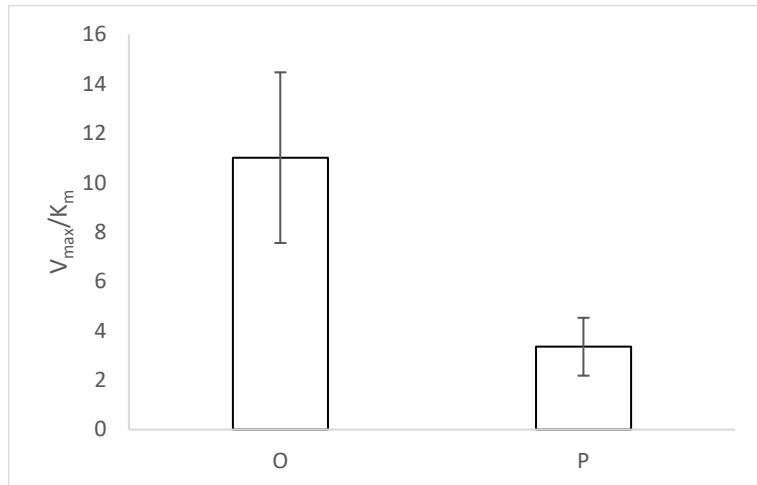
We compiled literature values for the nutrient uptake kinetic parameters  $V_{max}$ ,  $K_m$ , and  $V_{max}:k_m$  ratio for a range of Danish marine macroalgae along with information on the growth strategy (opportunist versus late-successional) of the same species based on the Steneck number (Table 1). The data on growth strategy was available from a previous work with macroalgae indicators in Denmark (Carstensen, 2017).

**Table 1.** Nutrient uptake kinetic parameters  $V_{max}$  ( $\mu\text{mol g dw}^{-1} \text{ h}^{-1}$ ),  $K_m$  ( $\mu\text{M}$ ), the  $V_{max}/K_m$ -ratio and their growth strategy (O-opportunistic, P=late-successional) for Danish marine macroalgae. Modified from Alwyn and Rees (2003).

Species	$V_{max}$ ( $\mu\text{mol g dw}^{-1} \text{ h}^{-1}$ )	$K_m$ ( $\mu\text{M}$ )	$V_{max}/K_m$	Growth strategy
<b>Rhodophyta</b>				
<i>Ceramium rubrum</i>	7.57	5.99	0.79	O
<i>Ceramium tenuicorne</i>	18.67	3.91	5.56	O
<i>Furcellaria lumbricalis</i>	3.19	15.29	0.19	P
<i>Phyllophora truncata</i>	1.69	9.21	0.18	P
<i>Rhodomela confervoides</i>	12.14	4.46	2.72	P
<b>Phaeophyta</b>				
<i>Chorda filum</i>	6.63	0.6	11.05	P
<i>Chordaria flagelliformis</i>	5.93	5.10	1.16	P
<i>Dictyosiphon foeniculaceus</i>	63.69	4.34	14.7	O
<i>Elachista fucicola</i>	17.57	1.94	9.06	O
<i>Eudesme virescens</i>	10.29	2.23	4.61	P
<i>Fucus spiralis</i>	17.56	6.7	2.62	P
<i>Fucus vesiculosus</i>	9.29	24.69	0.65	P
<i>Pilayella littoralis</i>	51.32	8.64	7.05	O
<i>Scytosiphon lomentaria</i>	59.32	6.92	8.58	P
<b>Chlorophyta</b>				
<i>Chaetomorpha linum</i>	30	3	10	O
<i>Cladophora glomerata</i>	115.72	5.27	40.18	O
<i>Cladophora sericea</i>	17	5	3.4	O
<i>Codium fragile</i>	9	5	1.8	P
<i>Ulva intestinalis</i>	64.65	17.22	3.75	O
<i>Ulva prolifera</i>	122.2	7.81	22.67	O
<i>Ulva lactuca</i>	20	5	4	O

Overall, the  $V_{max}:K_m$  ratio shows a clear pattern of higher levels for opportunists than for perennial species with late-successional growth or K-strategists (Fig. 5).

