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Incidence, occurrence and distribution of the nematode *Echinomermella matsi* in its echinoid host, *Strongylocentrotus droebachiensis*, in northern Norway

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Abstract The incidence, occurrence and distribution of the nematode *Echinomermella matsi* (Jones and Hagen) in its host, the echinoid *Strongylocentrotus droebachiensis* Müller, were examined in Norwegian waters from Nordmre (63°N) to the Russian border (70°N) in a range of habitats (e.g. kelp cover and community type) from 1982 to 1992. The results are used to examine the likely influence of the parasite on fitness (individual growth and gonad production) and its potential in regulating the population size of its echinoid host. The nematode infections are restricted to areas between Vikna (Vega) and middle Troms, with the highest prevalence (40 to 88% infected) in the Bodø area, the focus of the distribution. The prevalence rates are similar on kelp beds and barren grounds. No difference in growth rates between infected and noninfected sea urchins was found. Nematode-infected sea urchins in kelp bed populations had gonads weighing about one-sixth of those of equivalent uninfected individuals. This indicates that nematodes are really parasites causing reduced reproductive capacity. Areas with high prevalence (> 40% infected) of nematodes had low sea urchin densities. High nematode intensities were found in the areas with high prevalence. The mean abundance in high prevalence areas was highest (eight nematodes) in the 4- to 7-yr-old age group and decreased to zero among the oldest age groups. The ratio of variance/mean abundance was also highest among 5- to 8-yr-old sea urchins. At highly and slightly infected locations, the relationships between the log of the variance and the log of the mean abundance of parasites were 1.35 and 1.69, respectively. Measurements of the frequency distribution of nematodes in sea urchins and the corresponding estimates of the negative binomial distribution showed significantly higher counts in estimated than

observed subpopulations exceeding 20 nematodes per sea urchin. These results may explain nematode-induced sea urchin mortality. The low density of the host in the Bodø area, which had high prevalence, may be a result of increased host mortality caused by nematodes, by lower recruitment because of reduced gonad production, or by other factors. Low prevalence among older sea urchins may be caused by nematode-induced host mortality or by cycles in infection. However, studies on the life cycle of the nematode and long term investigations of host density and nematode intensity/prevalence will be needed before any true conclusions can be drawn.

Introduction

In theory, parasitic disease has the potential to regulate host population size. Its theoretical importance has been recognized for many years and has been restated by Anderson (1979, 1982) and Anderson and May (1979, 1981). Several approaches have been used to determine whether a parasitic infection is likely to affect the host mortality rate in a natural population. The importance of parasite-induced host mortality in the regulation of parasite population size has often been emphasized (Anderson 1978; Anderson and May 1978; May and Anderson 1978) as well as the need to quantify such mortality. Several methods have been developed to try to quantify parasite-induced natural mortality (Anderson and Gordon 1982; Gordon and Rau 1982; Lester 1984; Pacala and Dobson 1988). However, the importance of parasite infections in host population biology is equivocal (Holmes 1982; Kennedy 1984; Scott and Dobson 1989). Jangoux (1984, 1987a, b, c) has described diseases of the Echinodermata.

Recent studies demonstrate that sea urchins have grazed down the kelp beds along the Norwegian coast (Sivertsen 1982, in preparation; Hagen 1983, 1987; Skadsheim et al. 1995). This phenomenon has also been

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observed in other parts of the North Atlantic (Breen and Mann 1976a, b; Wharton and Mann 1981; reviews by Lawrence 1975; Lawrence and Sammarco 1982; Elner and Vadas 1990). On the coast of Nova Scotia, Canada, an amoeboid parasite, *Paramoeba invadence* Jones, in *Strongylocentrotus droebachiensis* (Jones and Scheibling 1985; Scheibling 1988) has caused dramatic reduction in sea urchin populations in barren grounds (Miller and Colodey 1983; Scheibling 1984; Scheibling and Stephenson 1984), followed by regrowth of kelp (Miller 1985; Scheibling 1986; Scheibling and Raymond 1990). During work with sea urchins in kelp beds and barren grounds on the Norwegian coast, populations of the green sea urchin *S. droebachiensis* were found infected by the mermitid nematode *Echinomermella matsi* (Benthimermithidae), recently described by Jones and Hagen (1987). Eggs, larvae, juveniles and adults of males and females of *E. matsi* were found, sometimes together, in the coelom of the sea urchins. The nematode males were 10 to 40 mm long, and females were 300 to 600 mm long. Stien (1993) suggested that the nematode multiplies in an individual host. This nematode is described in detail by Hagen (1987, 1996), Jones and Hagen (1987), and Stien et al. (1995, 1996).

By altering the fitness of the host, the nematode *Echinomermella matsi* might be able to change the population dynamics of *Strongylocentrotus droebachiensis*. *E. matsi* has only been observed on the coast of northern Norway. Extensive field studies of *S. droebachiensis* were conducted in order to elucidate the mechanisms responsible for fluctuations in kelp bed communities along the Norwegian coast (Sivertsen and Hopkins 1995; Sivertsen in preparation). The objectives of the present paper are thus to use data from these studies to examine the effects of nematode infection on individual host fitness (i.e. growth and reproduction of infected and noninfected individuals) and on the mortality of host populations.

