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ORIGINAL ARTICLE

The combined effect of canopy shading and sea urchin grazing on recruitment in kelp forest (*Laminaria hyperborea*)

KJERSTI SJØTUN¹, HARTVIG CHRISTIE² & JAN HELGE FOSSÅ¹

¹Institute of Marine Research, P.O. Box 1870 Nordnes, N-5817 Bergen, Norway, and ²Norwegian Institute for Water Research, P.O. Box 173 Kjelsås, N-0411 Oslo, Norway

Abstract

The aim of this study was to determine the impact of sea urchin grazing (*Echinus esculentus*) and canopy shading on the recruitment of the kelp *Laminaria hyperborea* in mid-Norway. A spatially variable distribution of sea urchins was observed, and recruitment processes were studied both after disturbance, caused by kelp harvesting removal of the canopy kelps, and in pristine kelp forests. The combination of sea urchin density and the density of canopy-forming kelps had the strongest influence on the density of small kelps in pristine kelp forest, suggesting that both grazing from sea urchins and shading from the canopy contributed to the mortality of small kelps. High densities of small kelps ($>20 \text{ m}^{-2}$) were only found in pristine kelp forest together with ≤ 6 canopy-forming kelps m^{-2} or < 3 sea urchins m^{-2} on average. However, within the observed range of sea urchin densities these had no effect on the density of large, canopy-forming kelps. Large *L. hyperborea* were apparently not subject to grazing. In addition, only a small number of surviving kelp recruits was needed to maintain the density of canopy-forming kelps, as *L. hyperborea* specimens may survive many years. These conditions result in high stability of the kelp forest. A different picture was seen after kelp harvesting, when high recruitment and survival of recruits are the conditions for rapid restoration of the kelp vegetation. After removal of the canopy-forming plants, the kelp recruits were temporarily released from high density-dependent mortality due to shading. Some influence of sea urchin grazing on the density of recruits was observed, but this was small compared with the strong canopy effect. However, the accumulated impact of grazing during a period of time had a strong overall effect on the regrowth of kelp. After 2.5 years the accumulated biomasses at the harvested stations were strongly related to average sea urchin density, and a density of between 4 and 5 sea urchins m^{-2} resulted in very little biomass accumulation. This suggests that the *L. hyperborea* kelp forest vegetation has a high degree of stability, but shows less resilience after disturbance, when exposed to moderate sea urchin grazing.

Key words: Canopy effect, *Echinus esculentus*, grazing, kelp recruitment, *Laminaria hyperborea*

Introduction

Recruitment success in kelp vegetation has been studied in several coastal ecosystems, and vast production and mortality in the microscopic and juvenile stages have often been demonstrated (Kain 1975; Chapman 1984). The mortality of microscopic and juvenile kelps may be caused by a number of external factors. Of the most important biotic ones are plant–animal interactions, such as grazing (Dean et al. 1989), and interactions among plants, such as density-dependent mortality. Density-dependent mortality may occur among benthic algae in the juvenile stage (Reed 1990; Steen & Scrosati 2004), or among individuals of different size co-

horts, where small plants suffer greater mortality when growing in competition with large plants than without (Graham et al. 1997; Creed et al. 1998). In addition to intraspecific competition, other plant interactions, such as sweeping (Dayton 1971; Santelices & Ojeda 1984; Kiirikki 1996), or interspecific competition for space may reduce recruitment. In a study of two species belonging to Laminariales (*Laminaria longicruris* (Hudson) J.V. Lamouroux and *L. digitata* Bachelot de la Pylaie), no effect on recruitment by the removal of large plants was found, while experimental removal of small and branched filamentous algae strongly enhanced recruitment (Chapman 1984).

Correspondence: Kjersti Sjøtun, Department of Biology, University of Bergen, P.O. Box 7800, N-5020 Bergen, Norway. E-mail: kjersti.sjotun@bio.uib.no

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Laminaria hyperborea (Gunnerus) Foslie dominates the kelp zone in outer coastal areas of the eastern part of the North Atlantic (Kain 1971). The relatively rigid stipe of the plants may reach a length of more than 2 m, and the laminae of large plants form a distinct canopy layer. In north Norway, the *L. hyperborea* kelp forests have been strongly affected by grazing of the green sea urchin, *Strongylocentrotus droebachiensis* (O.F. Müller), during the last 30 years, resulting in large areas totally devoid of kelp and with persisting high densities of *S. droebachiensis* (Sivertsen 1997). Large-scale decimation of kelp forests by sea urchin grazing has not been observed south of 63°N in Norway, and in southwest Norway *L. hyperborea* has been harvested for the production of alginate since the 1970s (Jensen 1998). During the 1990s, reduced populations of *S. droebachiensis* were observed in mid-Norway south of 65°N, together with a restoration of the kelp forests (Skadsheim et al. 1995). However, another sea urchin, *Echinus esculentus* L., was found in slightly increasing numbers in *L. hyperborea* kelp forests during the early 1990s (Christie & Rinde 1995). The ecological role of this grazer has been studied briefly, but Jones & Kain (1967) showed that *E. esculentus* grazing controlled the depth expansion of *L. hyperborea*. A restricted harvesting of *L. hyperborea* started in 1997 in the formerly overgrazed area in mid-Norway, accompanied by monitoring of sea urchin distribution, kelp recruitment and regrowth after harvesting.

