Population reductions of *Strongylocentrotus droebachiensis* (Echinodermata) in Norway and the distribution of its endoparasite *Echinomermella matsi* (Nematoda)

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ABSTRACT: Observations of sea urchin *Strongylocentrotus droebachiensis* (O. F. Müller) mass mortality at Vega island in mid Norway, and reduced sea urchin density in another area 280 km (aerial line) to the south, initiated a more extensive survey of sea urchin and kelp *Laminaria hyperborea* (Gunn.) Foslie forest distribution along 700 km of coastline. Records of the distribution and prevalence of the nematode *Echinomermella matsi* Jones & Hagen, 1987, an endoparasite of *S. droebachiensis*, were also included as the parasite has been postulated to cause sea urchin mass mortality. Sampling was concentrated in 5 areas of coastline along mid and northern Norway. Each area was studied along a wave exposure gradient. Old kelp forests have persisted along the outermost exposed parts of the coastline despite the 20 yr population outbreak of sea urchins. Inshore of the exposed kelp zone and towards the mainland, sea urchin dominated barren grounds still persisted. The distribution and abundance of *S. droebachiensis* in the southernmost area (Frøya) was greatly reduced, and expansion of kelp into former barren grounds resulted. Reduced numbers of sea urchins and some macroalgal regrowth also occurred in the 2 central areas 140 and 280 km north of Frøya, whilst high population densities of small sized *S. droebachiensis* on 'barrens' still dominated the inner zone in the 2 northern areas. The study indicated that *S. droebachiensis* populations, and hence the barren ground state, may be in a labile phase along the southern 300 km of the coast, whilst its state in the northern areas seems more persistent thus far. *E. matsi* was not found in the southernmost area. *S. droebachiensis* was heavily infested in the 2 central areas. In northern areas *E. matsi* was found only at a few sites. The pattern of parasite occurrence and sea urchin regression makes the role of *E. matsi* in this process questionable and indicates that 1 or more unidentified waterborne agents have been involved.

KEY WORDS: *Laminaria hyperborea* · *Strongylocentrotus droebachiensis* · Sea urchin mortality · Kelp revegetation · Sea urchin parasite · Norway

INTRODUCTION

For more than 20 yr high densities of the green sea urchin *Strongylocentrotus droebachiensis* (O. F. Müller) have reduced formerly luxuriant and highly productive kelp *Laminaria hyperborea* (Gunn.) Foslie forests to barren grounds of low productivity, *sensu* Pearse et al. (1970), along the Norwegian coast between 63° N and 71° N (Sivertsen 1982, Hagen 1983, 1987, Skadsheim et al. 1993). Large parts of the shallow coastal zone, which is up to 50 km wide, have been denuded, but kelp forests still persist on the outermost, wave-exposed areas. The size of the overgrazed area implies that this is among the largest sea urchin outbreaks reported. Both as a general ecological and as an environmental problem, it is important to understand the patterns of persistence of the kelp and barren states and the patterns of sea urchin mortality that may lead to kelp forest restoration.

Similar large scale outbreaks of *Strongylocentrotus droebachiensis* have been studied extensively in the northwestern Atlantic (Mann 1977, Scheibling 1986, 1988, Pringle 1986, Johnson & Mann 1988, Elner & Vadas 1990, Scheibling & Raymond 1990). There, a

severe sea urchin mortality, caused by an endoparasitic amoebae (Jones & Scheibling 1985), occurred over large areas some 10 to 15 yr after sea urchins had created barren grounds. The epizootic mortality, *sensu* Kinne (1980, p. 15), was then followed by a rapid restoration of kelp forests (Miller & Colodey 1983, Moore & Miller 1983, Scheibling 1984, 1986, Scheibling & Stephenson 1984, Miller 1985). These events were most pronounced on the east coast of Nova Scotia, Canada, while sea urchin dominated barren grounds remained further south and north (Pringle 1986, Keats 1991).

In early summer 1991, we observed a dramatic decline in numbers of *Strongylocentrotus droebachiensis* around several skerries in a barren area at Vega island in mid Norway (see Fig. 1) (H. Christie, H. P. Leinaas & A. Skadsheim unpubl.). Here we had studied sea urchins since 1988 without observing any marked perturbation in population densities until this event. The degree of sea urchin mortality varied considerably between skerries, ranging from small reductions restored within a few months, to near elimination of local populations with a subsequent establishment of kelp vegetation. Moreover, in 1990 we observed kelp regrowth (Røv et al. 1990) on a former barren ground (Sivertsen 1982) at Frøya island, 280 km south of Vega. These observations motivated us to carry out a survey on occurrence and population characteristics of kelps and sea urchins along 700 km of coastline (see Fig. 1) to search for evidence of reduced sea urchin populations outside the Vega area and possible regional trends in the phenomenon.

The survey covered the main area of extensive barren grounds created during the sea urchin outbreak in the 1970s. Less extensive barrens have been reported further to the north, past the northern tip of Norway (Sivertsen & Wentzel-Larsen 1989), while the Frøya area west of Trondheim city is in the southernmost area where barren grounds have been observed (Sivertsen 1982). Most of this coastline had been surveyed by Sivertsen (1982), whose estimates of distribution and abundance patterns of sea urchins and kelp forest destruction facilitated assessments of large-scale changes during the last 10 years.

