

## Overgrazing of kelp beds along the coast of Norway

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### Abstract

The aim of this study was to better understand the down-grazing of kelp beds by sea urchins (*Strongylocentrotus droebachiensis*) along the coast of Norway. Barren grounds were first observed in sheltered areas along the coast of the counties of Trøndelag, Nordland and Troms in 1974. In the 1980s, the barren grounds spread to areas more heavily exposed to waves. In the 1990s, the kelp beds were re-established in some localities in southern Trøndelag, initially in wave-exposed areas. In the northernmost parts of Norway, i.e. the counties of Troms and Finnmark, the barren ground areas may still be increasing. Crabs (*Cancer pagurus*) and common eiders are the most common predators on urchins. Predation on sea urchins in kelp beds is probably not among the factors that limit the sea urchin populations. Along the coast of Nordland and further north, sea urchins are infected by nematodes, resulting in a low, but significant increase in their mortality. No re-growth of kelp beds has been found in the most infected areas. In the late 1960s and the early 1970s, a high occurrence of echinoderm larvae was observed in deeper waters. This was a period with cold water, which may have caused high recruitment of sea urchins. The bet-hedging life strategy of sea urchins may account for the sudden increase in the size of the populations. In the present paper I propose the hypothesis that higher individual growth rates and higher mortality rates in the south than in the north may explain the decrease in the populations, which may in turn account for the re-growth of kelp in the southern areas.

### Introduction

Sea urchin populations are known to increase to such a high level that they overgraze the kelp beds in many temperate areas around the world, with barren grounds as a result. Several theories and critical reviews have been presented to explain why the densities of sea urchins have increased so dramatically (e.g. Lawrence, 1975; Dayton, 1985; Elnor & Vadas, 1990; Steneck et al., 2002). One frequently proposed explanation is low predation on sea urchins. High recruitment of sea urchin larvae in combination with favourable hydrographic conditions is another hypothesis (Forman, 1977; Ebert, 1983; Hart & Scheibling, 1988; Wing et al., 1995). Parasites in the sea urchins may also cause large oscillations in the size of the populations (Scheibling & Hennigar, 1997).

Re-growth of kelp beds in barren grounds dominated by sea urchins has been observed in several areas around the world, e.g. California and Nova Scotia (Hawkins & Hartnoll, 1983; Scheibling & Hennigar, 1997, respectively). Will variation in the factors that increase sea urchin populations (e.g. high recruitment, low predation, or low parasite infection) also cause a reduction in the populations? Will other factors such as abnormal weather events and changes in hydrographical conditions affect the populations (Parsons & Lear, 2001; Steneck et al., 2002), or may variation in the parameters related to population dynamics explain the oscillations (Ebert, 1985)?

The cycles from kelp beds to barren grounds and back again to kelp beds may be explained with reference to the life history of the sea urchins, which is characterised by bet-hedging strategies (Ebert, 1982, 1985).

The bet-hedging theory postulates that an extended reproductive life-span, a high rate of adult survival, and low annual reproductive effort are adaptations to compensate for the low and highly variable survival rate of first-year juveniles (Stearns, 1976, Roff, 1992).

The proliferation of barren grounds along the coast of Norway, from Nordmøre and further north to the Russian border, has been reported since the early 1980s (Skadsheim et al., 1995; Sivertsen, 1997a). Barren grounds have previously been observed in the areas around Stavanger by von Düben (1847) and around Tromsø by Döderlein (1900). Re-growth of kelp beds in barren ground areas, observed from the late 1980s, have been recorded in some overgrazed areas in the south, i.e. in Nordmøre, Trøndelag and southern Nordland (Hagen, 1995; Skadsheim et al., 1995; Christie et al., 1995; Sivertsen, 1997a).

The aim of this paper is to get a better understanding of the down-grazing and re-growth of kelp beds by the sea urchin *Strongylocentrotus droebachiensis* (O. F. Müller), in view of both its regional and local distribution on the coast of Norway. The focus will be on predation, parasitism, recruitment, population dynamics and the life history of the sea urchins.

## Materials and methods

The area investigated stretches from west of Lindesnes (58°N, the southernmost point of Norway) to the North Cape (71°N, the northernmost point of Norway) and eastwards to the Russian border. This coastline consists of large fjords and an archipelago of hundreds of thousands of large and small islands, some of them at a distance of more than 50 km from the mainland. The archipelago is here divided into three zones. The outer archipelago consists of areas where the swells frequently reach the shores. In the inner archipelago the sea water is influenced by fjord water. In between these zones is the middle archipelago, which is affected by swells and fjord waters to a lesser extent or not at all. This division is suitable for describing the pattern of barren grounds and of sea urchin density and size frequency (Sivertsen, 1997a; 2003). The Norwegian Coastal Current runs northwards along the entire coast.

*Laminaria hyperborea* (Gunn.) Foslie. dominates the kelp beds in wave-exposed areas, while *L. saccharina* (L.) Lamour. is most common in sheltered areas. *L. saccharina*, with its prostrate stipes and lamina may be easier for sea urchins to graze than *L. hyperborea*, with its stiff erect stipes. During the over-grazing process

the kelp and the undergrowth are first grazed. In wave-exposed areas juvenile *Laminaria* sp. were first grazed down, which inhibited their re-growth and left only remainders of canopy individuals, and gradually the canopy kelp disappeared (Sivertsen, 1997a).