Because of the vast number of spores produced by *L. hyperborea* during the seasonal period of sporulation (Kain 1975) and the relatively good dispersal ability of spores (Fredriksen et al. 1995), it is unlikely that recruitment within a population is limited by the production of gametophytes or microscopic sporophytes. When large canopy-forming plants are removed, for example after kelp harvesting, a dense carpet of juvenile *L. hyperborea* normally soon appears (Svendsen 1972; Christie et al. 1998). This suggests that the mortality of juveniles is strongly influenced by the amount of canopy-forming kelps present, presumably due to the shading effect by these. The long and relatively stiff stipes, carrying a much shorter lamina, will prevent scouring or sweeping effects on kelp recruits by the laminae. However, sea urchins, when present, probably affect recruitment through grazing of microscopic and juvenile kelps (Jones & Kain 1967; Sivertsen 1997). Much attention has been paid to extensive sea urchin populations grazing all the kelp vegetation and forming barren grounds, but small populations coexisting with stable kelp vegetation are probably more common. Under such circumstances the key questions are how moderate

grazing will interact with the canopy effect in regulating the density of kelp recruits, and whether high kelp recruitment as a result of the removal of the canopy-forming kelps may “swamp” the grazers (in a wide sense, *sensu* Vadas et al. 1992) and thereby reduce the effect of grazing on recruitment. Answering these questions is essential for understanding kelp forest persistence under different rates of sea urchin grazing, and for a sustainable management of kelp harvesting.

In this study we tested the possible impact of large grazers and canopy shading on kelp recruitment. Several localities were included, covering pristine *L. hyperborea* forest and areas subjected to harvesting. Kelp harvesting represents a disturbance in the kelp forests, by removing the canopy-forming kelps in large patches. Sea urchin density varied within a moderate density range within the study area, and this made it possible to study the combined effect of sea urchin grazing and canopy shading on kelp recruitment. We wanted to test if the relative importance of density-dependent and density-independent recruitment processes changed after disturbance of the kelp forest, and if a release from a potentially high density-dependent mortality could result in rapid regrowth due to kelp recruits “swamping” the grazers.

Material and methods

Kelp recruitment in unharvested areas

The densities of sea urchins and kelps were recorded in mid-Norway at three stations in 1997 and 1998 (Stns 3–5), 13 stations (including Stns 1–5) during August 1999, and five stations in August 2000 (Stns 1–5) (Figure 1). All recording was performed by SCUBA-diving. A sampling frame, covering 1 m² (0.5 m² in 2000), was placed randomly in the kelp vegetation, by dropping the frame while swimming above the lamina layer. All sea urchins and *L. hyperborea* kelps were counted within the sampling frame. This was repeated three to five times per locality. *Laminaria hyperborea* kelps were divided into three size categories: (1) small kelps, constituting all visible individuals with stipes less than about 10 cm, (2) intermediate-sized kelps, with stipe lengths normally up to around 1 m and (3) canopy-forming kelps, which have relatively uniform stipe lengths normally of around 1.5 m or more and form a distinct canopy layer (Sjötun & Fredriksen 1995). Separation of the kelps of the last two categories was performed by comparing stipe lengths of the plants, measured by eye, within the sample and assigning the kelps to canopy-forming kelps or intermediate-sized kelps. All recordings were carried