The population crash of *Strongylocentrotus droebachiensis* in Nova Scotia is the only case where the causal mechanism of sea urchin mass mortalty due to disease has been identified (Jones & Scheibling 1985, Jangoux 1987a, b, c, Peters 1993). In the Caribbean Sea the speed and direction of the spreading of a mass mortality incident exclusively affecting the black sea urchin *Diadema antillarum* Philippi indicated the involvement of a water-borne pathogen (Lessios et al. 1983, 1984). However, neither in this case (Bauer & Agerter 1987, 1994, Lessios 1988), nor in other

instances of more small-scale sea urchin die offs where diseases have been suspected (Johnson 1971, Pearse et al. 1977, Pearse & Hines 1979, Boudouresque et al. 1980, Maes & Jangoux 1984, Williams et al. 1991, Dayton et al. 1992), have the pathogens been identified.

All sea urchin populations in the Vega area were infested by the parasitic nematode *Echinomermella matsi* Jones & Hagen 1987 (Stien 1993, Christie et al. unpubl.) which Hagen (1992) suggested could cause mass mortality of *Strongylocentrotus droebachiensis* and thus terminate the barren ground state. Heavy infections of *E. matsi* have been reported from several places in northern Norway, the area from which this nematode was described (Jones & Hagen 1987). So far, however, its distribution along the coast has been poorly described, and we therefore included records of parasite prevalence in all sea urchin populations investigated.

METHODS

Sampling was carried out in June 1992, in 5 areas: Frøya, Vikna, Vega, Lofoten and Harstad (Fig. 1). In each area we selected 3 localities from west to east with
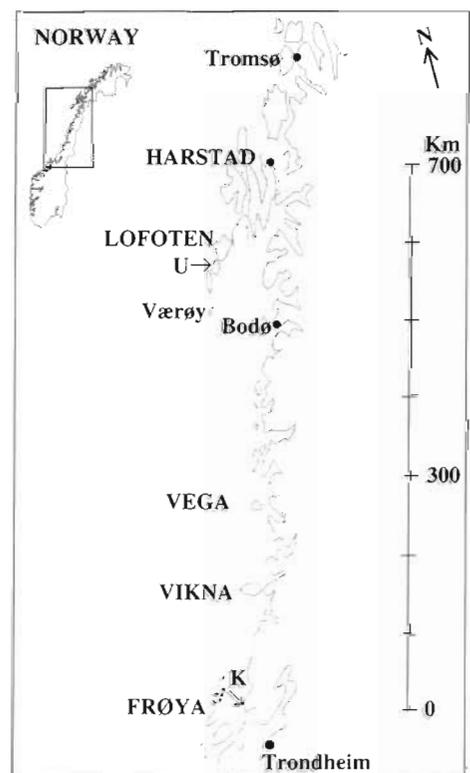

Fig. 1. Norway, showing the coastline with study areas (shaded). Arrows: extra sites (K: Kjeungskjæret; U: Utakleiv)

decreasing wave exposure. One locality was selected in the outer kelp forest. The other 2 were chosen so that the middle locality would represent the outer part of the zone of previous kelp forest destruction, while the inner locality was well inside the main barren ground described by Sivertsen (1982). We sampled 3 sites within each locality, except for Vega where 2 sites were sampled at the middle locality and 4 sites were sampled at the inner locality. Distances between areas were 100 km or more, localities were 3 to 20 km apart, whilst most sites were 200 to 700 m apart. We selected sloping rock walls at all sites to reduce variance due to topography and substrate. Accessibility was also important because the sites were intended to be used for long-term monitoring. Some sites were included because they had been sampled in earlier studies.

Population studies of the dominant kelp *Laminaria hyperborea* were done by sampling plants in 4 haphazardly placed frames (1×1 m^2) at 5 m depth. The stipe length of each plant in the canopy layer was measured and age was determined by growth ring analyses (Kain 1963). The same sampling was not done at Vega, where a demographic analysis of *L. hyperborea* already existed (Sjøtun et al. 1993). However, we present an age distribution based on plants that were collected for a study of the hapteron fauna since it agreed with the one obtained by Sjøtun et al. (1993) and thus seems respresentative for the area. The longevity of *L. hyperborea* in Norway, up to about 20 yr, together with the feasibility of demographic analyses of the species (Kain 1963, 1971), made it possible to estimate when kelp recovery began after populations of sea urchins were reduced on former barren grounds.

Sea urchin *Strongylocentrotus droebachiensis* densities were estimated by counting in frames (0.5×0.5 m^2) placed haphazardly 10 times on each of the depths 2, 5 and 10 m. At each site, ca 100 sea urchins were collected randomly at 5 m depth for measurement of diameter (by vernier calipers) and assessment of parasite *Echinomermella matsi* prevalence (by dissection). For comparative purposes, 100 sea urchins were collected at 3 additional sites, Håskjæra at Frøya (Fig. 2), Kjeungskjæret between Frøya and Vikna, and Utakleiv west of our study area in Lofoten (Fig. 1). Sea urchin density was recorded only at Håskjæra, whilst test diameters and parasite prevalence were measured at all 3 sites. We had sampled at Håskjæra in 1990 (Røv et al. 1990) and therefore could document changes which had occurred during the subsequent 2 yr.