Materials and methods

Study locations and data collection

This study of *Echinomermella matsi* infection in sea urchins is based on investigations in the areas Nordmøre (63°N) to North Cape (71°11'N) and eastwards to the Russian border (Fig. 1). The study was performed during investigations of destructive grazing by sea urchins on kelp beds (Sivertsen and Hopkins 1995; Sivertsen in preparation). The locations chosen represent 49 shallow-water (2 to 5 m depth) locations of which four in Bodø and three in Vega were visited two to five times, while the rest of the locations were visited only once. The locations were categorized into three types depending on the occurrence of kelp, sea urchins and the type of substratum. Dense kelp beds of *Laminaria hyperborea* (Gunn.) Foslie were found on a rocky or stony bottom and consisted of high densities of kelp in all size classes and low sea urchin densities. "Transition" areas were found between kelp beds and barren grounds, and consisted mainly of large (adult) *L. hyperborea* at reduced densities, and moderate to high sea urchin densities. "Barren ground" areas were those of rocky or stony bottoms, forming a habitat suitable for kelp

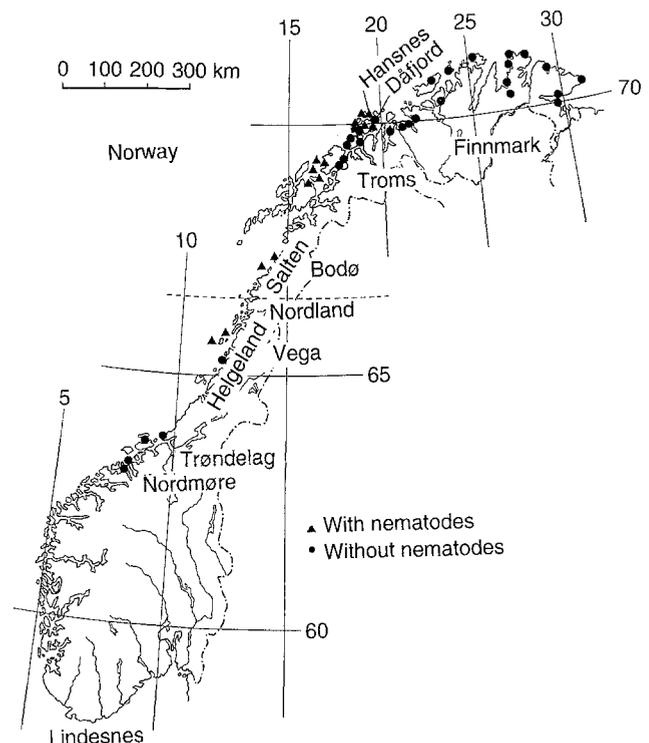


Fig. 1 Map of locations investigated for the endozoic nematode *Echinomermella matsi* in the sea urchin *Strongylocentrotus droebachiensis* on the Norwegian coast

attachment, but with an absence of kelp and a dominance of sea urchins. In these areas investigations of nematode infections in sea urchins were performed from September 1982 to February 1992 (Table 1). In addition 51 randomly distributed barren ground locations in Trøndelag and Nordland (Fig. 1) were investigated in June and July 1981 for the occurrence of sea urchins (Sivertsen 1982; Sivertsen in preparation). In these areas the infection of sea urchins by nematodes was not studied. However, results from these locations were used to compare possible changes in sea urchin densities with results obtained from later investigations in which nematodes were observed.

Nematode infection in sea urchin recruiting areas, dominated by small *Strongylocentrotus droebachiensis* at depths of 8 to 12 m, was recorded in the Bodø area in November 1989. A naturalist's dredge, towed at 1 knot for 5 to 10 min by a research vessel, was used to sample sea urchins. On board the vessel, the sea urchins were sorted from the dredge content and examined for nematodes. Registration and sampling of sea urchins and algae at each location were conducted at depths relative to "extreme" low water spring tides (ELWS) at the vernal equinox (Lewis 1976). Depths were measured either by divers or by means of an echo sounder. At each location the type of bottom was categorized as comprising either rock or stones (> 25 cm), or loose substrata such as gravel, dead shells and loose corallines (*Lithothamnium glaciale* Klellm.). Locations of the sites were given as distances in kilometers from Lindesnes (the southernmost point of Norway). For further explanations of selection of locations and density measurements, see Sivertsen and Hopkins (1995) and Sivertsen (in preparation).

The highest densities and largest individuals of *Strongylocentrotus droebachiensis* were found at shallow depths. Our investigations on nematode infections were therefore performed mainly at 2 and 5 m depths. To measure densities of sea urchins and algae at the locations, at those depths, transects were established horizontally along 50 or 100 m long ropes, which were marked randomly. At those locations where kelp was absent, 18 to 20 marks were made along

Table 1 Overview of the period and number of areas investigated for various categories of kelp beds