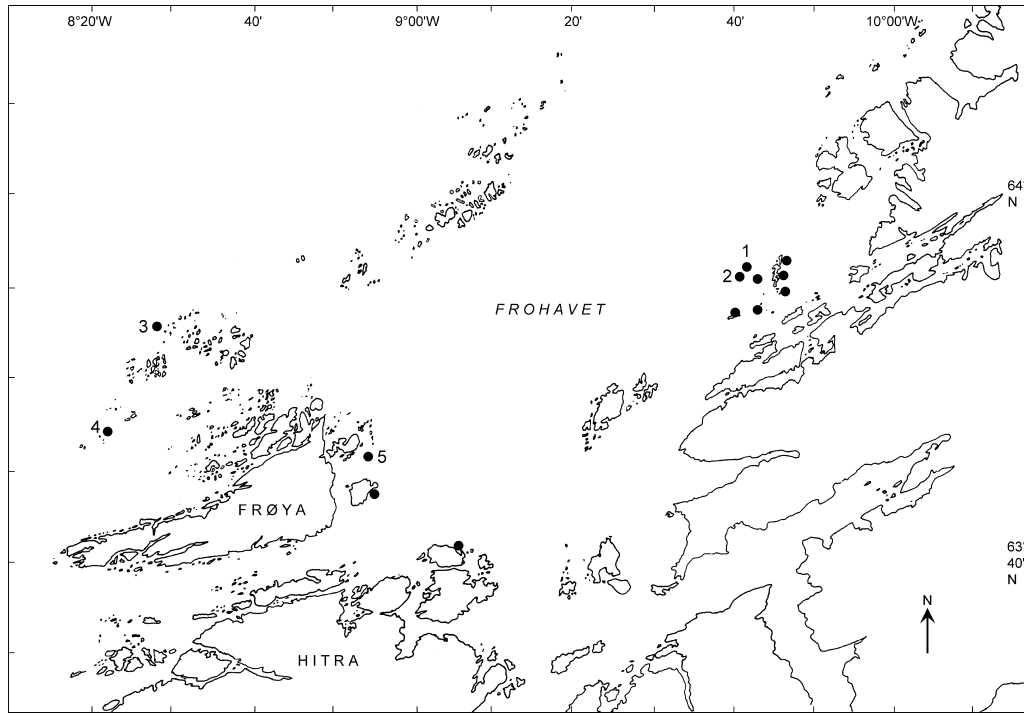


Figure 1. Study area in mid-Norway showing all stations where kelps (*Laminaria hyperborea*) and sea urchins (*Echinus esculentus*) were counted in unharvested kelp forest (black dots). At the numbered stations (Stns 1–5), additional recordings of kelp regrowth after kelp harvesting were carried out.

out between 3 and 9 m depth within an area not exceeding 30×30 m at each station.

Kelp recruitment in harvested areas

At Stns 1–5, kelp (*L. hyperborea*) was harvested within two periods during the winter 1997–1998 (17–26 November 1997 and 9–17 February 1998). Harvesting of *L. hyperborea* was carried out by using a dredge with pointed prongs, which was pulled through the kelp forest by boat (Briand 1991). The large kelps fastened between the prongs and were torn off the substrate, leaving open gaps in the closed kelp forest where the dredge had been pulled. All sampling of the regrowth of *L. hyperborea* was carried out within clearly harvested areas in the closed kelp forest at Stns 1–5.

Sampling was carried out in May 1998 (Stns 3–5), August 1999 (Stns 1–5) and August 2000 (Stns 1–5). A frame, covering 1 m^2 in 1998 and 1999 and 0.5 m^2 in 2000, was placed randomly on the bottom within the harvested areas between 4 and 11 m depth. We defined recruits as sporophytes up to about 10 cm long. All kelps longer than about 10 cm were collected within the sampling frame and taken to the surface. All sea urchins were counted, and the kelp recruits were counted in a total of five subareas (10×10 cm) within the frame. This was repeated three to four times per station. All collected kelps were counted and separated into hapteron, stipe and

lamina. Each separate part was weighed (only whole kelps at Stn 3 in 1998). The mortality of kelps may be related to the risk of being torn loose by drag forces by waves. Kain (1971) suggested that a high hapteron weight in relation to the weight of the rest of the kelp plants was crucial in avoiding being torn loose. This relationship was therefore examined. The age of each plant was determined by counting growth rings of the stipe, according to Kain (1963).

Statistics

Linear and multiple regressions were performed in order to examine the relationships between densities of kelp and sea urchins in unharvested kelp localities, and at the harvested sites between kelp recruits, biomass of kelp and density of sea urchins. Data were log transformed ($Y+1$) before regression analyses were carried out. Linear regressions were carried out on untransformed data to examine the relationship between accumulated kelp biomass and mean density of sea urchins at the harvested stations. Linear regressions were also performed on the relationship between hapteron weight and stipe and lamina weight of collected kelps from Stn 4 in 1998 and 1999. The portion of hapteron weight of regrowing kelps after harvesting at Stn 4 in 1998 and 1999 was compared in a t-test. Percentage values were arcsine transformed before the analysis.

Results

Kelp recruitment in unharvested areas

The recordings from Stns 1–5 do not represent totally independent samples, as the samplings were performed at the same stations during 1997–2000. However, as the purpose here is to examine a possible relationship between recordings of sea urchins and kelp density, all the recordings are included. The mean density of small *L. hyperborea* kelps varied between 0 and 118 m^{-2} on the unharvested sites, while the mean sea urchin density varied between 0.2 and 14.8 individuals m^{-2} (Figure 2A). Of the sea urchins, only *E. esculentus* was observed. More than 20 small kelps m^{-2} were only observed concurrently with densities of *E. esculentus* being <3 individuals m^{-2} (Figure 2A). A similar, but not so clear, negative relationship was observed between the density of *E. esculentus* and the density of intermediate-sized kelps, whereas no relationship was seen between the density of *E. esculentus* and the density of the canopy-forming kelps (Figure 2B, C, Table I).