**Figure 5.** Ratio between  $V_{max}:K_m$  for Danish macroalgae termed O=opportunists and P=late-successionals.



This is in contrast to the common observation that nutrient-poor coastal areas are dominated by slow-growing macroalgae. However, the ability of a species to sustain growth and therefore dominate in a nutrient-poor environment is not only governed by its nutrient uptake kinetics. The interplay between

growth rate and internal storage of nutrients has strong implications for a the ability of a species to survive/dominate in a nutrient-poor environment (Pedersen and Borum, 1997). A fast-growing species will quickly utilise the assimilated nutrients and therefore meet the levels critical for growth in contrast to slow-growing species that utilise their internal stores of nutrients more slowly and therefore are capable of sustaining growth for a longer period than a fast-growing species (Pedersen and Borum, 1997; Pedersen and Borum, 1996). A perennial species, like *F. vesiculosus* with a clear K-strategic life form, has a low  $V_{max}$  and a high  $K_m$  value, resulting in a very low  $V_{max}/K_m$ -ratio, but is highly competitive in a nutrient-poor environment due to its slow growth rate (Pedersen and Borum, 1996). Also, as opportunists are unable to maintain high growth rates in nutrient-poor environments, they often fail to escape grazing as they typically have a poor grazing defence (Geertz-Hansen et al., 1993).

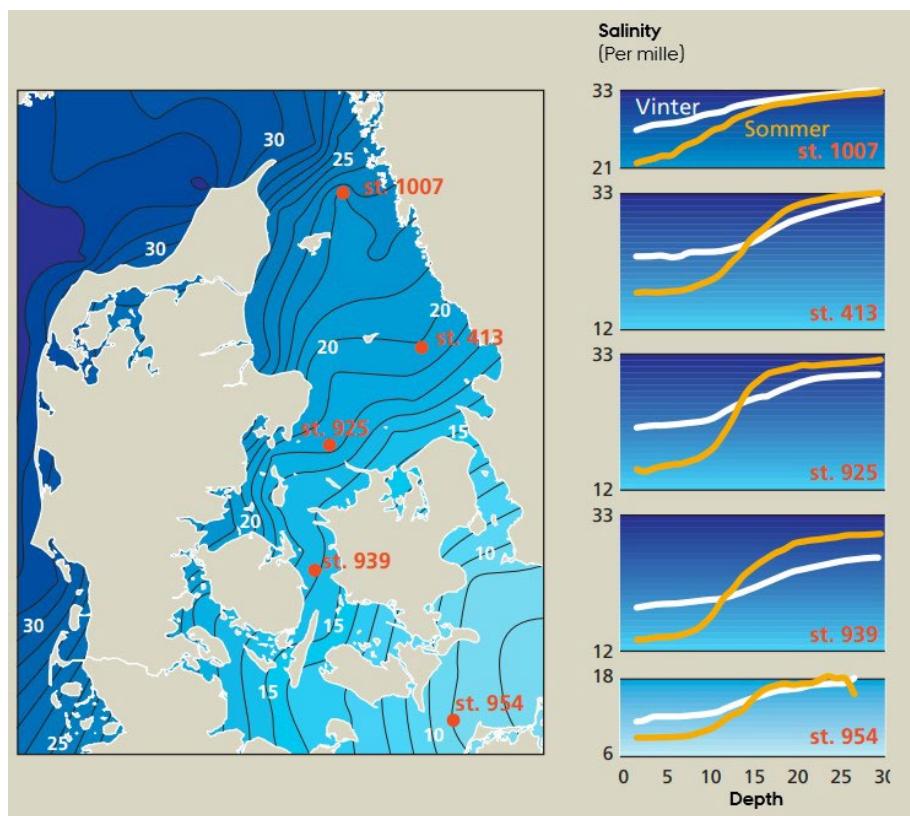
The nutrient levels in Danish waters typically increase from September, peak in January and reach a minimum from May to September due to the dynamics of pelagic phytoplankton growth (Hansen and Høglund, 2021). Average dissolved inorganic nitrogen levels generally reach a maximum of 400 µg L<sup>-1</sup> in fjord areas and 80 µg L<sup>-1</sup> in open water areas during winter and approach depletion during summer. Therefore, during summer in Danish waters, macroalgae are nutrient limited for various periods of time depending on the growth rates and nutrient levels critical to maintain growth (Pedersen and Borum, 1996). The temperature can also restrict the growth of some macroalgae within the summer period and therefore potentially lower the response of these to ambient nutrient levels during summer (Bolton & Lüning, 1982).