At Frøya, we chose the northern tip of Frøya as the middle locality, and the bay south of Dyrviksundet, on the east side of Frøya, was chosen as the inner locality. Due to the discovery of an apparently ongoing process of kelp recovery following sea urchin regression at Frøya, we also included an extra inner locality (Leksa),
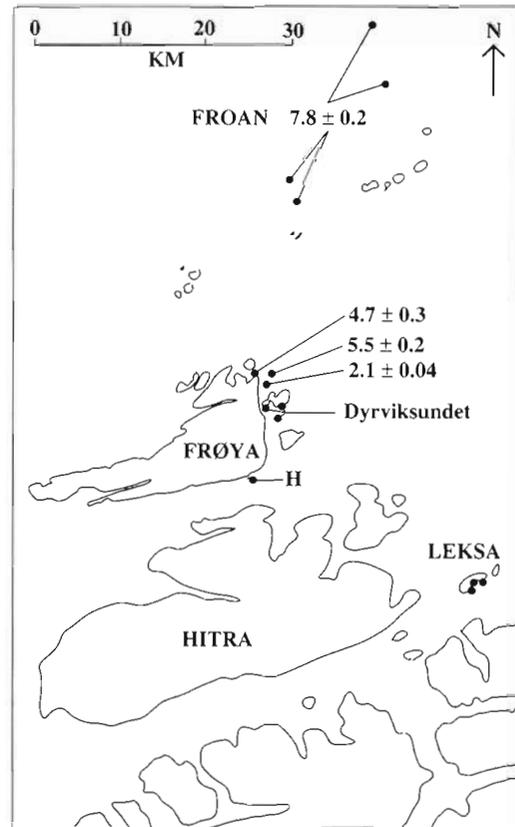

Fig. 2. The Frøya area. Dots show positions of sites. Values are mean age ± SE of kelp *Laminaria hyperborea* plants forming the canopy layer in the Froan archipelago and at the 3 sites on the revegetated locality near Frøya. H: Håskjæra. Positions of 3 sites just southeast of Dyrviksundet are also shown

closer to the mainland (Fig. 2). In addition, we also observed the occurrence of macroalgae and sea urchins across a transition zone from the kelp forest into the barren zone. These observations were made by looking through diving masks from a rubber boat or by short dives when organisms were difficult to see from the boat. The outer ungrazed kelp forest of this area was analysed at 4 sites in the Froan archipelago just north of Frøya in September 1993.

Density estimates and size frequency analyses of sea urchins were made on the data from the middle and inner localities in each area for comparison between areas. Thus, on Frøya the additional sites at Leksa and Håskjæra were used to trace trends in numbers of sea urchins in this area, but they were not included in the statistical analyses for comparison between areas.

Prior to statistical testing, data on kelp age and sea urchin diameter were square root transformed, whilst the density records were log(n + 1)-transformed. These transformations were found sufficient to homogenize the variances (Snedecor & Cochran 1981). Differences for kelp age between areas were tested by 1-way
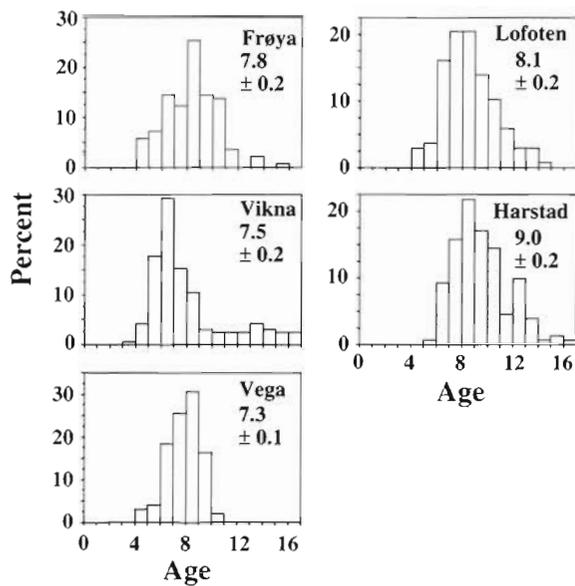
Fig. 3. *Laminaria hyperborea.* Age distribution of kelp plants forming the canopy layer in the 5 areas. Mean age ± SE are shown

analysis of variance (ANOVA) and differences between means at sites or areas were tested by Fisher's Protected Least Significant Difference (Fisher's PLSD). All *t*-tests were performed as ungrouped comparisons. Kelp age and size measurements from the Vega area were omitted from the statistical comparisons since the kelp data were not collected by the same method as elsewhere and because emphasis was on comparing northern and southern areas.