The mean density of large, canopy-forming kelps varied between 1 and 19 m^{-2} . A clear negative relationship between the density of small kelps and the density of canopy-forming kelps was found (Figure 3). More than 20 small kelps m^{-2} were only observed where the density of canopy-forming kelps was less than 7 m^{-2} .

A linear regression between observations of the density of small kelps and the concurrent density of *E. esculentus* at the stations did not show a significant result ($P=0.057$), while a regression between the density of small kelps and the concurrent density of canopy-forming kelps showed a significant relationship between the variables ($P=0.008$) (Table I). However, when plotting all residuals against the independent parameter values, a pattern of increasing values of the dependent parameters was observed in both regressions, suggesting that a multiple regression could be appropriate (Zar 1999). A multiple regression where both the density of *E. esculentus* and the density of canopy-forming kelps were independent parameters resulted in a lower P-value ($P=0.003$), and an increase in the adjusted coefficient of multiple determination (R_a^2)

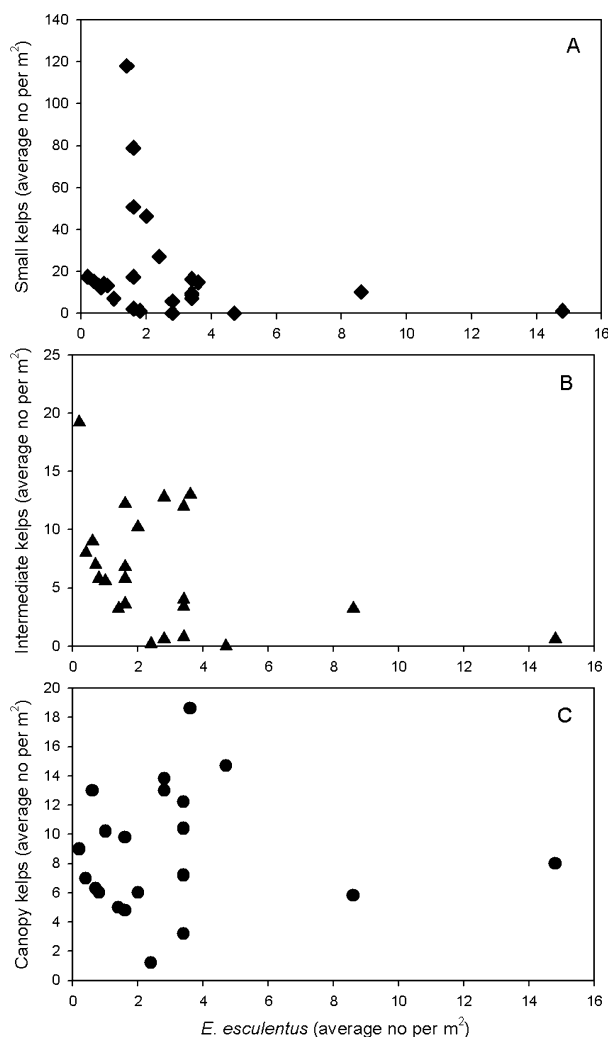


Figure 2. Relationships between the mean density of *Laminaria hyperborea* (A, B and C: different size categories) and sea urchins (*Echinus esculentus*) at 24 examined localities in pristine kelp forest 1997–2000.

value to 0.39 (Table I). This means that both parameters contributed to the variation in small kelps, and around 40% of the total variation in small kelps between the stations could be explained by the two parameters together.

Kelp recruitment in harvested areas

In May 1998, about 6 months after the kelp harvesting, up to 1500 recruits m^{-2} were observed

Table I. Regressions between the density of small kelps and independent factors in a natural kelp forest 1997–2000 ($n=24$). The type of analysis, P-value and r^2 or R_a^2 (adjusted coefficient of multiple determination) for each analysis are shown. A significant result ($P < 0.05$) is shown by an asterisk.

Dependent/independent factor	Type of analysis	P-value	r^2 or R_a^2
Small kelps/ <i>Echinus esculentus</i>	Linear regression	0.057	0.16
Small kelps/canopy-forming kelps	Linear regression	0.008*	0.29
Small kelps/ <i>E. esculentus</i> and canopy-forming kelps	Multiple regression	0.003*	0.39

at two of the three examined stations. The majority of these were recruits-of-the-year (<1 year). The mean density of 1-year-old kelps varied between 6 and 25 m⁻² at the stations (Figure 4). In addition, a cover of *Desmarestia* spp. was observed at the stations in 1998, especially at Stns 3 and 4 where *Desmarestia* spp. covered, on average, more than 50% of the substratum.

The density of *L. hyperborea* recruits was generally lower the following years, and in most cases less than 100 recruits m⁻². The age groups 1- and 2-year-old kelps dominated in the sampled kelp at the stations in both 1998 and 1999 (Figure 4). In 1999, overall higher densities of 1-year-old kelps (between 8 and 38 m⁻²) compared with 2-year-old kelps (between 1 and 17 m⁻²) were found, except at one station with very little regrowth (Stn 5). In 2000, about 2.5 years after the kelp harvesting, a more even-aged vegetation consisting of 1–3-year-old kelps dominated at most stations (Figure 4).