Area	Period	Category			Sum of stations	Source
		Kelp bed	Transition	Barren		
Random						
Trøndelag, Nordland	June–July 1981			51	51	Sivertsen (1982)
Troms	Aug–Sept 1990	0	0	18	18	Sivertsen (1991)
Finmark	Aug–Sept 1985	6	4	1	11	Lein et al. (1987)
Nonrandom						
Nordmøre, Trøndelag	July 1983		2	8	10	{ Sivertsen and Wentzel-Larsen (1989)
Nordland, Vega	Aug 1987		1	2	3	
Bodø	Feb–Nov 1982–84	8	0	10	18	{ Sivertsen and Hopkins (1985)
Troms	Jan–Feb 1992	1	1	2	4	
Finmark	Aug–Sept 1985	1	1	0	2	Lein et al. (1987); Sivertsen and Wentzel-Larsen (1989)

the rope. At each mark, an area of 50 × 75 cm was photographed by a scuba diver, and the density and cover of urchins and algae were obtained from magnified (1:1) projections. When kelp was present, ten marks were made at 2 and 5 m depths. At each mark an area of 1 m² was investigated visually by a diver, and quantitative measurements of the density and cover of sea urchins and algae were recorded. The median densities at depths of 2 and 5 m were used. The densities of *S. droebachiensis* and *Laminaria hyperborea* were measured as number of individuals m⁻².

At each location between 2 and 5 m depths, irrespective of the presence or absence of kelp, about 100 *Strongylocentrotus droebachiensis* and about 50 *Echinus esculentus* Linné were collected from randomly selected 50 × 50 cm quadrants and taken to the research vessel. Among the *S. droebachiensis* individuals collected, some *Strongylocentrotus pallidus* G. O. Sars were found, and the two species were separated on board and size–frequency distribution measured. Size was taken as test diameter (measured to the nearest millimeter). Individual total “live” (wet) weight, gonad wet weights, indices of gonad maturity, and nematode infection were also recorded.

Gonad indices

Gonads of *Strongylocentrotus droebachiensis* were sampled from individuals collected from November through February. The gonads were removed from the test. Excess water was removed with a paper towel, and the gonads were air-dried for about 15 min before wet weight was measured to the nearest 0.1 g. The gonad index (GI) was defined as the ratio of the weight of gonads/total live weight of each urchin × 100 (Gonor 1972; Falk-Petersen and Lønning 1983).

Nematode infection

The sea urchin species were examined for *Echinomermella matsi* nematode infection by eye. It is possible that microscopic nematodes were not counted, and large nematode females were counted as approximately 4 cm long fragments, so that the counts represented the burden of the nematodes. This approach is in accordance with Black and Lankester (1981) who found that the length of females of the nematode *Cystidicola cristivomeri* Withe in char was inversely related to the total number of worms. The actual number of nematode females might therefore be overestimated in some sea urchins, but the number of males and fragments of females are taken to provide indices of burden. However, results are presented as abundance (i.e. number of nematodes/sea urchin, infected and noninfected) and intensity (i.e. number of nematodes/infected sea

urchin). For further details on definitions of parasitological terms see Margolis et al. (1982). Since the degree of nematode infection depended on the size of the sea urchins, the size group 21 to 50 mm of *Strongylocentrotus droebachiensis* was used to show the prevalence (% sea urchins infected) of nematodes for studies of the geographic distribution.

Age determinations

The ages of individuals of *Strongylocentrotus droebachiensis* were estimated by recording the zonation/banding of the interambulacral plates of the test at two locations in the Troms area, and four in the Bodø area where both infected and noninfected sea urchins were found (see Jensen 1977; Gage 1985, 1991; Gage and Tyler 1985; Sivertsen and Hopkins 1995). Comparable techniques have been applied successfully to several echinoderm species (Gage and Tyler 1981, 1982a, b, 1985).

The tests were cleaned and stored frozen for subsequent age determination. The aging method described by Jensen (1977) was used with the following modifications. The tests were thawed at room temperature, washed in 96% ethanol, dried, and “burned” at 150°C for 70 min. After cooling, the tests were dipped into xylene in order to visualize the growth rings in the interambulacral plates. The 4th to 8th plate (usually the 5th) from the oral side of the test was used to count age-rings with a stereomicroscope. In order to avoid disturbing reflections, soya oil was added to the test.

Age estimates of presumptive cohorts of the *Strongylocentrotus droebachiensis* dredged from the “recruiting” area were made using size-based computer programs according to the methods implemented in ELEFAN (Gayanilo et al. 1988) and the modal class progression method of Bhattacharya (1967) (see also Hopkins and Nilssen 1990; Sivertsen and Hopkins 1995).

Growth and mortality

A von Bertalanffy growth function (VBGF) (Bertalanffy 1938) was fitted to the test diameter-at-age data using an iterative procedure in the SYSTAT module NONLIN (Wilkinson et al. 1992). The VBGF is formulated as:

$$L_t = L_\infty(1 - e^{-K(t-t_0)}), \quad (1)$$

where L_t = test diameter (cm) at age t years, L_∞ = the asymptotic test diameter, K = growth constant, and t_0 = origin of the growth curve. For further details and methods of linearization and tests of significance see Hopkins and Nilssen (1990) as well as Sivertsen and Hopkins (1995).