Differences between density measurements of *Strongylocentrotus droebachiensis* were tested by a nested 4-way ANOVA with a mixed model. The fixed variables were area, locality and depth. Site was nested within locality and area. The analyses were done using the SAS GLM procedure (Freund et al. 1986). Differences in densities between areas were compared by Scheffé's test. Vega was not included in this test, as the main purpose was to describe and compare the state (sea urchin density) of the 2 southern and the 2 northern areas. Through our long-term studies in Vega we had already documented a very patchy mortality there (Christie et al. unpubl.). For the other 4 areas, we used the 2 previously chosen localities per area in the originally overgrazed zone, keeping the 3 sites at each locality to maintain a balanced design in the 4-way ANOVA. We thus excluded the outer kelp localities with no sea urchins and the additional localities mentioned above because they were chosen

ad hoc to document the ongoing process at Frøya and parasite prevalence. The 4-way ANOVA was not completely balanced because shallows prevented density counts at 10 m depth at some sites.

RESULTS

Kelp along the coast

At all outer localities there were intact kelp *Laminaria hyperborea* forests free of green sea urchins *Strongylocentrotus droebachiensis*. The canopy layer was largely dominated by 6 to 12 yr old plants with a few reaching 15 yr or more. The age distribution of kelps in the various areas is shown in Fig. 3. The kelps in the southern areas (Frøya and Vikna) were significantly younger than those in the northern areas (Lofoten and Harstad); $t = 5.03$ and $p < 0.0001$ when kelp age records from Frøya and Vikna were pooled and compared to the pooled sample of Lofoten and Harstad. Excluding Vega, the mean kelp ages of the 4 areas, except for Frøya compared to Vikna and Lofoten respectively, were significantly different (Table 1). Our records (Fig. 3) and those of Sjøtun et al. (1993) indicate little variation in mean kelp age along the coast from Frøya to Vega. The stipe lengths of kelps decreased to the north with lengths falling into 2 groups, Frøya and Vikna versus Lofoten and Harstad (Table 2). The mean stipe length in each area was significantly different from the other 3 (Fisher's PLSD: $p < 0.0001$).

Barrens with high densities of sea urchins covered wider zones in the more sheltered part of the coast closer to the mainland. Between the outer kelp forest and the barrens there were zones or patchy areas in transition states, either as kelp forests subjected to sea urchin grazing, or former barrens in different stages of macroalgal regrowth.

Table 1. *Laminaria hyperborea.* One-way ANOVA for the effect of area on square-root-transformed values of kelp age and Fisher's PLSD for the square root of age and the effect of area

ANOVA Source	df	SS	MS	F	p
Kelp age	3	6.65	2.22	13.31	<0.0001
Error	584	97.27	0.17		

Fisher's PLSD					
			Areas compared:		
	Frøya- Vikna	Frøya- Lofoten	Frøya- Harstad	Vikna- Lofoten	Vikna- Harstad	Lofoten- Harstad
p	0.1040	0.3875	<0.0001	0.0113	<0.0001	0.0007

Table 2. *Laminaria hyperborea*. One-way ANOVA for the effect of area on square-root-transformed values of stipe length in the 4 areas Frøya, Vikna, Lofoten and Harstad and the mean values (cm) ± SE in the 4 areas

ANOVA Source	df	SS	MS	F	p
Stipe length	3	982.48	327.49	221.17	< 0.0001
Error	572	846.97	1.48		

Stipe length Frøya	Vikna	Lofoten	Harstad
105.9 ± 2.2	121.9 ± 2.0	58.5 ± 1.9	80.8 ± 1.4

Kelp and sea urchins at Frøya

At the northern tip of Frøya, the middle locality in this area (Fig. 2), a young to medium-aged forest of *Laminaria hyperborea* was established in an area where Sivertsen (1982) reported barren grounds. Mean ages of the canopy forming plants decreased from the most exposed site towards more sheltered ones to the west and southwest (Fig. 2). The decrease in age was significant (1-way ANOVA for the effect of site on age; df = 2, 135, SS = 21.612, MS = 10.806, F = 182.987, p < 0.0001) and all 3 mean kelp ages were significantly different (Fisher's PLSD; p ≤ 0.0005). Observations along a 3 km line transect southwards from the locality at the northern tip of Frøya showed that *L. hyperborea* extended almost to the Dyrviksun-det sound (Fig. 2). However, in this southern part of the transect the stands of *L. hyperborea* became more fragmented as they were replaced by the opportunistic *Laminaria saccharina* (L.) which dominated the inner-most part of this kelp forest. We did not find *Strongylocentrotus droebachiensis* in the pure forest of *L. hyperborea*, but we saw scattered aggregations of large sea urchins among the *L. saccharina* stands in the inner (southern) part of the transect.

No kelp forest was present in the locality in the bay south of Dyrviksundet. There, the upper 2 to 3 m were barren, and below this depth were patches of variable sizes covered by mixed vegetation of annual brown algae, small recruits of *Laminaria saccharina* and some scattered large *L. saccharina*. Correspondingly, most sea urchins were aggregated at ca 2 m depth in this bay. Sea urchin densities (mean ± SE) were 14.3 ± 4.0, 4.3 ± 2.1 and 0 specimens m⁻² at 2, 5 and 10 m depth respectively. No *L. hyperborea* was found inward of Dyrviksundet.