The age structure of the kelp vegetation in the harvested areas in 1998, about 6 months after the kelp harvesting, showed that even 6-year-old kelps were part of the remaining kelp understorey vegetation (Figure 4). In 1999, no kelps older than 4 years were found in samples from the harvested areas, suggesting a high mortality of kelps, especially among the eldest of the remaining kelps. In order to find possible intrinsic causes of mortality, the relationship between hapteron weight and the weight of the rest of individual plants was examined, and was found to change from 1998 to 1999 (Figure 5). The results showed a significant positive linear regression between the two variables in both years (P < 0.05), but with a higher regression coefficient in 1999 (0.08) than in 1998 (0.05), suggesting an overall increase in hapteron weight in relation to the

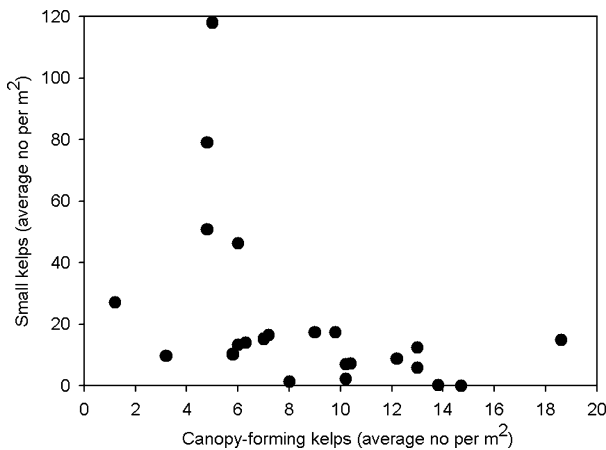


Figure 3. The mean density of small *Laminaria hyperborea* kelps plotted against the mean density of canopy-forming kelps. Data from a total of 24 recordings in pristine kelp forest 1997–2000. n = 3–5.

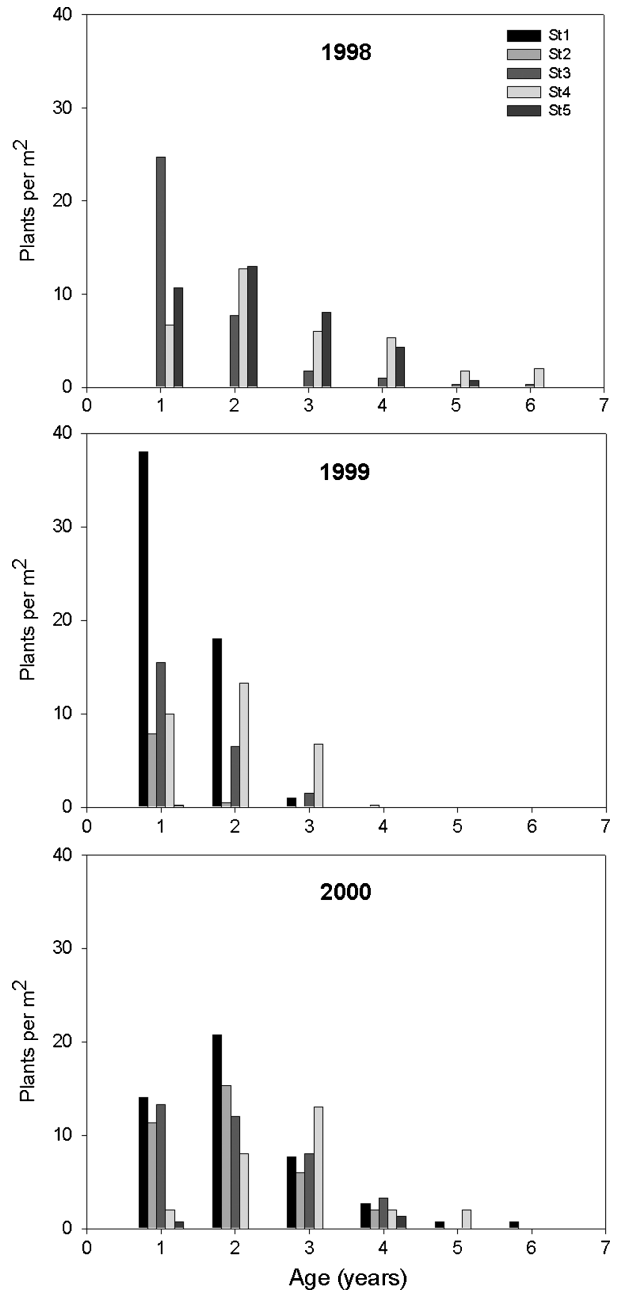


Figure 4. Age composition of *Laminaria hyperborea* from harvested sites 1998–2000. Samples were collected from three stations in 1998 and five stations in 1999 and 2000. Sites are separated by different histograms.

weight of the rest of the plant. The mean percentage hapteron weights of kelps from Stn 4 in 1998 and 1999 were compared by a students t-test after arcsine transforming the values. The test showed significantly different values between the years (P < 0.002), with hapteron weight consisting of 8.9% of the total weight in 1998 and 12.5% on average in 1999.