An Echinoderm larvae index (EI) was used to estimate the occurrence of Echinoderm larvae, based on unpublished zooplankton samples from 1969–1983 from The Institute of Marine Research (IMR) in Bergen. Plankton hauls were taken in six localities. Three southern localities were at 59°N, 61°N and 63°N respectively, and three northern localities at 68°N, 68°N and 71°N respectively (Figure 1). Two plankton net hauls were performed about twice per month, a shallow one from 50 m depth to the surface and a deep one from 300 m to the surface in each locality. A short-cut method was used to identify dominating plankton species in the samples. The names and stages of the first 100 individuals in sub-samples were identified microscopically, and then the number (N) of Echinoderm larvae out of 100 zooplankton individuals was counted. To estimate the number of Echinoderm larvae in a whole sample, the volume of the sub-sample, or the number and the volume of each identified species, is required (Hjort & Ruud, 1927; Wiborg, 1962). These estimates were not made here. Instead an EI (Echinoderm Index) was made. The Echinoderm larvae were not identified to each species, which brings an element of uncertainty into the data. The net volume (when large individuals such as medusae and large euphausiids were removed) in mL (V) of each sample was measured. The EI used was  $EI = N \cdot V$ . The average EI from samples taken in March, April and May (zero indices included) was used. Deep and shallow hauls were separated. At the same time temperature and salinity were measured close to the localities where the zooplankton samples were taken. The hydrographic data are stored, and mean values of temperature for March, April and May have been estimated by The Norwegian Oceanographic Datacenter at IMR.

Many species prey on sea urchins. Hooper (1980) lists e.g. *Tealia*, other anemones, small sea stars, *Solaster*, *Leptasterias*, crabs (*Hyas*, *Cancer*), lobsters, cod, flounders, wolf-fish and sea-birds as predators on sea urchins in the Newfoundland waters. These groups also occur on the coast of Norway. Predation on sea urchins was estimated from counts of sea birds and landings of fished stocks. Between 1983 and 1986 the sea-bird abundance was estimated in Trøndelag and Helgeland, 63°N–66°N (Follestad et al., 1986), both of which are large areas dominated by barren grounds

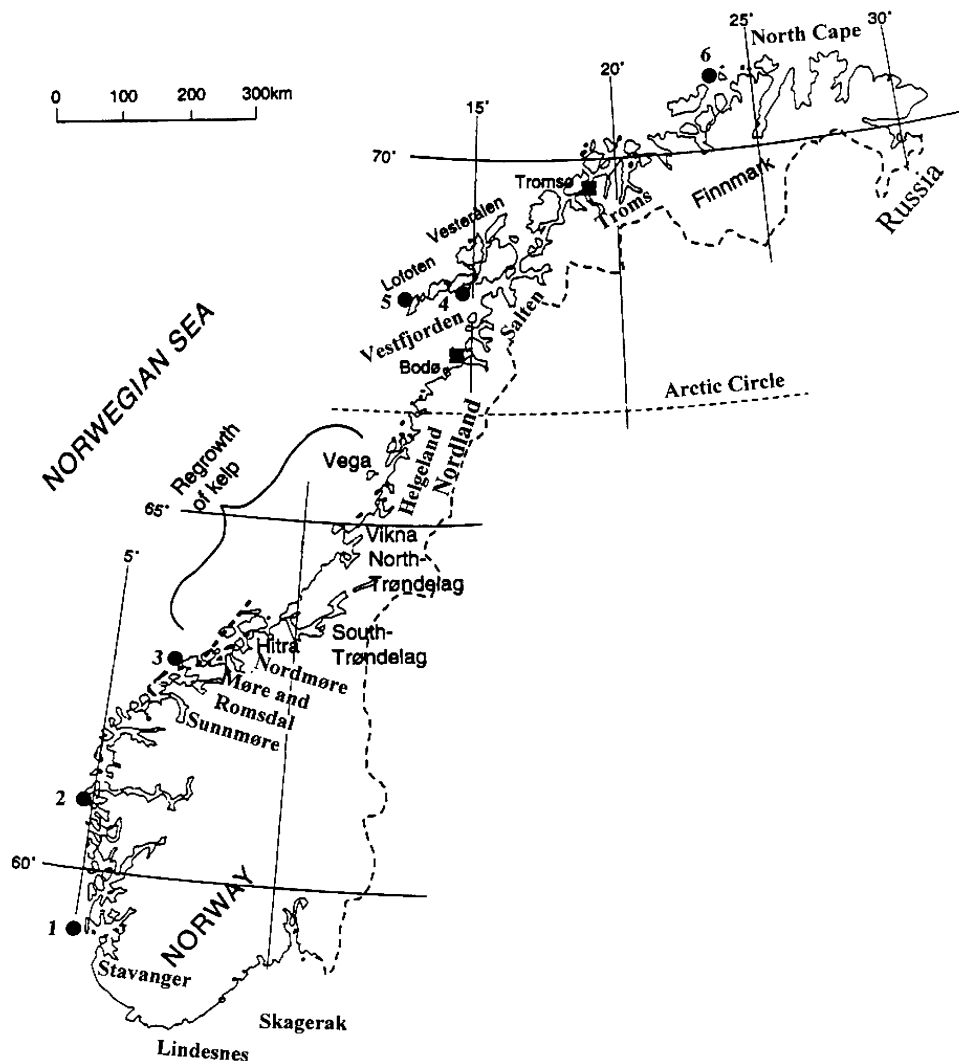


Figure 1. Map of the coast of Norway with reference to regions and localities. Broken line outside Nordmøre indicates southern border of barren grounds.

(Sivertsen, 1997a). These counts are of sea-bird numbers 10–20 years ago. Estimates of fishable stocks have not been made for this area. Landing statistics were therefore examined, assuming that the landings reflect variations in the size of the stocks (Fishery statistics, 1961–1973).