On the Leksa locality closer to the mainland (Fig. 2), the situation resembled that in the bay south of Dyrviksundet. Sea urchins and barrens dominated the upper 2 to 3 m. Below this zone ephemeral algae covered most of the bottom, while *Laminaria saccharina*

largely occurred as scattered groups of small and young plants. Hence, the macroalgal cover appeared to be in a somewhat younger stage of recovery at Leksa compared to that at Dyrvik-sundet. The density of *Strongylocentrotus droebachiensis* at Leksa was somewhat higher than at Dyrviksundet (mean sea urchin densities ± SE were 22.3 ± 4.6, 1.7 ± 1.3 and 0 specimens m⁻² at 2, 5 and 10 m depth respectively), but the differences between the 2 localities were not significant at any depth (t = 0.568, p = 0.579 at 2 m depth and t = 1.711, p = 0.092 at 5 m depth).

At the Håskjæra site (Fig. 2) the bottom was barren in 1990. Annual algae mixed with scattered stands of small *Laminaria saccharina* dominated the substrate up to 2 or 3 m depth in 1992. The sea urchin density decreased in the same period (Fig. 4). The reduction was greatest at 5 m depth; the density was significantly lower (t = 4.70, p = 0.0003) in 1992 than in 1990. In fact, the relatively high sea urchin density at this depth, even in 1992 (15.6 ± 13.0 specimens m⁻²), compared to other sites in the Frøya area, was mainly due to a single quadrat in which one of the few remaining sea urchin aggregations was sampled. If this outlier is omittted, the mean density estimated from the remaining 9 replicates (2.7 ± 1.9 m⁻²) indicate a 90% reduction (t = 6.08, p < 0.0001) at this depth. Sea urchin density was also lower in 1992 than in
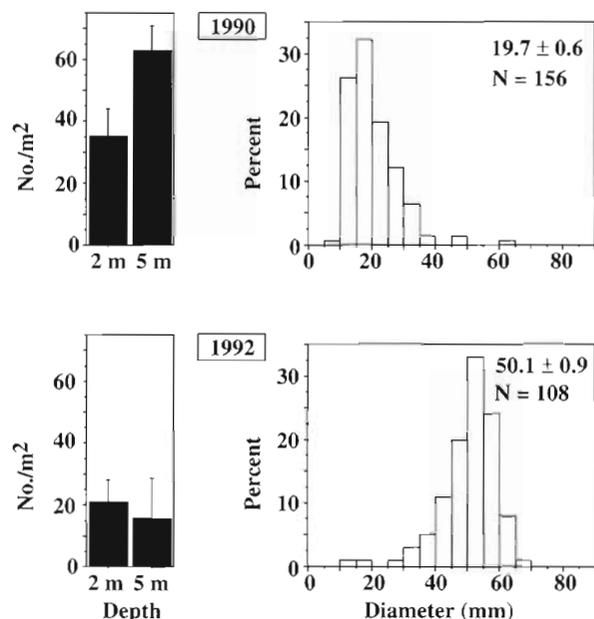

Fig. 4. *Strongylocentrotus droebachiensis*. Mean population density ± SE at 2 and 5 m depth and size distribution of samples from 5 m depth at Håskjæra in 1990 and 1992. Mean test diameters ± SE are shown

interaction term area × locality was not significant ($F =$ 1.99, p = 0.155). These interaction terms were therefore not included in the model of the analysis. There were significant differences in sea urchin densities between depths; but, most importantly, the sea urchin densities in the 2 southern areas were distinctly lower than those in the 2 most northern areas (Table 3). There were, in addition, 2 significant interaction terms, area × depth and locality × depth, which were included in the ANOVA model. The contrast test (Scheffé's test) on differences between mean sea urchin densities in the 4 areas showed significant differences between means in all areas as well as a significant density reduction with depth (Table 3). In the south, the 2 areas Frøya and Vikna showed similar patterns of reduced sea urchin density, except that there were some urchins still present in what we have defined as the middle locality at Vikna. However, the great differ-
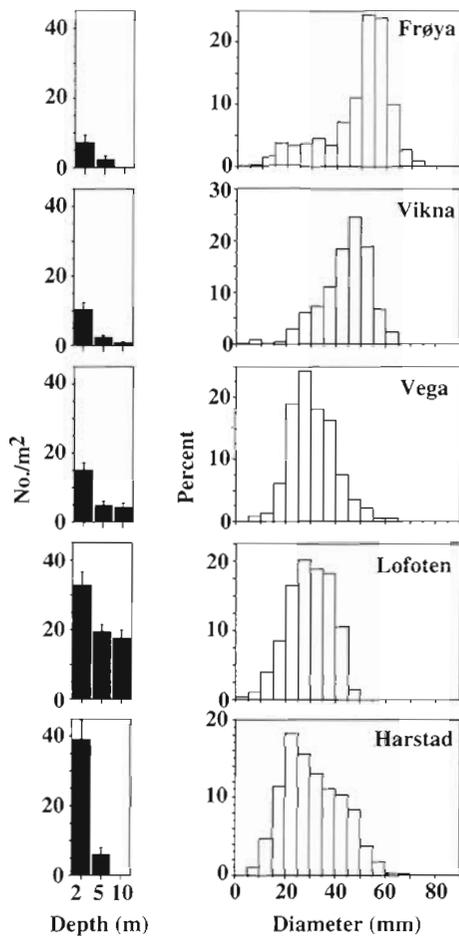

