

Research Article

Seasonal Patterns of Sporophyte Growth, Fertility, Fouling, and Mortality of *Saccharina latissima* in Skagerrak, Norway: Implications for Forest Recovery

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On the Skagerrak coast the kelp *Saccharina latissima* has suffered severe stand reductions over the last decade, resulting in loss of important habitats. In the present study, healthy kelp plants were transplanted into four deforested areas and their patterns of growth, reproduction, and survival were monitored through subsequent seasons. Our main objective was to establish whether the kelp plants were able to grow and mature in deforested areas. We observed normal patterns of growth and maturation at all study sites. However, heavy fouling by epiphytes occurred each summer, followed by high kelp mortality. The study shows that the seasonal variations and the life stage timing of *S. latissima* make formation of self-sustainable populations impossible in the present environment. Most noteworthy, we suggest that fouling by epiphytes is involved in the lack of kelp forest recovery in Skagerrak, Norway.

1. Introduction

Saccharina latissima (Linnaeus) C. E. Lane, C. Mayes, Druehl, and G. W. Saunders is a large (1–3 m) brown alga in the order Laminariales (kelps). The species is common, and often dominates the subtidal vegetation on sheltered rocky shores in Norway. In 2002, a dramatic decline of *S. latissima* was observed along the south coast of Norway (Moy and Christie, submitted). Areas previously (in the mid 1990s and before) dominated by dense stands of kelps are now almost exclusively dominated by annual filamentous algae. A report published by The Norwegian Climate and Pollution Agency (Klif) in 2009 revealed the vegetational shift as a geographically widespread phenomenon along the entire south coast of Norway, from the Swedish border in the east to (and including) the Møre og Romsdal region in the west. When islands and fjords are included this stretch has approximately 34 500 km of coastline.

According to Moy and Christie (submitted) the wave sheltered fjords have been more affected than wave exposed coastline. Scattered *S. latissima* individuals were observed at several of the stations in poor condition, but mainly at very shallow waters (0–2 m depth) (Moy and Christie, submitted). The mechanisms that drove the shift and the mechanisms currently preventing recolonisation of kelp have not been identified. Increasing water temperatures in Skagerrak over the past decades and a couple of particularly warm summers (in 1997 and 2002) preceding observations of deforestation has pointed toward elevated temperature as a probable culprit (Moy and Christie, submitted).

Large-scale shift from perennial macrophytes to short lived ephemeral algae is a global problem [1–4]. Events likely to be involved are increased temperatures, increased eutrophication, reduced light availability, increased sedimentation, and changes in grazing pressure. Most of these events

are probably related and caused by the synergy of several agents, many of which are anthropogenically induced [5].

In addition to being a widespread phenomenon, the shift from perennial (e.g., kelp) to annual foundation species appear to be persistent. Long-term ecosystem effects of kelp loss on higher trophic levels are poorly known. However, kelp forests serve key functions in the ecosystem as habitat builders and provide important feeding and nursery grounds for many invertebrate, mollusc, and fish species [6, 7]. Hence, substantial ecological effects across several trophic levels are expected (see e.g., [8]).

The kelp life cycle comprises multiple stages from the microscopic, gamet-producing gametophyte, to the macroscopic, spore-producing sporophyte [9]. The drivers of kelp death and preventives of recolonisation may act on any of these life stages. To be able to generate hypotheses addressing the deforestation and lack of recolonisation, we need knowledge of the viability and seasonality of the different life stages under the prevailing environmental conditions. In the present paper we focus on the sporophyte stage. Seasonality in *S. latissima* has been studied in other areas [10, 11], including the west coast of Norway [12]. However, the seasonal patterns in kelps in general are known to vary [9], even on local scales [13]. The aim of this study is firstly to establish whether adult kelp transplanted into a deforested area in Skagerrak (the south east coast of Norway) are able to survive. Secondly, it is to describe the timing and duration of frond elongation, meiospore formation and release, and fouling and longevity of the sporophytes. We will discuss the observed pattern of maturation and survival in relation to ambient temperature variations and fouling. The present study will offer plausible explanations for the lack of recovery of *S. latissima* beds in southern Norway.