The consumption of sea urchins has been estimated in relation to the size of the predator populations, the percentage of sea urchins in their diet, the number of days per year of feeding on sea urchins, and also the amount of food needed by the individual species assumed to prey most on sea urchins in the Trøndelag and Helgeland areas (presumably eight species altogether). Wolf-fish, plaice, lobsters and

crabs are assumed to be the most important fishable stocks consuming sea urchins. To estimate the size of fishable stocks, the mean landings in the areas in Trøndelag and Helgeland for the years 1961–74 were used (Fishery statistics, 1961–1973). The landings for plaice, wolf-fish, lobsters and crabs are multiplied by five, assuming a mortality of 0.2 for all of them. There are, however, obvious problems in using fish statistics for this purpose, since fishing gear, fishing intensity, prices, and management may influence landings as well as stock abundance. Plaice and wolf-fish feed in shallow areas half the year, and in this period 10% of their consumption is assumed to consist of sea urchins. Miller (1985) assumes that lobsters consume

an annual amount of sea urchins that corresponds to their own weight, and crabs one and a half times their own weight. These estimates are also applied here. It is assumed that 20–25% of the diet of common eiders and king eiders are sea urchins (Bustnes & Lønne, 1996) and that they feed 250 and 150 days a year, respectively (Mehlum & Gabrielsen, 1995). Sea urchins also constitute 5% of the food for gulls, and gulls feed every day throughout the year (Karl Birger Strand, personal communication). The physiological estimates for need of food for each species are shown in Sivertsen (1997b).

The pattern of barren grounds along the coast of Norway is based on the surveys in the 1980s and the 1990s by Sivertsen (1997a) and Skadsheim et al. (1995). While making these surveys in the early 1980s, we also interviewed fishermen, asking them when they had first observed barren grounds. In addition, we also investigated the occurrence of kelp beds and barren grounds at Hitra in South-Trøndelag (63°33'N) during summer time every second or third year since 1980. Bottom areas from low water tide to 5–7 m depth were investigated by using a small boat, going along the shoreline. Dominant kelp species, and densities and size distribution of sea urchins were recorded using a sea telescope (a tube with a transparent clear glass in the lower end). Sea urchin occurrence and the borders between kelp beds and barren grounds were registered.

## Results

### *Distribution of barren grounds*

From about 1974, barren grounds were seen by fishermen at Hitra (63°30'N), Vikna, Vega, Bodø and Troms (70°N). Surveys in 1980 and later showed that barren ground areas were dominated by large densities of sea urchins, *S. droebachiensis*, but *Echinus esculentus* Linné occurred frequently during the overgrazing process (Sivertsen, 1997a). Stretches of barren grounds now occur from Nordmøre (63°N) and further north along the entire coast to the Russian border (Figure 1). Along the entire stretch of this coastline, barren grounds occurred more frequently in the middle and inner archipelago than in the outer archipelago and were rare or absent in the fjords. In general, barren grounds occurred in sheltered and moderately exposed areas, but not in areas heavily exposed to waves (Sivertsen, 1997a, 2003).

### *Predation*

Common eiders and crabs are estimated to be the dominant predators on sea urchins along the coast of Trøndelag and Helgeland (Table 1). A total of 43,200,000 kg were consumed in the 2400 km<sup>2</sup> area, corresponding to 19 g m<sup>-2</sup> y<sup>-1</sup> or one individual of 46 mm in diameter m<sup>-2</sup> y<sup>-1</sup>. Wolf-fish, plaice, herring gulls, great black-backed gulls and common eiders are common all along the coast. Crabs and lobster are mainly found from Helgeland (66°N) and southwards, while king eiders are most common in the north.

### *Echinoderm larva recruitment*

EI ranged between 0.5 and 21, reaching its maximum at temperatures below 4 °C, while at higher surface temperatures EI exceeded 3.5 only twice (Figure 2). High EIs were found in deep waters in the northern area from 1969 to 1974. This was in the period prior to the first observations of sea urchins dominating barren ground areas. In the south (59°N–63°N), where no barren grounds were found, EI did not exceed 6 in the period before 1974, neither in samples from deep nor shallow water.

### *Re-growth of kelp beds*

Re-growth of kelp in previously barren ground areas dominated by sea urchin has been observed in the southern part of the overgrazed areas in Nordmøre,

Table 1. Predation on sea urchins on the coast of Trøndelag and Helgeland, an area of 2 400 km<sup>2</sup>. The consumption is estimated from the mean value of catches of fish and Crustacean populations from 1961–1973. Birds counted in 1983–1986.

Species	Consumption of sea urchins (1000 kg y <sup>-1</sup> )
Common eiders ( <i>Somateria mollissima</i> )	23 500
Crab ( <i>Cancer pagurus</i> )	11700
Herring gulls ( <i>Larus argentatus</i> )	2 650
Blackbacked gulls ( <i>L. marinus</i> )	2 250
Plaice ( <i>Pleuronectes platessa</i> )	1 215
King eiders ( <i>S. spectabilis</i> )	940
Wolf-fish ( <i>Anarchichas lupus</i> )	820
Lobster ( <i>Homarus vulgaris</i> )	125
Sum	43 200

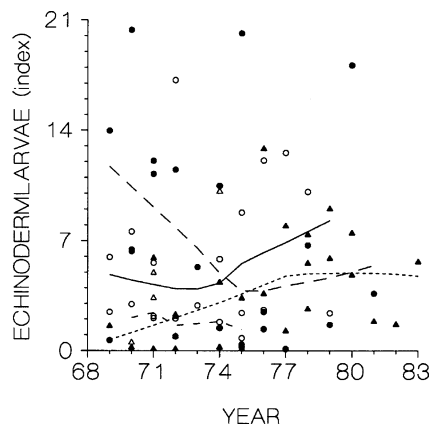


Figure 2. The Echinoderm larvae index (EI) is shown as a function of year of sampling (see text). Samples were taken by vertical plankton hauls in three locations (see Figure 1) at Vestlandet (1, 2, 3) and three locations (4, 5, 6) in northern Norway north of the Arctic Circle. The samples were pooled and divided into four groups to present EI in: 1) North-Norway, depth 50–0 m (empty circles and solid line). 2) North-Norway, depth 300–0 m (filled circles and large broken line). 3) Western Norway, depth 50–0 m (empty triangles and small heavy broken line). 4) Western Norway, depth 300–0 m (filled triangles and very small broken line).