Estimations of the distribution of numbers of nematodes in the *Strongylocentrotus droebachiensis* populations, assuming negative binomial distribution, are based on the number of hosts with zero nematodes out of the total number of hosts investigated (Elliott 1977; Rice 1987). The probability (p_0) of the count being zero is

$$p_0 = (1 + m/k)^{-k}, \quad (4)$$

where m is the sample mean of nematodes and

$$p_0 = N_0/N, \quad (5)$$

when there are N_0 zeros of N . Then k is estimated from Eqs. 4 and 5. To calculate the following probabilities of different amounts of nematodes in the sea urchins fitting the negative binomial distribution, we used a recursive relationship,

$$p_n = \frac{k+n-1}{n} \left(\frac{m}{k+m} \right) p_{n-1}, \quad (6)$$

where n is the number of the infection group ($n = 1$ means group number of urchins containing one to five nematodes, $n = 2$ containing six to ten nematodes, etc.). A χ^2 -test was performed to test significant difference between the estimated and the observed distributions.

Results

Geographic distribution and prevalence

Infections of *Echinomermella matsi* in sea urchins were recorded in the Nordmøre survey area (63°00' N) and northwards. Nematodes were found in Vega, Bodø and Troms, but not in Nordmøre, South Trøndelag, North Troms or Finnmark (Fig. 1). Prevalence of nematodes in *Strongylocentrotus droebachiensis* in the Bodø area (1335 km from Lindesnes) was very high (40 to 88%) in both kelp beds and barren grounds (Fig. 2A). In Vega and Troms the prevalences were less than 25% with only one exception (Dåfjord in Troms) where 50% was infected. There was no significant difference (t -test, $p = 0.658$, $n = 18$) in nematode prevalence in the *S. droebachiensis* populations from kelp beds or barren grounds in the Bodø area, but the prevalence was significantly higher (t -test, $p = 0.013$, $n = 36$) in transition areas than in barren grounds in the Vega and Troms areas that had low prevalence. Nematodes infected 49.9% of *S. droebachiensis* in areas with high prevalence and 9.3% in areas with low prevalence at 2 to 5 m depths (Table 2). Three individuals (2.8%) of *S. pallidus*

and no *Echinus esculentus* were found to be infected. All locations where the nematodes were observed are included.

The densities of *Strongylocentrotus droebachiensis* populations at the randomly distributed locations investigated in 1981 (see "Materials and methods") along the distance gradient showed a change around 1200 km (i.e. at the Arctic Circle) with significantly higher values

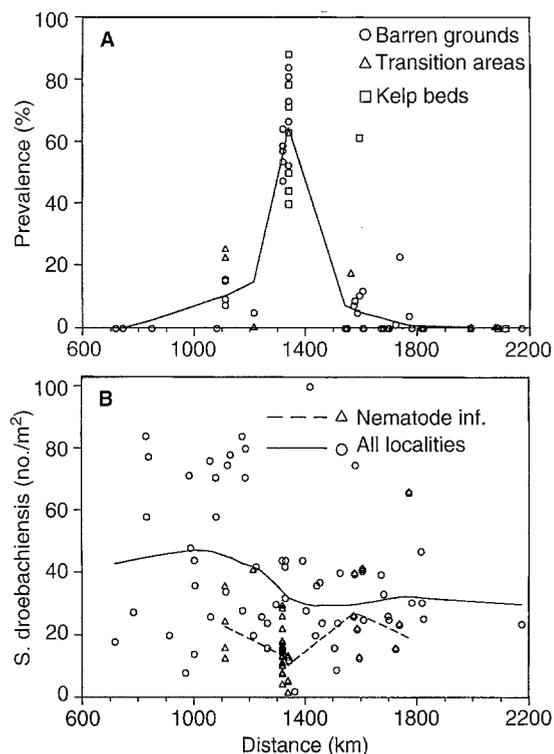


Fig. 2 A Prevalence (%) of the endozoic nematode *Echinomermella matsi* in the sea urchin *Strongylocentrotus droebachiensis* as a function of distance in kilometers from Lindesnes. Only individuals with test diameters of 21 to 50 mm were taken into account. Continuous line shows running mean of prevalence. B Density (ind m^{-2}) of *S. droebachiensis* in barren ground locations as a function of distance in kilometers from Lindesnes. Continuous line and circles show running mean of densities from randomly distributed locations investigated in 1981 in Nordmøre, Trøndelag and Nordland and in 1990 in Troms (Sivertsen in preparation). Dashed line and triangles show running densities for locations infected by nematodes (present paper)

Table 2 Total number of individuals investigated and of individuals infected with the nematode *Echinomermella matsi* for three species of sea urchins in northern Norway in the years 1982 to 1992. Individuals from all locations where nematodes were observed at depths of 2 to 5 m are taken into account (high = prevalence > 40%; low = prevalence < 25%)

Sea urchin species	With and without nematodes (no.)	With nematodes (no.)	Prevalence	
			Category	% infected
<i>Strongylocentrotus droebachiensis</i>	924	461	high	49.9
<i>S. droebachiensis</i>	1793	167	low	9.3
<i>S. pallidus</i>	106	3	high + low	2.8
<i>Echinus esculentus</i>	484	0	high + low	0

(t -test, $p = 0.014$, $n = 51$) in the south than in the north (Fig. 2B). At that time no investigations for *Echinomermella matsi* were performed. In later investigations nematode infections were recorded, and in the Bodø area, with high prevalence of nematodes, densities of *S. droebachiensis* were significantly lower (t -test, $p < 0.001$, $n = 41$) than in the randomly distributed locations in Salten (Fig. 2B). In the Vega area no significant difference in sea urchin densities occurred between the years 1983 and 1987 (t -test, $p = 0.904$, $n = 6$), or between 1981 and later investigations (t -test, $p = 0.105$, $n = 25$), and there was no significant difference between infected and noninfected locations studied in Troms in 1990 (t -test, $p = 0.809$, $n = 18$). Densities of *S. droebachiensis* decreased with time in areas with high prevalence ($> 40\%$) of nematodes, but not in areas with low prevalence ($< 25\%$) or absence.