In conclusion, literature values of the nutrient uptake kinetics for Danish macroalgae correspond well with the functional form and growth strategy of a species. The nutrient uptake kinetics of a species, together with other factors like growth rate and critical nutrient levels for growth, determine the ability of a species to compete in an environment with prolonged periods of nutrient starvation.

## 4 Salinity effect of species composition

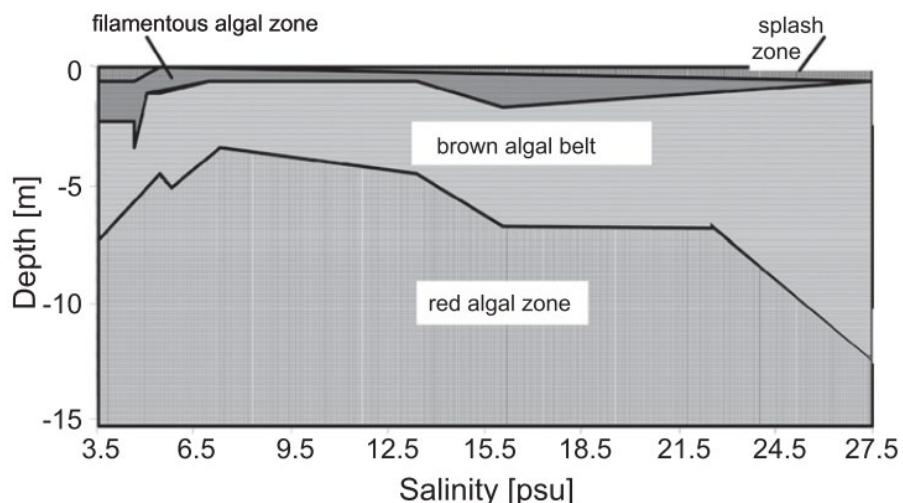
Salinity varies greatly within Danish marine waters from >30 PSU in the Skagerrak region to <10 PSU in the Baltic Sea area (Fig. 6), and the estuaries also show salinity gradients. The diversity of macroalgae decreases almost linearly from full salinity down to 0 PSU in Danish marine waters (Schubert et al., 2011; Middelboe et al., 1997). Consequently, the number of macroalgae species typically decline 3-8 times when moving from >30 PSU to <5 PSU (Schubert et al., 2011).

**Figure 6.** The map shows the average surface salinity (1-5 m depth) in Danish waters. The graphs show the average salinity from the surface to the bottom at selected stations in Kattegat during summer and winter. Modified from Dahl et al. (2003).



Seaweed enzymes can only function in a narrow salinity range of 6-12 PSU, and species have therefore developed various mechanisms to cope with salinity stress (van Ginneken, 2018). Generally, green algae are most tolerant to low salinity levels followed by brown and red algae (Larsen and Sand-Jensen, 2006; van Ginneken, 2018). Within the Kattegat-Baltic Sea area, the depth limit of brown algae decreases with decreasing salinity (Fig. 7). This happens due to a shift in foundation species from kelps such as *L. digitata*, *S. latissima* and *L. hyperborea* towards dominance of *F. vesiculosus*, which tolerates salinity levels <8 PSU (Schubert et al., 2011).

**Figure 7.** Changes in the depth range of algae from the splash zone, filamentous algae zone, the brown algae belt and the red algae zone along the salinity gradient in the Baltic Sea. From Schubert et al. (2011).



Salinity differences can greatly affect the growth rate of macroalgae species. For example, *S. latissima* has a 50% lower growth potential at a salinity of 16 PSU compared to 25 PSU (Broch et al., 2019). The biomass composition of macroalgae also changes along salinity gradients as shown for *L. digitata* and *S. latissima* in the Kattegat-Baltic Sea area, where the contents of both dry matter, nitrogen and phosphorous decrease with decreasing salinity (Nielsen et al., 2016). Decreasing salinity may also reduce the genetic diversity in species like *S. latissima*, which could affect the resilience with regard to, for instance, climate change. Despite the overall differences in salinity tolerance, there may be local adaptations. Both *S. latissima* and *F. vesiculosus* populations can adapt to the prevailing salinity levels (Gerard et al., 1987; Spurkland and Iken, 2011; Nygård and Dring, 2008; Bäck et al., 1992).