Trøndelag, and occasionally in the southern part of Nordland (Skadsheim, 1995; Stien et al., 1995; Hagen, 1995; Sivertsen, 1997a), but not further north (Sivertsen 1997a, 2003). Investigations in the early 1980s showed that higher densities of *S. droebachiensis* were found more frequently in barren ground areas south of the Arctic Circle ( $52.2 \pm 6.9$  individuals  $m^{-2}$ ) than north of it ( $26.1 \pm 2.5$  individuals  $m^{-2}$ ) (Sivertsen, 1997a). New investigations in 1992 showed a decrease in densities to about 20 individuals  $m^{-2}$  in the area south of the Arctic Circle (Skadsheim et al., 1995) to even lower densities than in the north. No changes in densities from the early 1980s to 1992 were observed in the north (Skadsheim et al., 1995; Sivertsen, 1997a). The size distribution of sea urchins in barren grounds, pooled from eight or more localities from eight geographical zones in the south-north gradient, showed that large sea urchins dominated in the south (Figure 3). The mean size gradually decreased northwards, where individuals of 20–30 mm in diameter dominated in the northern-most area.

In an area north of Hitra ( $63^{\circ}33'N$ ) in Trøndelag, which was investigated every second or third year since 1980, the extent of barren grounds increased through the 1980s, reaching a maximum around 1987 (Figures 4A). The barren grounds expanded gradually outwards to more wave-exposed localities. After 1987

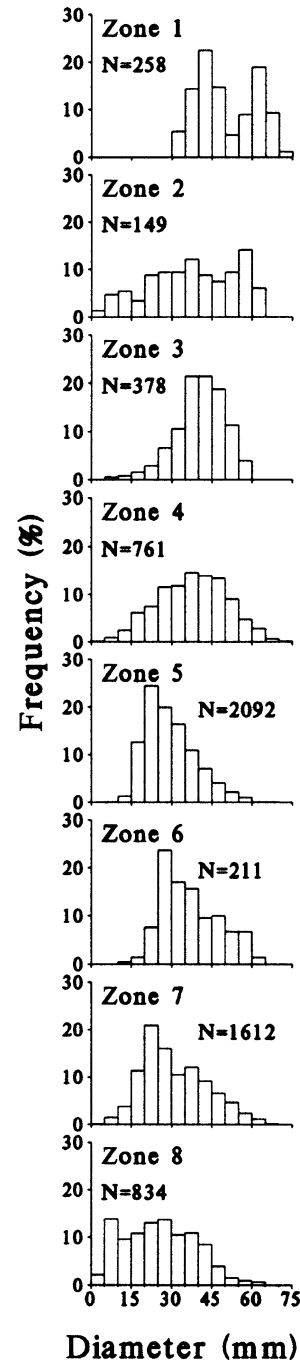


Figure 3. The size distribution of sea urchins (*S. droebachiensis*) on barren grounds along the coast of Norway. Zones refer to areas 1: Møre and Romsdal, 2: South Trøndelag, 3: North Trøndelag, 4: Helgeland, 5: Salten, 6: Lofoten and Vesterålen, 7: South Troms, and 8: North Troms. (From Sivertsen 1997).