The prevalence of nematode infection (30 to 85%) was highest among 2- to 7-yr-old sea urchins at the

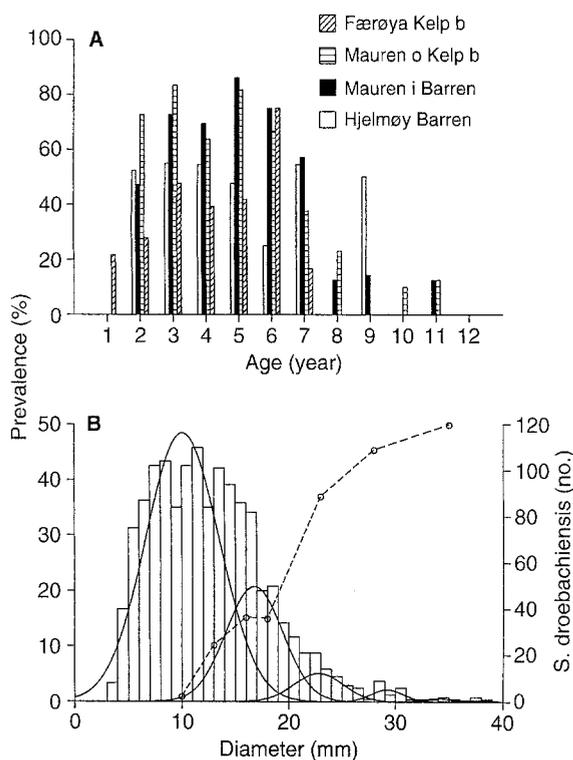


Fig. 3 **A** Prevalence (%) as a function of host age of the nematode *Echinomermella matsi* in the sea urchin *Strongylocentrotus droebachiensis* from two kelp bed locations (*Færøya*; *Mauren o* exposed shoreline at *Mauren* Island) and two barren ground locations (*Mauren i* sheltered shoreline at *Mauren* Island; *Hjelmøy*) at 2 to 5 m depth all found in the Bodø area. **B** Prevalence (dashed line) as a function of test diameter at a “recruiting” area for the sea urchin *S. droebachiensis* investigated in Bodø at depths of 8 to 12 m on 20 February 1989. Histogram shows the size distribution of *S. droebachiensis*; continuous lines show Gaussian curves delineating the separation of the five age groups from 0.8 to 4.8 years old from left to right, respectively, using the size-based technique of Bhat-tacharya (1967)

locations in Bodø (Fig. 3A). This included both kelp beds and barren grounds. Individuals younger than 2 yr or older than 7 yr old had little or no infection. Prevalence of small and young sea urchins from “recruiting” areas with a coralline bottom substrate at 8 to 12 m depth in Bodø showed that the infection started at about 10 mm and increased to 50% at 35 mm in diameter (Fig. 3B). At this location sea urchin age was determined using the size–frequency distribution method. In 1.8-yr-old sea urchins prevalence of infection increased from 0% for the smallest individuals to 15% for mean sized individuals. Among the 2.8-, 3.8- and 4.8-yr-old sea urchins prevalences were 37, 46 and 50% at their mean sizes. The prevalence increased sharply in the second- and third-year age classes (Fig. 3B), but more slowly in the older age groups (Fig. 3A, B).

Intensity

Of those infected, the intensity of parasitism increased, in general, proportionally to the test diameter/age of the sea urchins (Fig. 4A), except for large sea urchins at Vega and Hansnes. There was a significantly higher intensity in Bodø and Dåfjord than at Vega and the rest of Troms. The mean intensity of the different locations varies from 7 to 26 nematodes per sea urchin in high prevalence areas. The intensity decreased slowly over the study period both in kelp beds and transition areas in Bodø (Mann–Whitney, $p = 0.002$) from September 1982 to May 1984, and in Vega (Mann–Whitney, $p = 0.030$) from July 1983 to August 1987, respectively. No significant decreases were found in barren ground locations in Bodø (Mann–Whitney, $p = 0.633$) or Vega (Mann–Whitney, $p = 0.548$) over the same time periods.

Fitness

The effects of nematode infection on *Strongylocentrotus droebachiensis* fitness were measured in terms of both the individual growth rate of test (body) diameter and gonad production (Fig. 5A, B). The sea urchins showed significantly higher test-diameter growth rates in kelp beds than in barren grounds in Bodø areas (ANOVA, $p = 0.007$), but no significant differences were found between infected and noninfected subpopulations (ANOVA, $p > 0.070$) in the same location (Fig. 5A). Gonad production measured in Dåfjord in February 1992, a location with dense kelp beds and 50% prevalence, showed reduced gonad index in the infected subpopulation compared to the noninfected sea urchins (Fig. 5B). The gonad indices of age groups 3.8 to 8.8 yr were 12.8 and 2.2% in noninfected and infected sea urchins, respectively.