2. Materials and Methods

The present project was undertaken from 2005 to 2009 and intensified in December 2007, expanding monitoring from one site in one area (Arendal) to four sites situated in two areas (Arendal and Grimstad). All monitored kelp individuals were transplanted from areas with healthy *S. latissima* forests, which were only found on moderately exposed sites. Transplantation is a widely used methodology in studies of kelp biology (see e.g., [14–19]). In total, 16 kelp individuals were monitored each year from 2005 until 2007, and 31 kelp individuals were monitored each year from 2007 until 2009.

2.1. Arendal Area (2005–2009). Field experiments were initiated in November 2005 and continued until October 2009. *S. latissima* sporophytes were transplanted from a moderately exposed into a sheltered site outside Arendal (the Institute of Marine Research Field Station at Flødevigen), where stand reductions for this species had been observed (Moy and Christie, submitted). The kelps were mounted on vertical ropes along the quay outside the field station. The collected sporophytes were classified into two age groups, adults (>1 year old sporophytes) and prereproductive juveniles (<1 year old sporophytes) based on size (stipes diameter and

blade area) and presence/absence of reproductive tissue. Two vertical ropes were used for each of the two age groups, and four sporophytes were mounted (ca 5 cm apart) at 3 m depth on each rope (16 kelps in total each year).

Elongation rate and reproductive status of the sporophytes were monitored monthly for approximately one year, before new series were started with freshly collected sporophytes in the fall. Backup sporophytes were kept on a separate rope each year. A backup sporophyte was brought into the series if an individual was lost (died), until the supply of backup plants ran out. To be able to measure frond elongation, a small hole was punched at the middle of each blade, 10 cm above the meristematic transition zone between blade and stipe. Elongation rates between sampling dates were estimated, following the methodology of Fortes and Lüning [20]. Reproductive status of sporophytes was monitored by visual inspections. If sori (meiospore containing compartments) were observed, samples of sori tissue were collected. The samples were rinsed in tap water and gently patted dry with paper towels to induce sporulation. The spore's ability to form gametophytes and sporelings was determined after 14 days of cultivation in IMR 1/2 medium at 16 : 8 light-dark cycle under $50 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ (PAR) at 8°C.

Sea temperatures have been measured daily at 1 m depth at Flødevigen Research Station since 1960. A complete temperature dataset was provided by the Institute of Marine Research. In the present study, annual average, maximum and minimum temperatures as well as monthly count of days with temperatures exceeding 20°C each year were extracted for analytic purposes, as the summer isotherm of 19–21°C is limiting its southern distribution according to Müller et al. [21].

2.2. Grimstad Area (2007–2009). In December 2007, 15 individuals of *S. latissima* were transplanted from moderately exposed natural kelp forest sites nearby Grimstad to 3 sheltered deforested localities (>300 m apart) in Groosefjord. Five kelp plants were transplanted into each locality. Each individual was mounted onto a separate rig (Figure 1). The kelp hapteron was attached to the rig at approximately 3 m depth. A plate was mounted onto the rig beneath the kelp (at 5 m depth). At each sampling event, which occurred monthly, four plexi glass pieces (3 × 3 cm) were mounted onto the plate acting as spore collecting devices. The following month, the pieces were collected for further cultivation (in IMR 1/2 medium at 16 : 8 light-dark cycle under $50 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ (PAR) at 12°C) and inspection of spore settling by the use of a light microscope.

To avoid any whiplash effect on the spore collecting devices, kelps were trimmed down to 1 m length if necessary. Elongation and reproductive status of the sporophytes were monitored as described in the previous section (Arendal 2005–2009). Epiphyte densities were noted as percentage frond cover judged by eye.

By February 2008 four of the fifteen rigs had been lost. These were replaced by new rigs and kelp that had been kept as a backup on separate ropes since the initiation in December 2007. In March 2008 two of the lost rigs

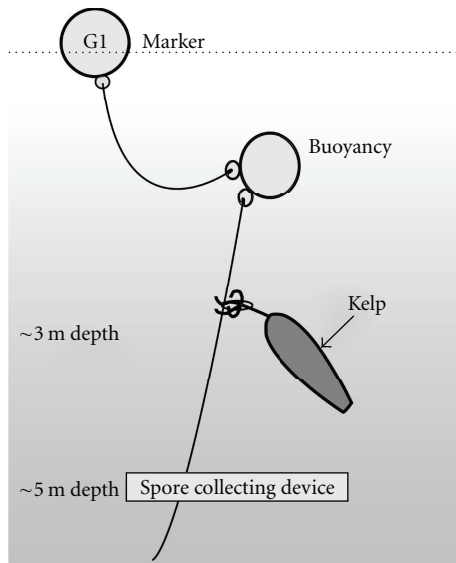


FIGURE 1: Grimstad rig with kelp and spore collecting device mounted at 3 m and 5 m depth, respectively.