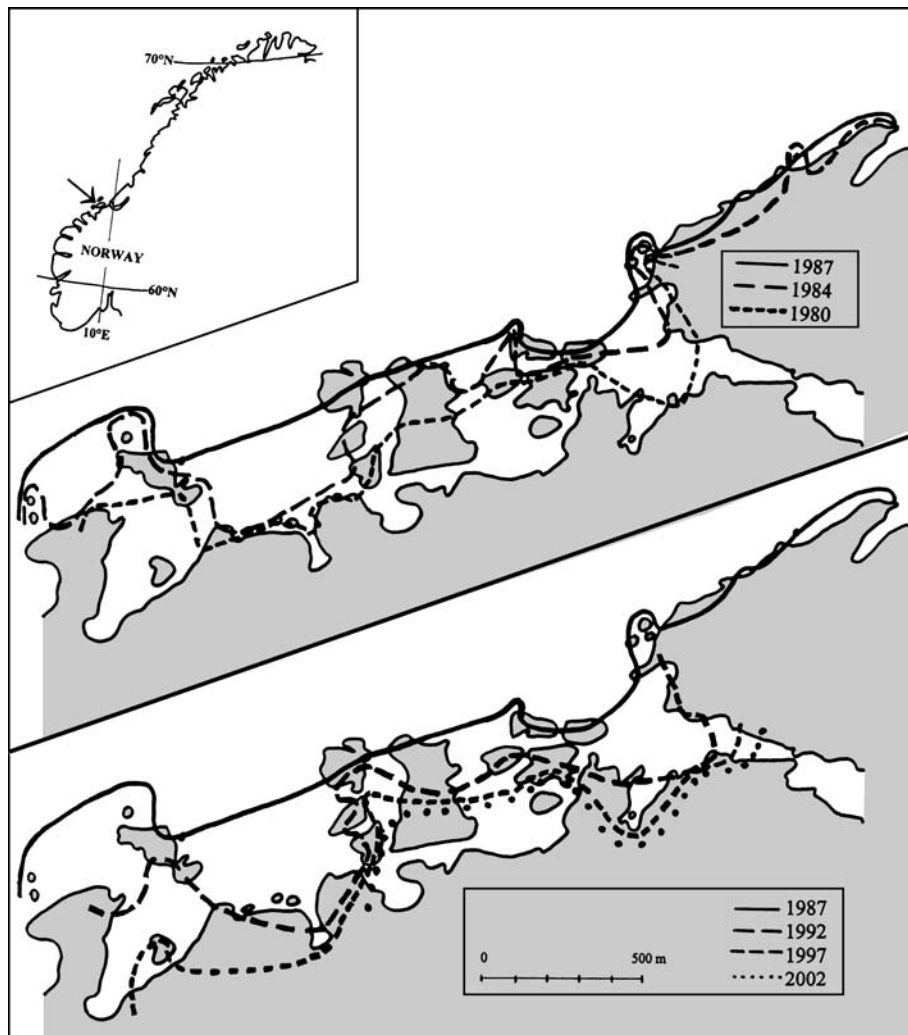


Figure 4. The extent of kelp beds and barren grounds in an area at Hitra, South-Trøndelag. Lines show the border between kelp beds and barren grounds in different years. Top: decrease of kelp beds, and increase of barren grounds from 1980 (small broken lines) 1984 (large broken lines) and 1987 (solid lines). Bottom: increase of kelp beds and decrease of barren grounds from 1987 (solid line), 1992 (large broken line), 1997 (small broken line) and 2002 (dotted lines).

the barren ground areas decreased, and kelp beds underwent a period of re-growth (Figures 4B). Re-growth was first observed in those wave-exposed areas that had become barren most recently. Barren grounds gradually retreated and prevailed only in sheltered areas. In some sheltered areas, where barren grounds were observed in the 1980s, areas of them still remain. One locality that was found barren in 1974 is still barren 30 years later. In localities with re-growth of kelp, *Saccorhoza polyschides* (Lightf.) Batt. often dominates together with *L. hyperborea*, but also *L. saccharina*, *Desmarestia aculeata* (L.) Lamour. *Halidrys siliquosa*

(L.) Lyngb. and annual brown algae frequently occur.

### Discussion

The fluctuations in densities and size distribution in sea urchin populations along the coast of Norway may be explained with reference to population dynamics. My hypothesis is that the bet-hedging strategy is a characteristic of sea urchin populations along the coast of Norway, and that predation and parasitism may have only minor influences.

### Predation

An estimate of predation on sea urchins was made in order to establish if low predation could account for the increase in sea urchin populations (Table 1). The eight species assumed to prey on sea urchins most effectively in the area Trøndelag and Helgeland (2400 km<sup>2</sup>), have a mean consumption of 43 200 000 kg y<sup>-1</sup> or 19 g m<sup>-2</sup> y<sup>-1</sup>. A production of 19 g m<sup>-2</sup> y<sup>-1</sup> is needed to compensate for this mortality. The mean annual mortality rate ( $Z$ ) of *S. droebachiensis* in kelp beds was estimated as 0.47, which corresponds to a 40 % mortality of standing stock of sea urchin per year (Sivertsen & Hopkins 1995). If  $Z = P/B$ , where  $P$  = productivity of *S. droebachiensis* and  $B$  = mean biomass of *S. droebachiensis* (Pitcher & Hart, 1982), and assuming that sea urchin mortality is caused exclusively by predation, the above equation gives  $B = 41 \text{ g m}^{-2}$ . Biomasses were estimated from individual densities and mean individual weight from localities described in Sivertsen (1997a). The mean sea urchin biomass was 400 g m<sup>-2</sup> in the area north of Bodø where there was no sign of overgrazing. During the overgrazing process, the mean sea urchin density was about 1500 g m<sup>-2</sup> both south and north of Bodø (Sivertsen, 1997b). These localities did not show any sign of overgrazing. The recorded biomass of sea urchins was 10–40 times larger than what is needed to compensate for the predation. From these estimates it may be concluded that the predation on sea urchin populations is too low to support claims that these populations are predator-limited, at least in the last years prior to the appearance of barren grounds. It is possible that predation affects only sparse populations of sea urchins. There is no indication that there are any keystone predators on the urchin populations along the coast of Norway, as is proposed in Nova Scotia (review in Elnor & Vadas, 1990). However, Jackson et al. (2001) have used historical data to show that in the West Atlantic there have been time-lags of decades or even centuries between the onset of over-fishing and consequent changes in the ecological communities.

It has been proposed that extensive fishing of cod (*Gadus morhua* L.) and other predatory fish in spawning aggregations in Maine and Nova Scotia in the Northwest Atlantic in the 1930s and later was accompanied by a rapid decline in the numbers and the body size of coastal cod in the Gulf of Main, and this coincided with their extirpation from the coastal zones (Steneck et al., 2002). Dominant fish predators in the coastal zone have been replaced by small, commercially less-important species, and large predatory finfish have

remained functionally absent from the coastal regions of the western North Atlantic (Steneck et al., 2002). The extirpation of coastal cod and other fishes by the 1940s in the Gulf of Maine has resulted in the functional loss of apex predators, which has fundamentally altered the coastal food web, as lobster, crabs and sea urchins have become more abundant (Steneck et al., 2002). This change was observed in the 1960s in the Gulf of Main and a decade later in Nova Scotia (Steneck et al., 2002). They conclude that after the loss of apex predators the high density of sea urchins caused the denudation of the coastal zone.