When choosing macroalgae indicators for Danish marine waters, it is highly important to consider the variability in species composition related to salinity. Due to the natural shift in species richness and dominant species with changing salinity, interpretation of macroalgae indicators must take salinity into account.

## 5 Pressures for marine macroalgae vegetation

### 5.1 Eutrophication

Eutrophication has been the main pressure in Danish coastal waters for decades and so it remains despite major reductions in nutrient levels since the peak in the 1980s (Riemann et al., 2016; Hansen and Høglund, 2021). The nutrient regime within the Danish marine waters is highly variable both on a seasonal, geographical and depth-dependent scale. During winter, the levels of inorganic nutrients are high, but during summer they are low because of phytoplankton uptake (Hansen and Høglund, 2021). Nutrient concentrations are higher in estuaries than in open waters, and due to the estuarine character of the Danish Baltic-Kattegat-Skagerrak transition, a shifting halocline contributes to differences in nutrient levels at a local depth-dependent scale. Macroalgae growing in Danish waters are mainly nitrogen limited, but a certain degree of P limitation occurs during spring in some areas (Hansen and Høglund, 2021).

Eutrophication generally decreases the macroalgae species richness, favouring dominance of a few species (Middelboe and Sand-Jensen, 2004). These species are typically fast-growing ones with thin leaves and efficient nutrient uptake and light capture characteristics and may generate macroalgae blooms (Duarte, 1995; Valiela et al., 1997; Thorsen et al., 2021; Middelboe and Sand-Jensen, 2000; Johansson et al., 1998).

A few studies have compared the macroalgae species composition in the Kattegat region before and after the peak of eutrophication. The abundance of macroalgae at several locations in the Swedish Kattegat region was, for example, compared from 1960-61 to 1997 (Johansson et al., 1998). The study found increased dominance of fast-growing red algae species with low light demands as an indirect effect of eutrophication. In some areas with high sedimentation, red algae species with tough thalli tolerating sedimentation were favoured. Another study from the inner and outer part of Isefjord and Roskilde Fjord compared macroalgae species abundance in 1941-43 with that in 1982-1994 (Middelboe and Sand-Jensen, 2000). Over this period, the abundance of green algae with opportunistic growth increased while that of large brown algae decreased. The effect of nutrient enrichment was highest in the area with the lowest initial nutrient concentration and less prominent in areas with a high nutrient baseline level (Middelboe and Sand-Jensen, 2000).

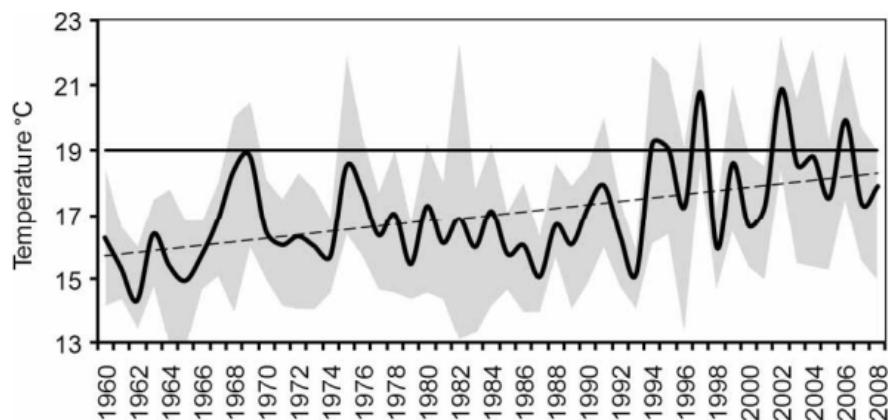
Due to the seasonal variability in nutrient level in Danish waters, the growth of macroalgae is often nutrient limited during summer. Fast-growing turf-forming species are nutrient limited for a longer period than slow-growing perennial species due to their high growth rates relative to nutrient storage capacity (Pedersen and Borum, 1996; Pedersen and Borum, 1997). Therefore, fast-growing species will be favoured over slow-growing species by nutrient enrichment of Danish marine waters.