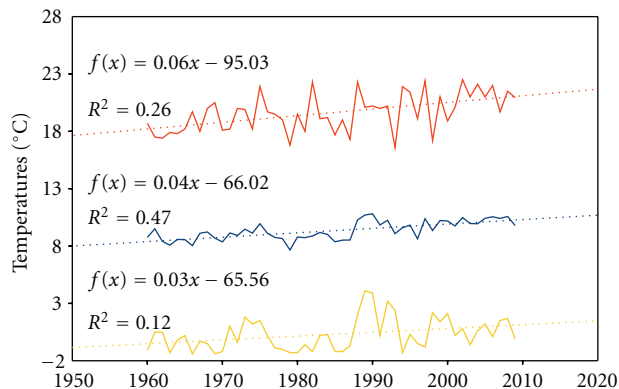


FIGURE 2: Minimum, mean, and maximum yearly temperatures measured at 1 m depth in Arendal from 1960 to 2009. $f(x)$ are the linear regressions.

reappeared, and we continued to measure kelp growth on them. However, these were excluded from the monitoring of sporulation. In October 2008 the series from December 2007 was terminated. Monitoring of growth and sori formation in a new series of 15 newly harvested individuals was initiated at that time. Monitoring of this series continued until April 2009. Spore settling was not investigated in the latter series due to time limitations.

Positive controls were not performed. Monitoring kelp growing on natural substrate as well as on rigs in forested areas would have greatly improved the design. However, rigs located in the exposed areas of healthy kelp forests frequently disappeared after periods of bad weather, and diving in these areas to measure monthly growth on individuals still attached to substratum was considered too costly.

HOBO-loggers measuring temperature every 15 minutes were mounted onto each rig in March 2008. Temperatures

were logged until April 2009. The data from the 15 loggers were used to validate a temperature model for the area retrieved from the operational ocean forecast database at the Norwegian Meteorological Institute [22] (made available by Jon Albretsen), which provided a complete dataset for the monitored period.

In 2009 two additional, independent HOBO-loggers measuring light (lx) at 3 m depth every 30 minutes was placed in two of the study sites. The loggers were maintained by wiping them clean in late February (winter), late March (early spring), late May (early summer), and mid-August (early fall). Light data measured for one week after cleaning were retrieved and pooled giving intensities hour by hour through the average day.

3. Results

3.1. Temperature and Light. A linear regression of modelled temperatures at 5 m depth against the measured temperature (15 HOBO loggers) from the Grimstad area gave convincing results ($r^2 = 0.92$ and $P < 0.001$). Also, the modelled temperatures for Grimstad fitted significantly to measured temperatures at 1 m depth at Flødevigen Station of Marine Research in Arendal ($r^2 = 0.93$ and $P < 0.001$).

Annual maximum, mean, and minimum sea temperatures measured, at 1 m depth increased in the period from 1960 to 2009 (Figure 2). Years with sea temperatures above 20°C have increased in frequency and so has the duration of the warm periods. Particularly warm summers were recorded in 1997, 2002, and 2006 where the temperature at 1 m depth rose above 20°C for 39, 24, and 23 days, and maximum temperatures reached 22.4 , 22.5 , and 22°C , respectively.

Temperatures measured in Arendal in the period of the present study are presented in Figure 3. The warmest periods were recorded in the summer months from July to September. The number of days where recorded temperatures exceeded 20°C was 23 in 2006, none in 2007, four in 2008, and six in 2009. The coldest periods were recorded in late winter/early spring between February and April (except in 2008). In general, considerable year to year variation occurred (Figure 3).

Daily hour-by-hour light intensities from HOBO-loggers indicating winter, spring, summer, and fall situations are presented graphically using the smooth spline function available in R [23] (Figure 4).

3.2. Frond Elongation. A distinct seasonal pattern of frond elongation was observed in the period from 2005 to 2009 in Arendal (Figure 5). The observations at all field sites in Grimstad from 2007 to 2009 also fit this pattern (Figure 6). Elongation in both young (~ 1 year) and older (> 1 year) sporophytes in Skagerrak reached a peak in April/May and paused in June/July. The elongation rates remained very low from August to November/December.