Fig. 5. *Strongylocentrotus droebachiensis*. Mean density ± SE at 2, 5 and 10 m depth and size distribution in each area. Density estimates are based on 6 sites with 10 observations per site in each area, except for Vega where 4 sites were recorded. For sample sizes of diameter see Table 4

1990 at 2 m depth, but not significantly so ($t = 1.26$, p = 0.223). If densities at 2 and 5 m depth at Håskjæra were pooled prior to testing and the outlier was included, then density was significantly lower in 1992 than in 1990 ($t =$ 4.29, p < 0.0001). In the same period there was a strong increase in the mean test size of remaining sea urchins ($t = 27.66$, p < 0.0001) (Fig. 4).

Sea urchins along the coast

The mean sea urchin densities of the pooled data from the middle and inner localities in the 5 areas are shown in Fig. 5. The mean sea urchin densities [as $\log(n+1)$] for the 2 southern and the 2 northern areas included in the 4-way nested ANOVA of density are shown in Table 3. The interaction term area × locality × depth was not significant ($F = 1.165$, p = 0.354), and the

Table 3. *Strongylocentrotus droebachiensis*. ANOVA table for tests of $\log(n+1)$-transformed sea urchin densities on sites; see last part of 'Methods' Scheffé's test tested for differences between mean sea urchin density in areas following the nested ANOVA. CL: confidence limits. Diff. means: difference between means. $\log(n+1)$ of mean sea urchin density and SE in each area is included for the sake of comparison

ANOVA Source	df	MS	F	p
Depth	2	115.25	42.94	<0.0001
Error[a]	32.96	2.68		
Area	3	174.19	22.50	<0.0001
Error[a]	19.20	7.74		
Locality	1	5.10	0.66	0.4559
Error[a]	19.24	7.70		
Area × Locality	6	17.84	6.67	<0.0001
Error[a]	33.06	2.68		
Locality × Depth	2	14.36	5.38	0.0095
Error[a]	33.14	2.67		

Scheffé's test	Lower CL	Diff. means	Upper CL	p
Frøya-Vikna	−0.5779	−0.2911	−0.0043	<0.05
Frøya-Lofoten	−2.5648	−2.2760	−1.9873	<0.05
Frøya-Harstad	−1.4171	−1.1111	−0.8050	<0.05
Vikna-Lofoten	−2.2696	−1.9849	−1.7003	<0.05
Vikna-Harstad	−1.1221	−0.8200	−0.5178	<0.05
Lofoten-Harstad	0.8609	1.1650	1.4690	<0.05

$\log(n+1)$ of:	Mean density	SE
Frøya	0.4457	0.0795
Vikna	0.7368	0.0898
Lofoten	2.7217	0.0862
Harstad	1.5568	0.1497

[a]Values come from the type III model

Table 4. *Strongylocentrotus droebachiensis*. One-way ANOVA for the effect of area on square-root-transformed measurements of sea urchin test diameter. Mean test diameter (mm) ± SE in each area. N: number of sea urchins measured in each area

ANOVA Source	df	SS	MS	F	p
Diameter	4	1261.49	315.37	342.84	<0.0001
Error	2820	2594.09	0.92		

Test diameter Area:	Frøya	Vikna	Vega	Lofoten	Harstad
Diameter	48.2 ± 0.5	43.3 ± 0.4	30.3 ± 0.6	29.1 ± 0.4	30.7 ± 1.2
N	719	621	227	628	630

ence between the 2 areas was that all sites in the middle and inner zones of Vikna were still barren, in spite of a very low sea urchin density. The 2 northern areas were characterized by high densities of sea urchins and extensive barrens.

The intermediately positioned Vega area (not included in the 4-way ANOVA; see 'Methods') clearly was in a transition state. It differed somewhat from the patterns observed further to the south. In the inner locality very patchy mass mortality had led to a variable sea urchin distribution pattern that, within short distances, ranged from local extinction and kelp recovery to sites with dense sea urchin populations on barren grounds (Christie et al. unpubl.). No algal revegetation on former barren grounds was seen in the Lofoten and Harstad areas. Remaining stands of kelp around Harstad were comprised of old plants.

The mean sea urchin test sizes in the 5 areas differed significantly (Table 4) (sea urchins from barrens at Vega were also included in this comparison). Mean test diameter decreased as sea urchin density increased (Fig. 4, Table 4). Mean test diameters were significantly different when most areas were compared by Fisher's PLSD (Table 5) following the 1-way ANOVA, except for diameters at Vega compared to those at Lofoten and Harstad respectively. Thus the 2 southern areas, Frøya and Vikna, contained mainly large sea urchins, compared to the 2 northern areas, Lofoten and Harstad, that contained small sea urchins.