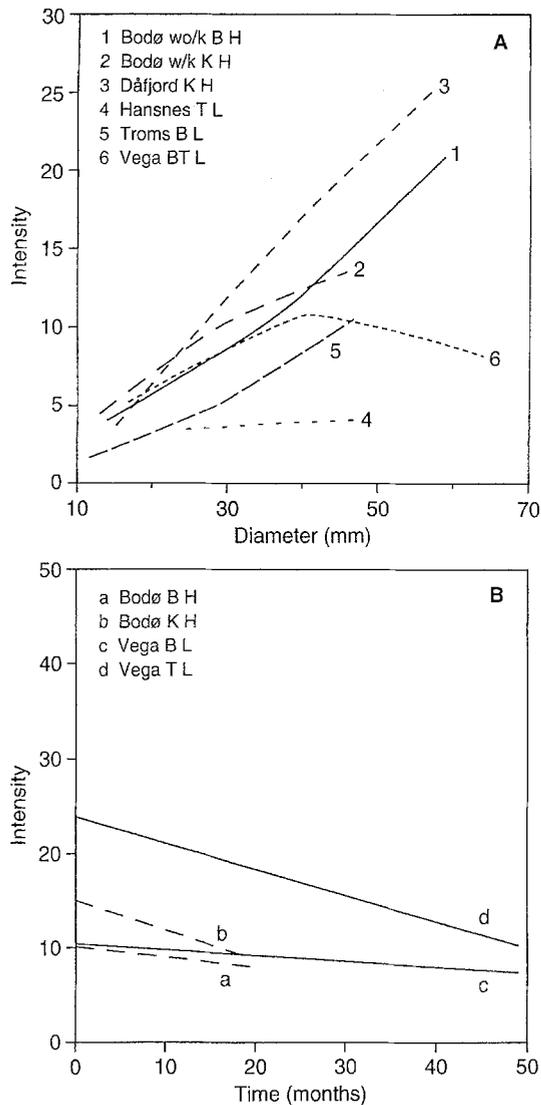


Fig. 4 Intensity of the endozoic nematode *Echinomermella matsi* in the sea urchin *Strongylocentrotus droebachiensis*. **A** Intensity in six different areas as a function of sea urchin test diameter. **B** Intensity at two types of location in Bodø investigated between September 1982 and May 1984, and two types of location in Vega investigated in July 1983 and August 1987, as a function of time (*K* = kelp beds; *T* = transition areas; *B* = barren grounds; *H* = high-prevalence areas; *L* = low-prevalence areas)

Parasite burden

In order to demonstrate variations in abundance with age/size of *Strongylocentrotus droebachiensis*, the locations were divided into two groups, those with high prevalence (Bodø and Dáfjord in Troms) and those with low prevalence (Vega and rest of Troms). In high-prevalence areas (Fig. 6A) the abundance reached eight in the age classes 4 to 6 yr, but decreased significantly to between one and two in age classes 9 to 11 yr, and was zero in older individuals. The ratio of variance/mean abundance was highest (25) in 5- to 8-yr-old sea urchins, and decreased slowly among older individuals.

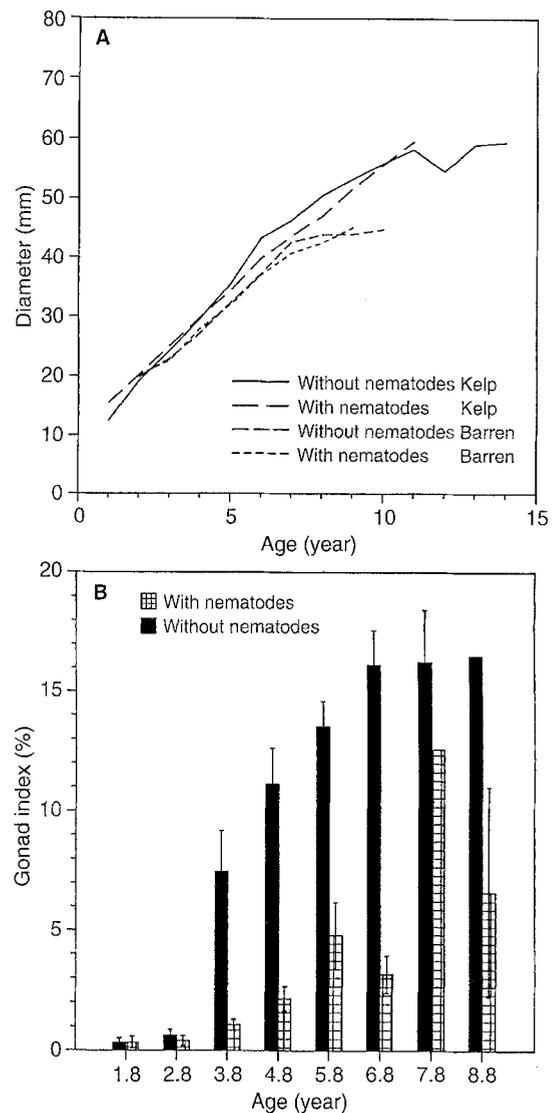


Fig. 5A Growth as a function of age of the sea urchin *Strongylocentrotus droebachiensis* infected or noninfected by *Echinomermella matsi*. Upper two lines represent kelp beds and lower two lines represent barren ground locations in the Bodø area. **B** Gonad index (gonad wet weight/total live weight \times 100) of *S. droebachiensis* individuals infected and noninfected by the nematode at different ages. Investigations were performed in kelp beds at depths of 2 to 5 m in Dáfjord on 10 February 1992, approximately 1 mo before breeding. Error bars indicate 1 SE; only one individual was measured where lines are missing