3.3. Mortality and Fouling. Mortality rates seemed generally higher in fall (August–November) in both the adult and the juvenile group in Arendal, although some year-to-year

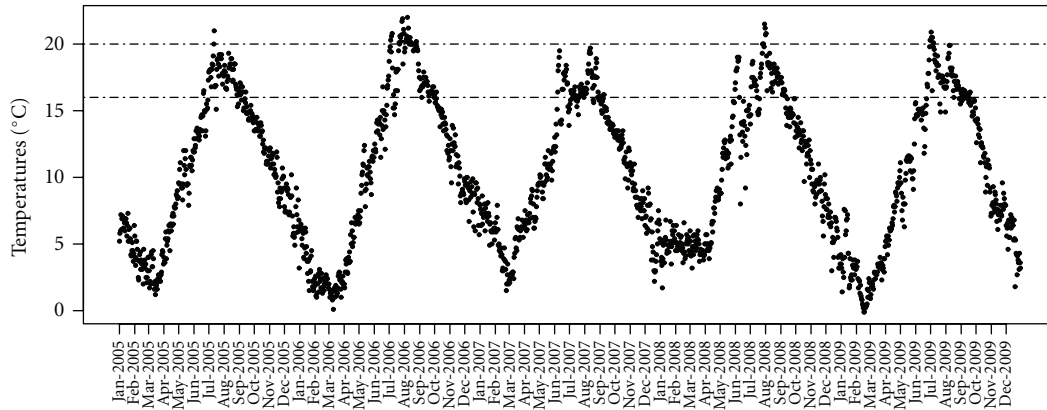


FIGURE 3: Temperatures measured at 1 m depth in Arendal from January 2005 to December 2009. Horizontal lines are drawn at 16°C and 20°C.

TABLE 1: Mortality of juvenile (J) and adult (Ad) kelp (% of population) in Arendal. (See text for results from Grimstad.) Values higher than 25% are marked in bold italic formatting. Blank fields means no data.

Year	Age	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Des
2006	Ad	12.5	12.5	0	0	0	0	0	0	0	50		
	J	25	0	0	0	0	0	0	12.5		57.14	100	0
2007	Ad		0	0	0	0	12.5	0	0	25	16.67	8.33	0
	J	0	0	0	0	0	0	0	0	0	0	12.5	7.14
2008	Ad	50	0	25		0	25	0	50	33.33	25	25	25
	J	0	12.5	0		0	0	0	25	25	20		
2009	Ad	0	0	12.5	33.33								
	J	0	0	25	0	0			12.5	12.5	22.5	0	

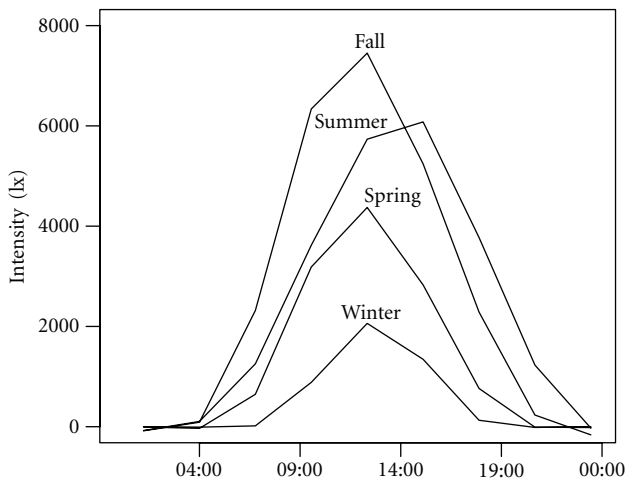


FIGURE 4: Light intensities at 3 m depth (in Grimstad) in winter (late February), spring (late March), early summer (late May), and fall (mid August). Time along the x-axis is displayed in a 24-hour format (HH:MM).