Fast-growing turf-forming species are characterised by low-lying algae that form pervasive mats of algae filaments, branches and associated sediment,

often covering areas in the order of m<sup>2</sup> or larger (Connell et al., 2014). In Danish waters, turf-forming species like *Ectocarpus* spp., *Ceramium* spp., *Cladophora* spp. and *Ulva* spp. occur.

## 5.2 Temperature

The world's kelp forests are affected by multiple stressors that may alter the state of many presently kelp-dominated sites (Wernberg et al., 2018). As kelps are foundation species that shape the environment that they occupy, changes in their distribution may have major ecosystem effects. During the last decade, there have been many reports of vast losses of kelp habitats in temperate marine areas around the world, especially at the equatorial warm edge of their distribution (Wernberg et al., 2018). Along the coast of Western Australia, 100 km of kelp forest was lost in 2010-2011, possibly due to a heat wave (Smale and Wernberg, 2013). Following the kelp loss, the abundance of turf species increased from 10 to 80% coverage in two years (Wernberg et al., 2013; Filbee-Dexter and Wernberg, 2018). Kelps in Nova Scotia have also shown a 89% reduction in canopy cover since 1982 and a vast change towards dominance of turf species, also likely due to warming (Filbee-Dexter et al., 2016). The persistent turf cover increased local sedimentation, which prevents kelp species from recolonising. A significant 80% loss of *Saccharina latissima* cover accompanied by an increase in turf algae species also occurred on the west coast of Norway, especially in the Skagerrak area, probably due to a combination of eutrophication and high summer temperatures (Moy and Christie, 2012) (Fig. 8).



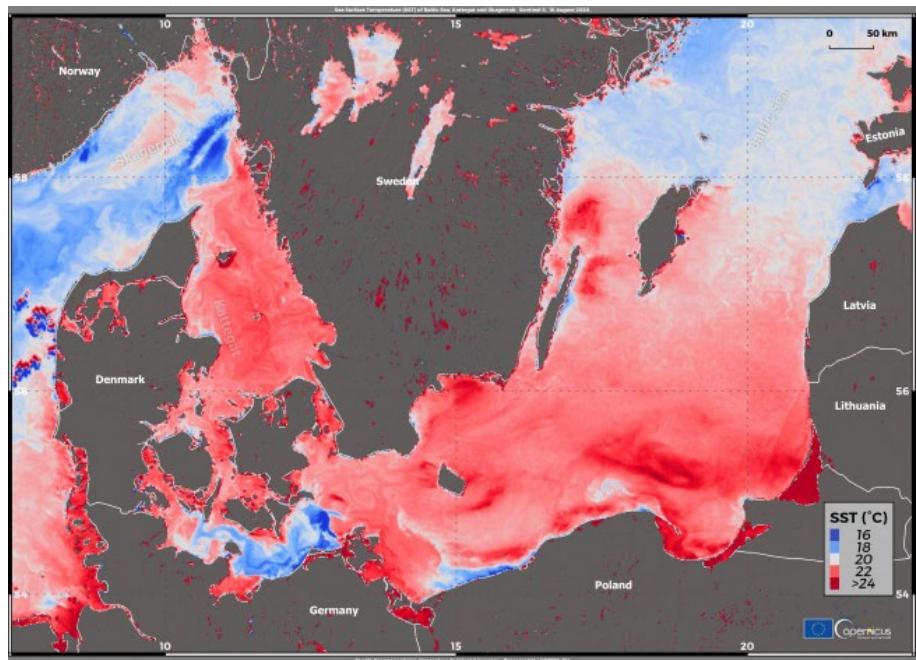
**Figure 8.** Sea surface temperature in August (the warmest summer month) measured daily between 1960 and 2008 at 1 m depth at Flodevigen Field Station at the Skagerrak coast (source: Institute of Marine Research, Norway). The solid line is monthly average, and the grey area is monthly maximum and minimum temperatures. The dotted line is the linear regression of the average August temperature. The line at 19.8 °C indicates a temperature limit of *Saccharina latissima*. From Moy & Christie (2012).