Increasing kelp biomasses accompanied by decreasing numbers of recruits after harvesting suggested a negative relationship between regrowth

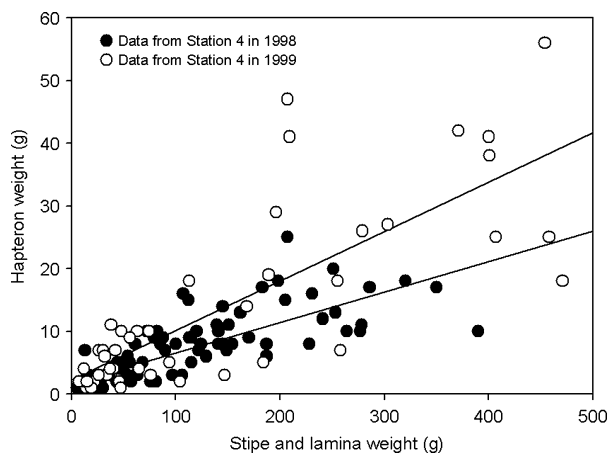


Figure 5. Hapteron weight in relation to the weight of the rest of the kelp in individual *Laminaria hyperborea* kelps harvested at Stn 4 in 1998 (filled circles) and 1999 (open circles). Linear regression equations are shown: 1998: $Y = 1.7 + 0.05X$ ($r^2 = 0.67$), 1999: $Y = 2.33 + 0.08X$ ($r^2 = 0.62$).

biomass and recruitment density. In order to test this, a regression between the density of recruits and kelp biomass on the harvested stations was carried out. Recruitment data from 1999 were omitted, as a fraction of the recruits-of-the-year had grown larger than the size we had defined as recruits, and had become part of the size fraction that was sampled in the squares. The data from 1998 and 2000 showed a significant negative relationship between regrowth biomass and recruitment density (Table II).

In order to test if there was a significant influence of sea urchin occurrence on recruitment density, a regression between the density of recruits and sea urchins at the harvested stations was carried out on data from 1998 and 2000. We observed a generally lower density of sea urchins in the harvested spots than in the surrounding kelp forests during 1998 and 1999, while the reverse was true at most of the harvested stations in 2000. In order to test if grazing activity from sea urchins both in and in the vicinity of the kelp harvested spots could influence the survival of kelp recruits we carried out regressions while using recorded densities of sea urchins within the harvested spots, recorded densities of sea urchins in the surrounding kelp forest nearby and average values of all sea urchin recordings per station

(Table II). No significant results were obtained in any of the three regressions, but the lowest P-value of the regressions was obtained with the sea urchin density in the harvested spots as the independent factor. When combining sea urchin density in the harvested spots and total biomass density as independent factors in a multiple regression, a significant relationship between these two factors and the density of recruits was found (Table II). In addition, the multiple regression showed an increase in the adjusted coefficient of determination for the multiple regression compared with the coefficient of determination for the linear regression between regrowth biomass and recruitment density (Table II), which suggests that both factors contribute to the variation in recruitment at the stations (according to Zar 1999).

In order to test the effect of accumulated sea urchin grazing on the regrowth of *L. hyperborea* at the harvested stations, a linear regression between kelp biomass in 2000 in relation to mean sea urchin density during the total observation period was carried out. The overall mean density of sea urchins at the stations during 1998–2000 ranged from 0.5 to 4.6 individuals m^{-2} (Figure 6). A significant linear regression was found ($P < 0.008$, $r = 0.96$), with around 1 kg *L. hyperborea* m^{-2} at the station with the highest density of sea urchins and around 18 kg *L. hyperborea* m^{-2} at the station with the lowest density of sea urchins (Figure 6).

Discussion

In the present study, the highest density of small kelps was found together with a low density of canopy-forming kelps or after removal of these. A relatively sharp limit of influence on the density of small kelps was found, with the highest densities of small kelps ($> 20 m^{-2}$) occurring when the canopy-forming plants grew sparser than 7 kelps m^{-2} in pristine kelp forest. The observed negative canopy effect was probably due to shading. A high density of canopy-forming *L. hyperborea* kelps has been shown to reduce the growth rate of understory plants strongly (Sjötun et al. 1998), and it has also been shown that in dense benthic algae vegetations, a

Table II. Regressions between the density of recruits and independent factors from kelp harvested sites in 1998 and 2000 ($n = 8$). The type of analysis, P-value and r^2 or R_a^2 (adjusted coefficient of multiple determination) for each analysis are shown. A significant result ($P < 0.05$) is shown by an asterisk.