variation occurred (Table 1). Occasional high mortality at other times was most likely due to episodes of bad weather causing increased drag and loss of kelp plants. The specimens in Arendal and the specimens IN Grimstad showed similar

patterns of mortality. By September most kelps at the rigs in Grimstad had been lost or were considered deceased. The number of kelp individuals was reduced from 17 (15 original + 2 replacements) in March 2008 to 13 in July 2008 and to six in September 2008 (~65% reduction in all). The survivors at all sites (including Arendal) were heavily overgrown by floral and faunal epiphytes which had accumulated since June. Epiphytes were estimated to cover between 80 and 100% of the kelp fronds in Grimstad in September 2008 (Figure 7). The epiphyte communities consisted of various combinations of blue mussels (*Mytilus edulis*), sponges, bryozoans (mostly *Membranipora membranacea* and some *Electra pilosa*), filamentous algae, and an enormous invasion (especially in Grimstad) of the vase tunicate (*Ciona intestinalis*). The few kelp plants that survived the fouling period were observed to form healthy tissue free of epiphytes in the following elongation season. However, elongation was no longer measured on these individuals after the initiation of the new series.

3.4. Fertility and Spore Production. Spore producing tissue (sori) was generally present from October and until March. The timing and the duration of sori formation seem to vary somewhat but still, the pattern was largely the same at all sites. The sporophytes released viable spores that were able

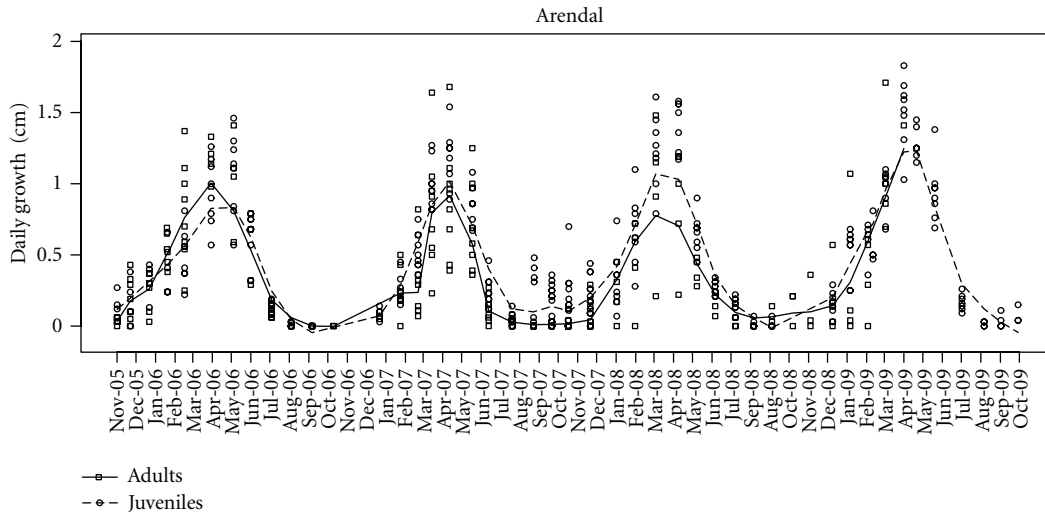


FIGURE 5: Frond elongation of adult and juvenile kelp at 3 m depth in Arendal from November 2005 to December 2009. Elongation rates are expressed as daily growth (cm).

TABLE 2: Adults able to provide viable spores (% of populations) in Arendal (A) and Grimstad (G). Values higher than 25% are marked in bold italic formatting. Blank fields means no data.

Year	Site	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	OCT	Nov	Dec
2005	A										75	100	100
2006	A	100	75	100	50		0	0	0		0	50	
2007	A	87.5	75	12.5	0	0	0	0	0	16.67	45.83	77.5	67.5
	G										0	100	100
2008	A	75	100	50		0	0	0	0	0	33.33	100	75
	G	100	100	13	0	0	0	0	0	0			

to settle and germinate all through the sori forming period (Table 2).

4. Discussion

The present study showed that kelp translocated into deforested areas were able to grow and mature, and that high kelp mortality in summer coincided with heavy epiphytic fouling as well as high water temperatures.

The most popularly stated comments in media on why the *Saccharina latissima* kelp forests in Skagerrak struggle have put great emphasis on the effect of global warming and high summer temperatures. This emphasis is natural considering studies like that by Müller et al. [21]. The observed deforestation could be the consequence of particularly warm summers in 1997 and 2002. Indeed, negative effects of elevated sea temperatures on both growth and longevity of kelps are to be expected (see e.g., [24]). Bolton and Lüning [25] found the optimum growth temperatures of *S. latissima* sporophytes to span from 10 to 15°C. Growth was reduced by 50–70% at 20°C, and the specimens completely disintegrated after 7 days at 23°C [25]. Gerard and Du Bois [16] investigated two populations of *S. latissima* and found marked differences in their responses to temperatures. Specimens