In areas with low prevalence (Fig. 6B), the abundance increased with increasing test diameter, reaching two nematodes in size groups exceeding 65 mm, and the ratio of variance/mean abundance increased proportionally from 2 to 45 with increasing test diameter.

The relationships between the log of the variance and the log of the mean abundance are shown (Fig. 7A), and the slopes (*a*) were 1.35 and 1.69 for the areas with high and low prevalence, respectively. The frequency of the parasites in sea urchin populations from areas with high and low prevalence are described by a negative

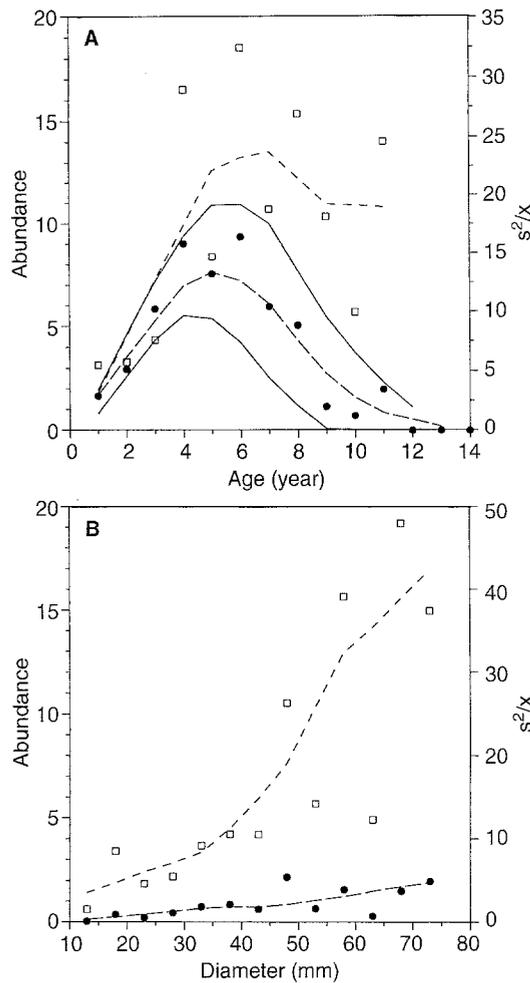


Fig. 6 Parasite (*Echinomermella matsi*) abundance and parasite dispersion (s^2/x) as a function of **A** age of the host (*Strongylocentrotus droebachiensis*) in high-prevalence areas (Bodø and Dajford) and **B** test diameter of the host (*S. droebachiensis*) in low-prevalence areas (Vega and Troms). Wide dashed lines and circles represent abundance; narrow dashed lines and squares represent dispersion; continuous lines represent 1 SE of abundance in high-prevalence areas

binomial distribution. An estimated distribution of nematodes using a negative binomial formula, where X = mean abundance, k = negative binomial parameter and n = number of individuals investigated gave the values $X = 5.087$ and $k = 0.216$ for $n = 924$ in areas with high prevalence and $X = 0.815$ and $k = 0.029$ for $n = 1793$ in areas with low prevalence, respectively (Fig. 7B). There was no significant difference between the observed and estimated frequency distributions in low prevalence areas (χ^2 -test, $0.05 < p < 0.10$), but there was in high prevalence areas (χ^2 -test, $p < 0.001$). There was a significant difference (χ^2 -test, $p < 0.001$) between areas with high and low prevalence. There is significant difference between the observed and expected numbers of sea urchins with intensity > 20 (Fig. 7B). In locations with high prevalence the numbers of sea urchins were 65.7 and 31 (χ^2 -test, $p < 0.001$), and at locations with low prevalence the numbers of