In a large research program on the sea-ranching of cod on the coast of Norway (PUSH), during the 1990s, the diet of cod was investigated (Svåsand et al., 1998). Three of the regions investigated were in North Norway where large areas were overgrazed and dominated by sea urchins. Cod at the age of two years or younger, and smaller than 30 cm, mainly fed on benthic invertebrates. According to Svåsand et al. (1998), Echinoderms and Mollusca are not important as food for cod. As cod grow, first krill and later fish become a more important part of their diet. The Norwegian Coastal cod is managed separately from the Norwegian Arctic cod. The quota for harvest is 40,000,000 kg a year, and 30–40,000,000 kg have been harvested yearly since the 1950s. Cod has probably little or no direct influence on the occurrence of sea urchins on the coast of Norway.

### Recruitment

The first observations of barren grounds were made in several localities along the coast of Norway at about the same time, in 1974. High densities of sea urchins may be caused by high recruitment of sea urchin larvae that have spread with the Norwegian Coastal Current. A high occurrence of Echinoderm larvae was found in North Norway in the late 1960s and early 1970s. These larvae were not identified to species. However, *S. droebachiensis* spawns in March, and its larvae have a pelagic stage for 6–8 weeks (Emlet et al., 1987). Ophiuroids spawn in late April, and the sea cucumber *Cucumaria frondosa* spawns at the end of March, and the larvae settle in May in the Tromsø area (Falk-Petersen, 1982). No large increases in these Echinoderm species (other than sea urchins) have been reported on the coast of Norway. However, it cannot be definitely concluded that the observed larvae were sea urchin larvae.

If environmental factors affect recruitment, growth and mortality of Echinoderm larvae, then it might be possible to explain temporal variations in recruitment in the benthic populations in terms of large-scale oceanographic events such as temperature anomalies (Hart & Scheibling, 1988). Ebert (1983) has reviewed the episodic nature of annual recruitment of echinoids, and considers the most important factors to be upwelling, the abundance of planktonic and benthic predators, and transport by water currents. He also reviews evidence for correlations between temperature and recruitment anomalies. His results indicate that strong high-temperature abnormalities correlate with high recruitment for some sea urchins, but that recruitment of *S. purpuratus* off southern California may be inversely related to temperature: in this area recruitment is most abundant after the coldest winters. Forman (1977) observed unusually large populations of *S. droebachiensis* in locations in the Strait of Georgia, British Columbia. These populations consisted mainly of a single cohort that settled in 1969. He suggests that the spring temperature normally is marginal for the development of *S. droebachiensis* larvae, and that 10 °C is an upper limit for larval development in that area. He concludes that record low spring temperatures in 1969 probably led to intensive recruitment that year. Wing et al. (1995) monitored settlement of sea urchins (*Strongylocentrotus* spp.) and crabs (*Cancer* spp.) and concurrent physical variables in northern California. Winds favourable to upwelling led to lower temperatures, higher salinities, and lower subsurface pressure, while periods of relaxation from upwelling typically caused a lagged reversal of each of these trends. Sea urchins settled primarily during an event of unusual relaxation which possibly involved remote physical forcing. Sea urchin and crab settlement were negatively correlated. Barren grounds were first reported from St. Margaret's Bay, Nova Scotia, in 1968, but the overgrazing probably began a few years earlier (Breen & Mann, 1976a,b). Hart and Scheibling (1988) investigated deviations from long-term monthly mean spring temperature in Halifax Harbor, Nova Scotia, Canada, in the period 1952 to 1986 and found a single large positive deviation of 3.5 °C higher than normal in June 1960. This was eight years before the first report of destructive grazing, and Hart and Scheibling (1988) propose that high urchin recruitment in 1960 as a result of high temperature caused the subsequent high population densities of sea urchins.

Braarud and Nygaard (1980) studied the phytoplankton communities in coastal waters off

the coast from Møre and Romsdal to Vesterålen in the years 1968–1971. In the Vestfjord – Vesterålen area they found a mixed spring diatom community during the four-year period. Here they found remains of the same plankton association that they found on the coast of Møre and Romsdal and Trøndelag one month earlier, suggesting that Helgeland is a transition area for the two regions. This shows that offshore transport of plankton takes place, and in some years this transport is sufficiently strong to be identified far from its source. Braarud and Nygaard (1980) suggest that these “offshore coastal areas” may become far more extensively influenced by such long-distance transport than the shore regions from Møre to Vesterålen. Variability in the meteorological and hydrographical situations may lead to different effects from year to year. This transport shows that plankton communities can spread over long distances with the Norwegian Coastal Current.

Fishermen were interviewed randomly as we met them during our research, but the interviews were not performed in a systematic way. Doubt about larval species and the haphazard way in which the interviews on observations of barren grounds were made obviously weaken the claim that barren grounds appeared simultaneously along the coast of Norway. Therefore it seems reasonable to question the importance of these two factors for the increase in the size of sea urchin populations causing the overgrazing of kelp beds on the coast of Norway.