that came from an area with ambient summer temperatures exceeding 20°C one and a half month (New York) seemed more temperature tolerant than specimens from an area rarely experiencing temperatures above 17°C (Maine). While >50% of the New York plants survived three weeks of temperatures above 20°C in field experiments, the Maine plants suffered 100% mortality. Both groups suffered 100% mortality after 3 days at 24°C in laboratory experiments [26]. *In situ* studies of *S. latissima* at its southern distribution in the Long Island sound, New York, showed decreased frond growth as the temperature exceeded 16°C and ceased growth when it exceeded 20°C [27]. Our results from the elongation studies in the deforested Skagerrak area are in concurrence with the patterns of growth described in the previously mentioned studies. The elongation rates were high in the cold periods (March to May), and reduced in June/July as the temperature rose (Figures 5 and 6). The concurring patterns indicate that for our interpretative purpose the data are reliable. Our main objective was to establish whether the kelp plants were able to grow and mature in deforested areas. In that respect, we do not consider the lack of positive controls a serious problem for the validity of our conclusion.

During the present project only July and August 2006 had particularly many days of high temperatures (23 days of temperatures above 20°C). Although kelp mortality was

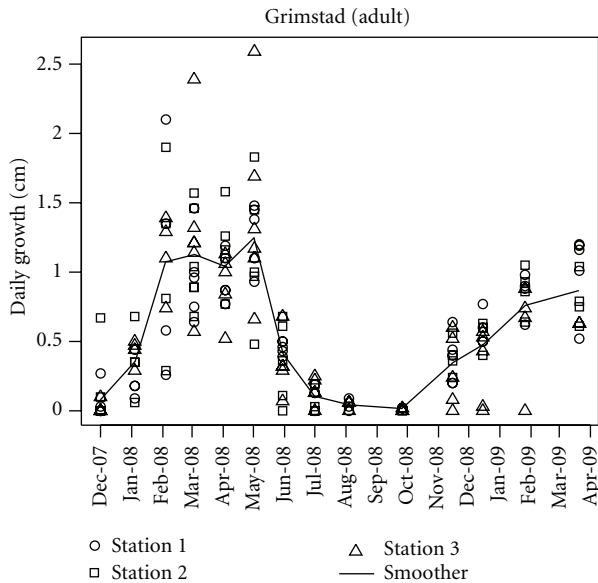


FIGURE 6: Frond elongation of adult kelp at 3 m depth in Grimstad. Elongation rates are expressed as daily growth (cm).

high after the warm summer of 2006, high mortality rates were also recorded in 2008, a year when the temperature exceeded 20°C for only four days (Table 1). Furthermore, high mortality occurred earlier in 2008 than in 2006, even though the maximum temperatures were recorded in the same period (Figure 3). The disappearance of *S. latissima* is by far most extensive in wave sheltered areas, where the water temperatures in summer are relatively high (Moy and Christie, submitted). However, near the surface where the water temperatures usually are the highest, the situation is far less severe (Moy and Christie, submitted). This fact along with our results suggests that even *if* a couple of warm summers in the late 1990s and early 2000s was the cause of the extensive deforestation observed in Skagerrak, it is less likely to be the preventer of kelp forest recovery at present.

Most organisms experience increased respiration as their surrounding temperature rises (see [28] for kelp example). One could therefore hypothesise that in low-light conditions of deeper waters, the kelp may not be able to photosynthesise sufficiently to support its respiration at elevated temperatures. This would explain why kelp populations in shallow waters, where light conditions are better, appear healthier. However, Davison et al. [29] found variation in respiratory rates of *S. latissima* grown at 15°C to be insignificant in the range from 10°C to 25°C. Daily water temperature as high as 25°C has not been recorded in Arendal in the period from 1960 and to this date. Furthermore, the respiratory rates were very similar to those measured for *S. latissima* grown and measured in cold water (5°C) [29]. Hence, variation in water temperatures in the range experienced in Skagerrak must have little effect on the kelps respiration. Irradiance required for compensation (5 and 25 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ measured at 5 and 25°C, resp.) was also similar in the two groups. Light saturated photosynthesis for kelps grown at 15°C occurred approximately 50 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$