Dependent/independent factor	Type of analysis	P-value	r^2 or R_a^2
Recruits/canopy biomass	Linear regression	0.018*	0.64
Recruits/ <i>E. esculentus</i> in kelp harvested area	Linear regression	0.312	0.17
Recruits/ <i>E. esculentus</i> in kelp forest	Linear regression	0.551	0.06
Recruits/ <i>E. esculentus</i> mean	Linear regression	0.400	0.12
Recruits/ <i>E. esculentus</i> in kelp harvested area and canopy biomass	Multiple regression	0.017*	0.73

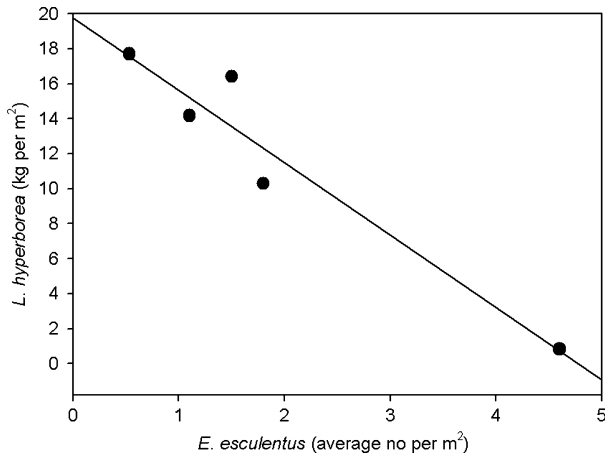


Figure 6. Mean *Laminaria hyperborea* biomass at the harvested stations 2.5 years after harvesting in relation to the mean density of sea urchins (*Echinus esculentus*) per station. Regression line is shown ($Y = 19.8 - 4.14X$), $r^2 = 0.93$.

period of no growth occurs before selective mortality of small plants takes place (Creed et al. 1998). At the observed limit of canopy kelp density, the photon fluence rates reaching the bottom may be below the minimum value needed to sustain growth in small kelps. Density-dependent mortality of small plants seems to be a common feature in most monospecific benthic algal vegetations (e.g. Graham et al. 1997; Creed et al. 1998).

Some small kelps were also recorded in our samples at stations with a very high average density of canopy-forming plants. This can be due to the temporarily variable light environment in the kelp forest. Occasionally a canopy plant may die, and leave a small opening in the closed canopy. In addition, in a wave-exposed kelp forest, waves constantly move the laminae and light flecks can reach the bottom, even in very dense canopies (Wing et al. 1993). Light conditions will therefore fluctuate and vary temporarily, even in a dense kelp forest, and on a small spatial scale there may be patches on the bottom that get sufficient light over a period of time for some recruiting kelps to survive.

The present study showed a clear canopy effect on kelp recruitment. However, in both pristine kelp forests and during regrowth after kelp harvesting, some effect of sea urchin grazing on the density of small kelps was evident, and the highest impact on recruitment was caused by the density of canopy-forming kelps and sea urchins in combination. In pristine kelp forest, a high density of small kelps ($>20 \text{ m}^{-2}$) was never recorded when the density of sea urchins exceeded around 3 *E. esculentus* m^{-2} . The density of *E. esculentus* varied spatially in the area, but the sea urchin densities were relatively low compared with what has been recorded in north Norway, where on average around 15 *S. droebachiensis*

and around 4 *E. esculentus* m^{-2} are reported from kelp forests close to overgrazed areas (Sivertsen 1997).

Even though sea urchin grazing had some negative effect on the density of small kelps in a pristine kelp forest, no effect was seen on the density of large kelps. This may partly be ascribed to the fact that *E. esculentus* has not been observed grazing on large plants, as *S. droebachiensis* has been shown to do (Hagen 1983; Hjørleifsson et al. 1995). Another point is that little recruitment is needed to maintain the density of canopy kelps, as these may persist for many years. In Norway, the mean age of canopy plants varies between 6 and 11 years, depending on geographical area (Rinde & Sjøtun 2005). Also, the density of *E. esculentus* has not been observed to be constantly high over long time periods, but may vary from one year to another at a locality (Sjøtun et al. 2000). This suggests that grazing pressure on recruits at a site may be relieved in periods. Thus, over a longer time period, a sufficient number of recruits may survive to replace dead canopy-forming kelps. In addition, we will expect that when there is insufficient kelp recruitment due to grazing, the canopy layer will become thinner after a while. This will provide more light and higher survival and growth of kelp recruits, and an increasing portion of recruits may escape grazing and result in recruitment to the canopy-forming plants. These conditions probably explain why an intact canopy layer was observed even at a sea urchin density of around 15 *E. esculentus* m^{-2} .