In 1970 the temperature both at the surface and in deep areas along the Coast of Norway was 1–2 °C lower than the normal annual mean value, and the Atlantic water had a cold period from 1965 to 1970, followed by a warmer period (Asplin & Dahl, 2003). The North Atlantic Oscillation index (NAO) is used to explain large-scale oscillations of many important species in the North Atlantic (Parsons & Lear, 2001). High NAO indices benefit some species while low indices benefit others. The NAO index was at an extreme low in the 1960s; it changed to positive after 1970 and reached its positive extreme during the late 1980s (Parsons & Lear, 2001). It may be possible to explain temporal variations in recruitment in terms of abnormal oceanographic events, as proposed by Hart and Scheibling (1988), or of long-term oceanographic events such as temperature variation, as explained by the NAO index. Larvae in areas along the northern coast can be spread over long distances by the Norwegian Coastal Current. High larval recruitment along the coast of Norway may have occurred in periods of cold water in the late



1960s. Fast individual growth of sea urchins to adult size may have occurred in the warm period in the early 1970s. From 1974 on, this may have led to a rapid increase in the sea urchin population, which became high enough to overgraze the kelp beds, resulting in barren grounds.

#### *Re-growth of kelp beds*

The patterns of density, the size distribution of sea urchins, and the re-growth of kelp in previously barren ground areas may yield important knowledge about the sea urchin populations and the dynamics between sea urchins and kelp beds. The densities and size distribution of the populations vary along the coast. North of 67°N small individuals were more abundant than larger ones, and the densities were relatively constant over time. This may explain the stability in populations with good recruitment. South of the Arctic Circle large individuals were more abundant than smaller ones, and the densities of urchins decreased significantly since the early 1980s (Sivertsen, 1997a) to 1992 (Skadsheim et al., 1995). This may indicate unstable populations with low recruitment, and the sea urchin populations may die out as the individuals become old and die. These results may explain differences in the population dynamics of sea urchins from the south to the north. Differences in mean annual temperature may explain these changes. At 63°N, the mean annual water temperature is 2.5 °C higher than at 71°N. As a consequence of physiological processes in sea urchins, the higher temperature in the south may account for the higher somatic growth rates and higher mortality rates of the sea urchins in the south than in the north (e.s. Pauly, 1982; Roff, 1992). Thus the duration of the life cycle for the sea urchin may be shorter in the south than in the north. Stability in the sea urchin populations in the southern areas may not be attained until the first few cohorts have gone through their life cycle and died. When the old individuals die, the densities may decrease to a level at which the re-growth of kelp will start.

Growth rates of sea urchins have been measured only in the areas from Bodø to Tromsø (Sivertsen & Hopkins, 1995), a distance which is too short to predict anything about the variation along the coast as a whole. Therefore growth parameters for cod and prawn (*Pandalus borealis* Krøyer) are here used for comparison. Growth rates of cod have been investigated in Vestlandet (60°N) and Troms (70°N) in the PUSH program (Svåsand, 1998). Mean individual length at the same

age were about 30% shorter in Troms than in Vestlandet. Rasmussen (1967) found that female prawns normally spawn at the age of 2.5 y in Skagerak when the temperature is 6 °C. In the period 1963 to 1966 the bottom temperature in Skagerak decreased by two degrees, and the females did not spawn until the age of 3.5 to 4.5 y. Hopkins and Nilssen (1990) found prawns spawning at the age of 4 at 4–5 °C and at the age of five at 2 °C in Troms. The mean carapace length increased 1–1.5 mM in the spawning stock in warm waters. If sea urchins follow the same patterns of growth rates and population dynamics parameters as cod and prawn, it would indicate that they grow faster and develop to maturity at a younger age in Nordmøre and Trøndelag than in areas further north.

The local pattern of overgrazing and subsequent re-growth of kelp beds shows that barren grounds first appeared in sheltered areas and gradually extended to moderately wave-exposed areas. This may be explained in view of the following factors: sea urchin recruitment, kelp bed productivity, wave activity, and adaptation to the areas most preferred by the sea urchins. Sea urchins are probably best adapted to sheltered areas. Here they are less disturbed by wave activity. Here also the bottom substrate is probably most suitable for juveniles to settle in and survive. Kelp beds have the lowest productivity in sheltered areas, increasing gradually to the highest level in heavily wave-exposed areas. *L. saccharina* usually dominates the kelp beds in sheltered areas. This kelp is prostrate and therefore more readily grazed by the sea urchins than *L. hyperborea*. Sea urchins may be abundantly recruited by one or a few cohorts both in sheltered and wave-exposed areas. As the sea urchins become large in test size, they may overgraze the kelp beds, but as kelp beds are more productive, or the sea urchins more disturbed by increased exposure to waves, the sea urchins need more time to graze down the kelp beds. Possibly, they graze on the juvenile kelp, thereby inhibiting the recruitment of kelp (Sivertsen, 1997a). In localities with heavy wave activity, fewer sea urchins may survive to maintain a high density long enough to graze down the kelp beds. Juvenile sea urchins live cryptically. They may find shelter in the kelp haptera or hide in crevices; they are rarely found in such places, though. In barren grounds the small individuals are very rare or, usually, not found at all. It is more probable that juveniles settle and survive on substrata of gravel, dead shells or loose coralline algae. As they become 15–20 mM in diameter they move upwards to rocky and stony bottoms and join the adult populations (Sivertsen & Hopkins, 1995). As

kelp beds disappear in a locality, the effects of the surge increase at the bottom. In moderately wave-exposed areas the juveniles may have difficulties in recruiting on the barren grounds. The recruitment in these areas may be too low to sustain the sea urchin populations, and then the grazing pressure can decrease to a level where re-growth can start, while in sheltered localities the recruitment is sufficient to maintain a stable population.