The parasite

The endoparasitic nematode *Echinomermella matsi* was not found in sea urchins from the Frøya area or at Kjeungskjæret close to the mainland between Frøya and Vikna. It was found at all sites at Vikna and Vega (Table 6) with a similar mean prevalence in the 2 areas. The prevalence of *E. matsi* ranged from 12.4 to 43.3 % at Vikna and from 18.2 to 53.3 % at Vega. In Lofoten the parasite was not recorded at any of the 6 sites in the main study area. As *E. matsi* had been found at Værøy at the southwestern tip of Lofoten (Hagen 1983, 1987), we took an extra sample from Utakleiv (Fig. 1). At this site the prevalence of *E. matsi* was 13.6 %. The parasite was present at 3 of 7 sites around Harstad (5 to 20 % prevalence).

DISCUSSION

Strongylocentrotus droebachiensis had not established dense populations in the outer, most exposed parts of the coast where kelp *Laminaria hyperborea* forests still persist. This agrees with Sivertsen (1982) who did not record barrens in this zone during a survey along the same coastline in 1981. The demography of *L. hyperborea* in our outer localities, therefore, probably reflected mature kelp forests which are little affected by sea urchin grazing. The latitudinal trend in kelp demography with smaller size and increased age to the north was also recorded by Sjøtun et al. (1993). Temperature and light may thus be important factors affecting kelp growth, and kelp vulnerability to sea urchin grazing may, therefore, increase to the north.

The records of kelp distribution presented here and those of Sivertsen (1982), Røv et al. (1990), and Skadsheim & Rinde (1995), show that *Laminaria hyperborea* persisted in a belt at all depths in the outer, most wave-exposed coastal zone. The zone seems to represent a refugium from where kelp may increase its distribution landwards when populations of *Strongylocentrotus droebachiensis* on adjacent barren grounds decline. This zone differs from that described by Johnson & Mann (1988). During the sea urchin outbreak in Nova

Table 5. *Strongylocentrotus droebachiensis*. Fisher's PLSD for the square root of sea urchin test diameter and the effect of area

	Frøya-Vikna	Frøya-Vega	Frøya-Lofoten	Frøya-Harstad	Vikna-Vega	Vikna-Lofoten	Vikna-Harstad	Vega-Lofoten	Vega-Harstad	Lofoten-Harstad
p	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.1111	0.9803	0.0263

Table 6. *Echinomermella matsi*. Prevalence (% of sea urchins infected) of the parasite in the different areas. No. of *S. droebachiensis*: number of *S. droebachiensis* examined. No. of sites: number of sites sampled in an area

Area	% E. matsi	No. of S. droe- bachiensis	No. of sites	No. of sites with E. matsi
Frøya	0	719	7	0
Vikna	24.3	621	6	6
Vega	27.4	529	7	7
Lofoten	2.1	746	7	1
Harstad	4.2	669	7	3

Scotia, *Laminaria longicruris* Pyl. maintained refuge populations in a narrow band confined to the low intertidal and shallow subtidal zones from where kelp recovery was rapid and widespread following the demise of the sea urchins.

In the Frøya area, the kelp forest had advanced closer to the mainland compared to the state described by Sivertsen (1982). He reported extensive barren grounds and estimated sea urchin densities of about 70 specimens m^{-2} where we found 2 to 6 yr old kelp forests. In this locality, *Laminaria hyperborea* became younger with decreasing exposure and was finally replaced by more opportunistic species. This age and species cline might reflect the time the slowly dispersing, but competitively dominant, *L. hyperborea* needs to expand when an area becomes free of sea urchins. However, the observed gradient apparently also reflected a gradual sea urchin decline. At the Håskjæra site the change took place after 1990 (Røv et al. 1990), i.e. several years after the forest of *L. hyperborea* had become restablished on the northern tip of Frøya. Moreover, the early stage of macroalgal recovery at Leksa indicated a more recent reduction of numbers of sea urchin at this innermost locality. The general aggregation of *Strongylocentrotus droebachiensis* in the shallows and a density decline with increasing water depth in all areas comply with observations made elsewhere (Himmelman 1986) and with those of Sivertsen (1982).

The increase in mean sea urchin test size observed at Håskjæra is explicable in terms of improved foraging conditions for the remaining individuals after the density reductions. Specimens of ca 20 mm may increase their test diameter by 10 to 20 mm yr^{-1} (Swan 1961, Larson et al. 1980), which would be equivalent to the changes observed at Håskjæra. Size-specific mortality, as observed for *Diadema antillarum* by Hunte et al. (1986), cannot explain the change in test size distribution between the 2 dates, because the dominant, large size classes of 1992 were hardly present in 1990. Immigration from deeper waters is unlikely, because we

saw only small sea urchins at 5 m and towards deeper waters in 1990.