The first two summers after harvesting, less sea urchins were observed in the open areas than in the natural kelp forest, but the reason for this is not clear. It is possible that the occurrence of *Desmarestia* spp. in the harvested spots to some extent may have prevented sea urchins from entering these during the first summer after the kelp harvesting. *Desmarestia* spp. contain sulphuric acid and are thus avoided by grazers. Interestingly, Dayton (1985) showed that recruits of *Macrocystis pyrifera* in South America only survived when growing together with *Desmarestia ligulata*, which prevented sea urchin grazing.

Our study shows that both density-dependent mortality (due to high canopy density) and density-independent mortality (due to sea urchin grazing) may contribute to the overall mortality of juvenile kelps in pristine kelp vegetation. However, as only a few recruits are needed to replace dead canopy kelps, the canopy-forming layer will persist, even under a relatively high grazing pressure. A different pattern was seen during the regrowth process of the whole canopy layer. While a few surviving recruits are sufficient to replace dead canopy plants in a

closed kelp forest, a rapid restoration of the kelp biomass after canopy removal is dependent on a high survival of recruits. Removal of the canopy plants through harvesting temporarily released the recruits from light limitation, which resulted in increased survival of recruits the following year. Our results indicate that the increased recruitment caused some “swamping” of the grazers (*sensu* Vadas et al. 1992), as we observed relatively little influence of sea urchin grazing compared with the canopy effect on recruitment. However, the accumulated grazing activity over a period of time had a strong impact on the kelp regrowth. About 2.5 years after harvesting, a close relationship between the accumulated kelp biomass and grazing intensity at the stations was evident. The apparent contradiction in the influence of sea urchin grazing can be explained by the fact that density-dependent and density-independent mortality of kelp recruits are different processes. Density-dependent mortality is self-regulating and causes the mortality of recruits until the limiting factor is eliminated. In the present study, a new canopy layer rapidly formed at the stations with the lowest sea urchin densities, and this caused a high mortality of recruits. This strongly reduced the “swamping” effect. In addition grazers, when present, will remove recruits at a constant rate according to the grazing intensity, and when density-dependent mortality is eliminated, the grazers will continue to eliminate recruits. Presumably, larger kelps than those included in the “recruit” group in the present study may also be susceptible to grazing. This explains the fact that the formation of a new canopy had the largest influence on recruitment density, at the same time as kelp biomass accumulation was found to be directly related to accumulated grazing intensity.

The present study shows that the effect of sea urchin grazing on the regrowth of kelp biomass needs to be taken into account when planning and regulating kelp harvesting. Relatively modest densities of *E. esculentus* have an impact on the accumulated biomass of *L. hyperborea* after harvesting, and may consequently slow down the process of kelp regrowth and result in less harvestable biomass the following harvesting cycle.

We also identified a possible additional source of density-independent mortality of small plants. Our results from one of the kelp harvested stations showed that the hapteron weight constituted more of the total plant weight 1.5 years after the harvesting than at about 6 months after harvesting. This can be a result of selective mortality of plants with a small hapteron in relation to the total plant size after the removal of the canopy-forming plants, due to increased drag forces from waves after removal of

canopy plants. A relatively small hapteron will result in less area for attachment of a kelp to the substratum, and increase the chances of detachment for the kelp when exposed to strong wave forces. The results suggest that a high fraction of the oldest kelps disappeared from 1998 to 1999, and the regrowth vegetation thus contained younger kelps in 1999 than in 1998. However, an earlier study suggests that hapteron growth is relatively constant in all age groups in *L. hyperborea*, whereas it increases with overall increasing wave exposure (Sjøtun & Fredriksen 1995). Within a natural kelp forest, the water velocity is lower than it would have been without the kelp forest (Løvås 2000), and consequently the understory kelps grow in a relatively sheltered environment. Removal of the canopy-forming kelps probably results in a more wave-exposed environment for the understory kelps, which may have resulted in both selective removal of plants with a small hapteron in relation to total plant size and higher allocation of growth to the hapteron.

This study demonstrates that the *L. hyperborea* kelp forest has a generally high stability (persistent *sensu* Connell & Sousa 1983), mainly due to the annual excess production of recruits and survival of a number of recruits as part of the understory. Recruitment is not dependent on annual success; here we have found recruits to persist in the understory for 6 years, waiting for an opportunity to grow under improved light conditions. High recruitment will ensure kelp dominance, even by a relatively high grazing pressure. However, grazing from sea urchins, even in modest densities, influences biomass accumulation strongly in a negative way during regrowth of the canopy plants. In the present study, the disturbance is caused by harvesting, but we expect that similar processes and interactions with grazers can be found, e.g. during regrowth after a heavy storm causing kelp mortality. An average density of 4.5 *E. esculentus* m⁻² was observed to prevent the re-establishment of kelp biomass during a period of 2.5 years after canopy plant removal. For *S. droebachiensis*, a similar critical density was found at a population density of 10 individuals m⁻² (Christie et al. 1995). This means that the *L. hyperborea* kelp forest has high stability, but less resilience, when it comes to the effects of sea urchin grazing.

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