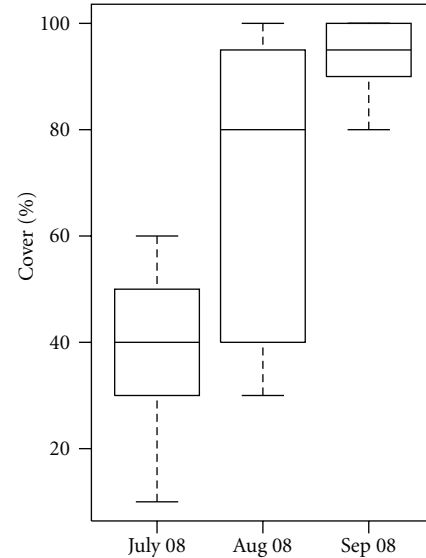


FIGURE 7: Estimated epiphyte cover on kelp fronds in Grimstad in 2008. Boxplots based on monitoring of 13 kelp individuals in July, 8 in August, and 6 individuals in September. The median value is marked by a horizontal line in the middle of each box. The boxes include the lower and the upper quartile. The whiskers extend to the extreme values.

when measured at 25°C [29]. Evidently, little light is necessary for the kelp to uphold a positive carbon budget. Considering all years, the present study documented a high mortality in summer/fall and generally low mortality in spring at 3 m depth. Since ambient temperatures seem to have little effect, the light conditions would have to be considerably worse in summer/fall than in spring to explain the seasonal kelp die-off by insufficient photosynthesis. Less light was available in spring than in summer/fall in 2009 (Figure 4), so we find such a scenario highly unlikely to be the case. Moreover, the light required for compensation and saturation of photosynthesis (as reported by Davison et al. [29]) roughly converts to 1320 and 2630 lx, respectively. Although the conversions are crude, the intensities were well above both levels for a longer period in summer/fall than in spring (Figure 4).

If not failure to compensate for respiration, what may explain the seeming correlation between deforestation and high sea temperatures? Increased sea temperatures appear to affect the growth of *S. latissima* negatively. Slow growth or elongation rate is not necessarily an indication of poor condition. However, reduced production of new thallus leaves the kelp more vulnerable to epiphytism and possibly to bacterial attacks and viral infections. In fact, along with elevated summer temperatures comes an increase in epiphytic load on the kelps. High mortality of kelp after heavy epiphytism has been reported from the northeastern coast of America [2, 10, 30]. Accumulating epiphytes cause increased brittleness resulting in defoliation, especially under increased mechanical disturbance at high energy events like storms [31]. Continuous exposure to moderate wave activity, however, may contribute in epiphyte control by washing

away new settlers [32, 33]. Such a mechanism could explain why kelps close to the surface and in relatively exposed areas are in better condition than deeper and more wave sheltered populations.

Observations of prominent epiphyte cover on kelps are very common in Skagerrak (Moy and Christie, submitted). In the present study, heavy fouling by epiphytes was observed at all sites by August. The epiphyte densities in Grimstad increased, covering 80 to 100% of each frond by September in 2008. Epiphyte densities were probably just as prominent in Arendal the other years (though actual cover was not estimated). Subjected to light limitations and increased drag disturbances caused by epiphytes, chances of survival seem drastically reduced. We do not know if translocation of kelp may affect the density of epiphytes growing on them. However, procedural control in another study has indicated that dislodgement and transplantation of kelps have no direct effect on the cover of epifauna [19]. Hence, we consider the cover of epiphytes likely to be the effect of the habitat rather than the methodology applied.

The present study showed that transplanted individuals free from epiphytes became fertile produced and released viable spores for five months in the deforested areas. It is evident that spores in the area are able to settle on clean substrate (spore collecting devices) and develop into small recruits. Still, we do not know if the spores are able to settle and germinate on the sea floor. Increasing amounts of sediments and a dense cover of filamentous algae may obstruct both settlement and germination [34]. Regardless, if recruits are formed, fouling may make them unlikely to survive until maturity (>1 year). Furthermore, if bryozoan cover cause reduced reproductive output, as reported by Saier and Chapman [35] the chances of reproductive success seems vanishingly small. Self-sustainable populations will not be able to form and full recovery of the kelp beds will not occur.

In conclusion, we consider the effects of heavy fouling in depriving the *S. latissima* sporophyte of light and in obstructing completion of the kelps life cycle likely to be the most important mechanism preventing recolonisation and recovery of *S. latissima* beds in the Skagerrak area.

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