Our study suggests that a gradual large-scale decrease in density of *Strongylocentrotus droebachiensis* proceeds northwards. A distinct reduction in sea urchin densities occurred at Vikna too. Both barren ground localities lay within the barren ground zone where Sivertsen (1982) reported *S. droebachiensis* at >70 ind. m^{-2}. Except for the upper 2 m at the inner locality, all Vikna sites showed sea urchin densities well below the level (ca 10 ind. m^{-2}) that induced macroalgal recovery at Vega (Christie et al. unpubl.). Prevailing barrens at Vikna in 1992 may reflect a recent population decline in the area. However, predominance of similarly large sized sea urchins at Vikna, as at Frøya, may indicate that a reduction in sea urchin density at Vikna occurred somewhat earlier than indicated by the still persisting barren ground.

Whether the patchy mortality observed at Vega will continue and eventually result in a general decline of sea urchin densities in this area is still unclear. Increased growth of opportunistic brown algae on several former barren grounds in 1992 to 1993, indicated continued decreases of sea urchin densities, while other barrens still persisted with high sea urchin densities at the end of 1993 at Vega (Christie et al. unpubl.). In the 2 northern areas, Lofoten and Harstad, our findings were more in accordance with those of Sivertsen (1982) and Hagen (1983, 1987), with no signs of sea urchin regression. These areas were dominated by small sea urchins, as observed at Håskjæra in 1990. Such a state characterizes barrens that have persisted for some years with high sea urchin densities (Lang & Mann 1976, Johnson & Mann 1982).

We found that the endoparasitic nematode *Echinomermella matsi* has a limited distribution compared to its host, *Strongylocentrotus droebachiensis*, which is widely distributed in the North Atlantic, the Barents Sea and the Northeast Pacific (Vasseur 1952, Jensen 1974, Propp 1977, Gagnon & Gilkinson 1994). In contrast, the parasite has only been found in Norway, with a main range by 1992 from Vikna to Bodø and Værøy (Fig. 1), a distance of about 400 km.

The present distribution of *Echinomermella matsi* might be of recent origin and related to the sea urchin outbreak in the 1970s. The southern limit of *E. matsi* seems rather sharp, as sea urchin fishermen operating north of Frøya to about 50 km south of Vikna have not found the parasite (K. & R. Svenning pers. comm.). In contrast, our northern records of scattered occurrences of *E. matsi* at low prevalence in the Lofoten and Harstad areas agree with observations of K. Sivertsen (pers. comm.) who found the parasite sparsely distrib-

uted ca 10 to 20 km north of Tromsø. Such differences in southern and northern distribution limits might indicate dispersal along the northgoing Norwegian coastal current. In 1981 K. Sivertsen (pers. comm.) found only a few parasitised sea urchins at Vega. Hagen (1992) reported increased parasite prevalence from 6 to 65 % in 7.5 yr at one site near Bodø. Falk-Petersen & Lønning (1983) did not observe *E. matsi* in *Strongylocentrotus droebachiensis* at Tromsø, whilst K. Sivertsen (pers. comm.) observed it there more recently.

Hagen (1992) proposed that *Echinomermella matsi* could terminate population outbreaks of *Strongylocentrotus droebachiensis*. We have no evidence for such a mechanism at any locality of this study. The extensive population decline of *S. droebachiensis* in the Frøya area occurred south of the range of *E. matsi*. At Vega, a prevalence ranging from 25 to 60 % between sites (Stien 1993) could hardly explain the up to 90 % mortality observed on some skerries in 1991 (Christie et al. unpubl.). We do not, however, reject the possibility that heavy infection may lead to an increased host mortality. *E. matsi* affects *S. droebachiensis* by reducing its gonads (Hagen 1992, Skadsheim et al. 1993, Stien 1993), which function as a reproductive organ and as the primary energy storage organ (Stott 1931, Gonor 1973). However, the parasite has to grow quite large before gonad damage is observed (Stien 1993).

The large-scale pattern in sea urchin reduction may suggest involvement of a waterborne agent that has gradually proceeded northwards with the Norwegian coastal current. On a smaller scale (km), such a mechanism might also explain the spatial distribution of mortality on Vega in 1991. There, the most heavily affected populations were found on skerries grouped along the direction of the water current through a sound (Christie et al. unpubl.). However, the trend of sea urchin mortality gradually expanding over large areas in the south might not necessarily represent the same phenomenon as the patchy mortality we have observed in the Vega area.

Mann (1977), Scheibling (1986, 1988), Elner & Vadas (1990) and Scheibling & Raymond (1990) discussed a possible cyclical alternation between kelp forests or sea urchin dominated barrens in the Northwestern Atlantic. There is no evidence for such a cyclicity along the Norwegian coastline. Long-term observations of local fishermen, who use the kelp forest as fishing grounds, suggest that the surveyed coastline was persistently dominated by kelp forests for generations (of fishermen) until the major sea urchin outbreak in the 1970s. Our observations indicate that the resulting barren state dominated by sea urchins may have an inherent instability. During the last years population reductions of sea uchins have led to large effects on algal growth and kelp recovery over large areas. This implies greatly improved foraging conditions and increased growth rate and gonad production among remaining sea urchins. We have not, however, observed that this has resulted in increased numbers of sea urchins and renewed high grazing pressure on reestablished kelp forest.

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