Generally, kelps of the order *Laminariales* are distributed in regions having temperatures between -1.8 °C at northern latitudes to 20 °C at southern latitudes (Müller et al., 2009). The upper lethal temperature for kelp species such as *L. digitata*, *S. latissima* and *L. hyperborea* lies around 20-24 °C (Lüning, 1984; Bolton and Lüning, 1982; Müller et al., 2009). Species growing close in shallow waters in near-shore stone reefs are especially vulnerable to high temperatures as the combination of high temperatures and high light can cause long-term changes in their photosystem performance, which may lead to loss of biomass (Nepper-Davidsen et al., 2019). Lethal effects of temperature possibly

increase when kelps are overgrown with bryozoans like *Menbranipora membranacea* (Brien, 2018).

Temperatures in Danish marine waters are increasing, and heat waves with water temperatures above 24 are getting more frequent (Fig. 9). Therefore warming is potentially a major pressure for especially near-shore and shallow-water stone reefs in Danish marine waters.

**Figure 9.** Sea Surface Temperature (SST) measured by one of the Copernicus Sentinel-3 satellites on 16 August 2020 in the southern part of the Baltic Sea and the Kattegat and Skagerrak straits. From Copernicus.eu.



Canopy-forming brown algae species like *S. latissima* and *L. digitata* have a negative effect on the colonisation of turf-forming algae due to shadowing (Brien, 2018). However, dieback of kelp species enables colonisation by turf algae. After their colonisation, kelp recolonisation is impaired due to space limitation and shadowing (Brien, 2018; Barner and Muth, 2020; Torp, 2018). However, in the Skagerrak area, there have been several regime shifts back and forth between kelp and turf algae species during the last decade (Christie et al., 2019). A possible reason for this is that the Skagerrak and Danish waters are cold during winter, which favours the growth of kelp species over turf-forming algae species (Moy and Christie, 2012).

Reproduction of *S. latissima* starts in October, peaks in November/December and prevails until March in Danish waters (Boderskov et al., 2021; Andersen, 2013). *Laminaria digitata* reproduces earlier with a peak in reproduction in late summer and ends in December (Bartsch et al., 2013). As turf-forming species may dominate in late summer, the recruitment of *L. digitata* could be more impaired than that of *S. latissima* in future high temperature climate scenarios.

As discussed above, rising sea temperatures and future heat waves may have significant negative effects on foundation kelp species. However, other foundation species like *F. vesiculosus* are not as sensitive to high summer temperatures, and areas dominated by *F. vesiculosus* are therefore not expected to be as strongly affected as kelps by warming (Mahasweta et al., 2018).

## 6 Conclusion

Literature values of light requirements and nutrient uptake rates can, to some extent, be used to divide algae into functional groups, but they cannot directly predict the potential distribution of a species in a natural environment. Because of interactions with other abiotic and biotic factors, the photosynthetic responses of multi-species communities relate better to the natural situation than the photosynthetic responses of single thalli. Therefore, the cumulative cover of macroalgae relates better than the cover of single algae species to light conditions and is therefore a better indicator of environmental water quality.

Literature values of nutrient uptake rates may be used to divide the algae into functional groups, but direct predictions of the distribution of species in a changing nutrient environment demand more variables. Other factors like the growth rate of a species and critical nutrient requirements for growth will determine the ability of species to compete in a changing nutrient environment.

Due to the estuarine nature of Danish marine waters, the salinity is highly variable and can be expected to play an essential role in species abundance and composition. Therefore, salinity should be included when using macroalgae indicators in Danish waters.

Eutrophication can generally be expected to favour fast-growing species with a high surface area to volume ratio, such as opportunistic turf algae. Therefore, eutrophication will likely result in increased dominance of a few algae species. However, the eutrophication effect may differ depending on the previous nutrient state of an environment.

Temperature increases are globally and locally coupled with regime shifts between kelp-dominated turf algae-dominated macroalgae communities. In Danish marine waters, future increases in temperature will expectedly have great effects on the kelp communities, especially on shallow water stone reefs where kelp species abundance may diminish during summer, giving way to turf-algae species.