#### Parasites

Hagen (1987) and Stien et al. (1995) propose the hypothesis that infection by the nematode *Echinomermella matsi* in sea urchins increases the mortality to a level where re-growth of kelp beds can start. However, no support has been found for this hypothesis to date (Hagen, 1987; Christie et al., 1995; Sivertsen, 1996). Re-growth of kelp was found in the Trøndelag areas where nematodes were *not* found. Low sea urchin densities were found in the Bodøareas, where the occurrence of nematodes was highest, the prevalence ranging from 40 % to 88 %, but here there were no observations of re-growth of kelp (Hagen, 1987; Sivertsen, 1996). A sudden decrease to a fourth in the density of sea urchins in less than 6 months was found in an area in Helgeland, where re-growth of kelp was observed. (Stien et al., 1995). About 60% of the sea urchins were infected by nematodes in both samples, and the occurrence of nematode-infected individuals tended to increase rather than decrease. Here, there was no evidence that the nematodes were a factor causing a decrease in the sea urchin population; the prevalence of nematodes was unchanged after the decrease in sea the urchin density (Stien et al., 1995).

#### Population dynamics

The cycles from kelp beds to barren grounds and back again to kelp beds may be explained with reference to the population dynamics and the life history of the sea urchins, which is characterised by bet-hedging strategies (Ebert, 1982, 1985). The annual growth rate of a population, as presented by Schaffer (1974) and Schaffer and Gadgil (1975), is:

$$= cB + p \quad (1)$$

where  $B$  is the total number of new-born individuals,  $c$  is the juvenile survival rate to the age of first repro-

duction, and  $p$  is the adult survival rate. Growth and mortality factors change with temperature variation. As temperature increases, growth and mortality rates also increase (Roff, 1992). Increased mortality leads to shorter life length, corresponding to a decrease of  $p$  in (1). To compensate for a low  $p$ , then  $c$  or  $B$ , or both, may increase to keep the size of the population constant.

Ebert (1982) proposes that sea urchins may have a bet-hedging life history. This postulates that an extended reproductive life-span, a high rate of adult survival, and low annual reproductive effort are an adaptation to the low and highly variable survival rates of first-year juveniles (Stearns, 1976, Roff, 1992). According to the bet-hedging theory, longevity is a response that reflects variations in juvenile survival (Murphy, 1968; Schaffer, 1974; Ebert, 1982). If  $c$  is very small, then one way of having 1 is for  $p$  to be large. Large  $p$  means long life. Very high but constant juvenile mortality may act as a constraint on longevity in this, in different species, this may reflect the presence of the barrier at different positions in the species' adapted space. These are the design constraints (Schaffer, 1974; Stearns, 1977; Ebert, 1982). Long-lived species, operating under the rule of bet-hedging populations, will usually be declining (births < deaths), but there will be occasional recruitment episodes that increase stability in the population (Ebert, 1982).

The bet-hedging life history model may explain the cycles in the size of sea urchin populations found on the coast of Norway. The low predation found on sea urchins (Table 1) indicates that if the populations are not predator-controlled, there may be other factors that limit the increase in the size of the population. An event that triggers a very successful recruitment may lead to a sharp increase in the juvenile sea urchin population, which in turn will lead to a large increase in the adult population. This is what may have occurred in the late 1960s to early 1970s along the coast of Norway. High occurrence of Echinoderm larvae (although whether it was sea urchin larvae is unproved) was found in the coastal waters from 1969 to 1973, i.e. some years prior to the first observations of the emergence of barren grounds along the coast. This may be an indication (albeit weakly supported in our material) that the sea urchin populations had increased, with barren grounds as a result.

Re-growth of kelp beds has occurred in the southern parts of the overgrazed areas since the late 1980s. In the south we may find shorter life length, as a consequence of warmer water, and the short life expectancy may

prevent the size of the population from being sustained at a high level. In Trøndelag where a decrease in the sea urchin populations was observed in some localities, the sea urchins compensate with higher recruitment or lower mortality only in those biotopes that they are best adapted to. In sheltered areas they still appear, while they have disappeared in marginal biotopes, such as wave-exposed areas.

The mean predation pressure on the sea urchins over the last 13 years prior to the appearance of barren ground was found to be 10–40 times lower than the mean live weight of sea urchin found in kelp beds and therefore too low to hold down the sea urchin populations. In some localities high parasite infection has been found to decrease the density and the mean size of the sea urchins significantly, but the decrease in the grazing pressure has not encouraged re-growth of kelp. Re-growth is usually found in areas where parasites have not been observed. Growth and mortality rates in a population are generally higher in warm than in cold environments. Variation in the water temperatures may consequently be a plausible explanation of the natural regulation of sea urchin populations; the decrease in the populations and the re-growth of kelp in Nordmøre, Trøndelag and Helgeland, which are the southernmost overgrazed areas, may be a result of higher water temperatures.

A sudden occurrence of high recruitment may be the most important factor for increase in the sea urchin populations. My hypothesis is that a sudden high recruitment in a population, followed by reduced recruitment with reduction of the population, is a result of the bet-hedging life strategy of sea urchins. This may explain the cyclical variation between kelp beds and barren grounds. The variations in population parameters discussed here are of a general character. The parameters should be estimated for each sea urchin species, in a temperature gradient that covers the whole range of distribution of the species in question.

Kelp beds have a primary productivity similar to cultivated areas ashore. The kelp production contributes to the benthic food chain in shallow areas. The fact that half of the kelp beds investigated in North Norway were grazed down indicates that in this area the food chain capacity has been reduced dramatically. Kelp beds are also important as habitats for many invertebrates and as nursery areas for fish. To test the hypothesis of bet-hedging we need studies on the recruitment of sea urchin larvae and on population parameters such as growth and mortality, covering the whole range of distribution of the species.

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