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## Appendix 1

Table 1: Literature values of light compensation ( $I_c$ ) and saturation ( $I_k$ ) points of marine macroalgae abundant in Danish marine waters. When values have several sources, the value represents the mean with the range of all values given in brackets

**Table 2.** Literature values of light compensation ( $I_c$ ) and saturation ( $I_k$ ) points of marine macroalgae abundant in Danish marine waters. When values have several sources, the value represents the mean with the range of all values given in brackets.

Species	$I_c$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	$I_k$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	Reference
<b>Rhodophyta</b>			
<i>Brongniartella byssoides</i>	25	122	[1]
<i>Ceramium nodulosum</i>	32	107	[1]
<i>Ceramium tenuicorne</i>	22	93	[1]
<i>Chondrus crispus</i>	22.5 (5-40)	171 (42-300)	[1-8]
<i>Coccotylus truncatus</i>	21	69	[1]
<i>Corallina officinalis</i>		396.5 (385-408)	[8]
<i>Cystoclonium purpureum</i>	32	139	[1]
<i>Delesseria sanguinea</i>	9.5 (4-15)	61 (60-62)	[4,9]
<i>Dilsea carnosa</i>	14	95	[1]
<i>Furcellaria lumbricalis</i>	10.2 (0.4-20)	208 (116-300)	[1,4,10]
<i>Lomentaria clavellosa</i>	18	72	[1]
<i>Membran optera alata</i>	13	72	[1]
<i>Palmaria palmata</i>	5.5 (5-6)	125	[4,9]
<i>Phycodrys rubens</i>	9.5 (3-16)	141.5 (44-239)	[1,4,11]
<i>Phyllophora crispa</i>	4	44	[1]
<i>Phyllophora pseudoceranoides</i>	22	82	[1]
<i>Plumaria plumosa</i>		259.5 (238-281)	[11]
<i>Polysiphonia fucoides</i>	23	100	[1]
<i>Porphyra umbilicalis</i>	37	277	[1]
<i>Rhodomela confervoides</i>	24	74	[1]
<i>Spermothamnion repens</i>	28	103	[1]
<b>Phaeophyta</b>			
<i>Chorda filum</i>	46	139.5 (95-184)	[1,12]
<i>Desmarestia aculeata</i>	17	238.5 (80-397)	[1,11,13]
<i>Dictyosiphon foeniculaceus</i>	95	446	[1]
<i>Ectocarpus confervoides</i>	6		[4]
<i>Ectocarpus siliculosus</i>	76 (51-101)	441.5 (396-487)	[14]
<i>Fucus serratus</i>	38.5 (6-71)	300 (100-500)	[1,4,9]
<i>Fucus vesiculosus</i>	32 (4-60)	313.5 (27-600)	[1,4,15-19]
<i>Halidrys siliquosa</i>	33	148	[1]
<i>Laminaria digitata</i>	8 (3-13)	121	[4,20]
<i>Laminaria hyperborea</i>	22.5 (3-42)	108.5 (17-200)	[1,4,21]
<i>Laminaria saccharina</i>	13.5 (2-25)	203.5 (7-400)	[1,22]
<i>Sargassum muticum</i>	55	237	[1]
<i>Scytoniphon lomentaria</i>	11		[4]

<i>Sphaerelaria arctica</i>	34	113	[1]
<i>Sphaerelaria cirrosa</i>	30	136	[1]
<b>Chlorophyta</b>			
<i>Bryopsis plumosa</i>		216.5 (117-316)	[14]
<i>Chaetomorpha linum</i>	17.5 (15-20)	541 (82-1000)	[12,23,24]
<i>Cladophora sericea</i>	10	750	[25]
<i>Codium fragile</i>		50	[4,23]
<i>Ulva intestinalis</i>	12.5 (5-20)	528 (56-1000)	[4,23,24]
<i>Ulva linza</i>		214.5 (50-379)	[14]
<i>Ulva prolifera</i>		157.5 (49-266)	[14]
<i>Ulva lactuca</i>	2-8	115 (30-200)	[2,26]

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