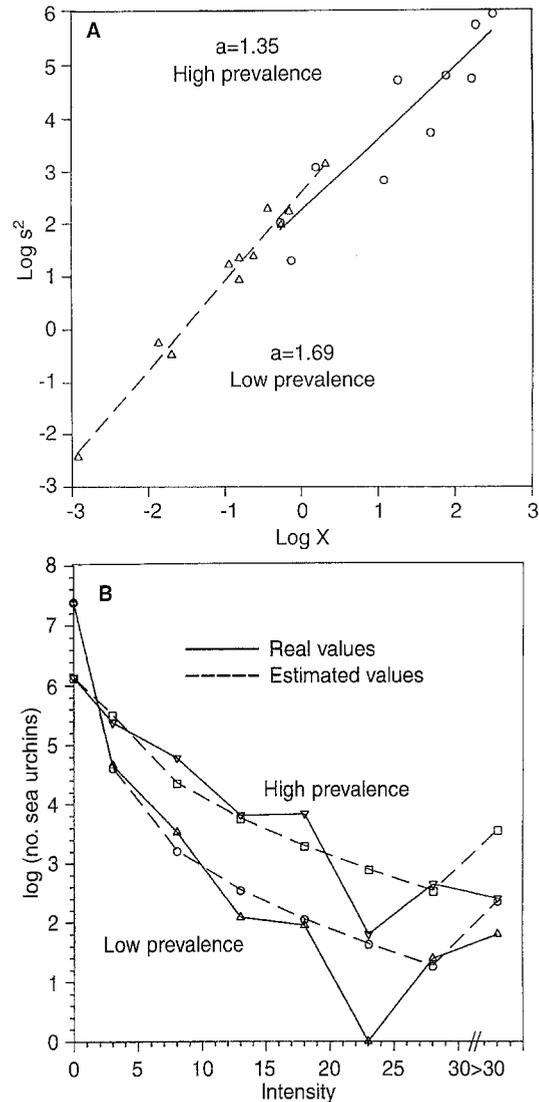


Fig. 7 **A** Relationship between the mean abundance (X) of parasites (*Echinomermella matsi*) per host (*Strongylocentrotus droebachiensis*) and the variance (s^2) plotted in log scales. Continuous lines and circles represent high-prevalence areas (Bodø and Dajford); dashed lines and triangles represent low-prevalence areas (Vega and Troms). (a = slope of the lines). **B** Frequency distribution of *E. matsi* as a function of intensity. Continuous lines show observed frequency; dashed lines represent estimated result, assuming a negative binomial frequency distribution; upper two lines represent high-prevalence areas; lower two lines represent low-prevalence areas

sea urchins were 19.2 and 11 (χ^2 -test, $0.025 < p < 0.05$), respectively, for estimated and observed infections of individuals hosting > 20 nematodes per sea urchin.

Nematode infection and host density

The abundance, intensity and prevalence of nematodes in *Strongylocentrotus droebachiensis* were negatively correlated with host density in barren ground areas (Fig. 8A to C), and were significantly higher in the

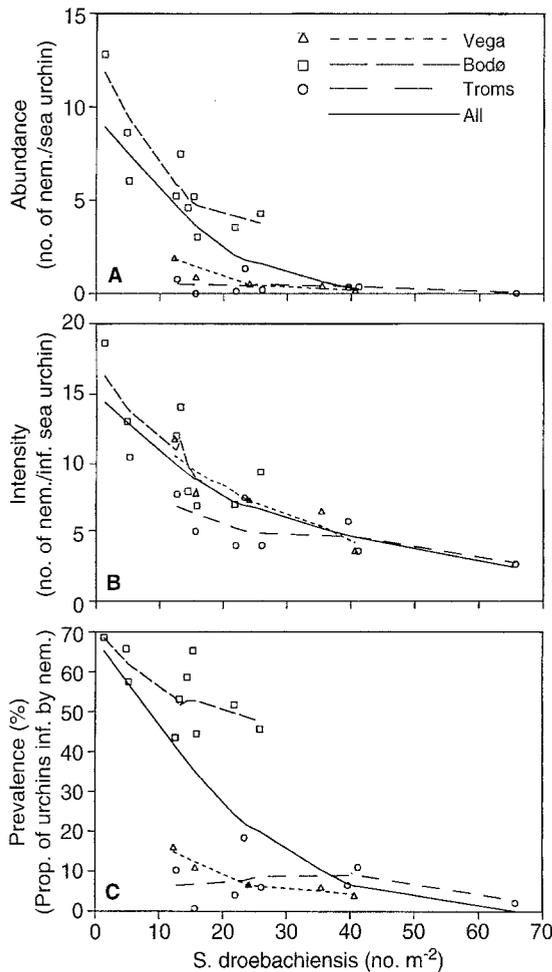


Fig. 8 **A** Abundance, **B** intensity and **C** prevalence of the endozoic nematode *Echinomermella matsi* in *Strongylocentrotus droebachiensis* in barren ground areas as a function of host density

Bodø area, where the host densities were lower (t -test, $p = 0.004$, $n = 23$) than in Vega and Troms. The significance values for abundance, intensity and prevalence were $p < 0.001$, $p = 0.003$ and $p < 0.001$, respectively (t -tests, $n = 23$). With decreasing density of *S. droebachiensis*, abundance increased from 0.1 to 13 nematodes per sea urchin, intensity increased from 4 to 19 nematodes per infected sea urchin and the prevalence increased from 1 to 69%. The mean density (± 1 SE) of *S. droebachiensis* on barren ground areas was 13.0 ± 2.5 ind m^{-2} at Bodø and 28.8 ± 4.4 ind m^{-2} at Vega and Troms areas.

Discussion

Geographic distribution

The infection of *Strongylocentrotus droebachiensis* by *Echinomermella matsi* was first observed in 1981 and

has not been recorded outside Norway (Hagen 1983; author's observations). The present investigation shows that the affected area extends from Vega to middle Troms. However, barren ground areas dominated by *S. droebachiensis* were found from Nordmøre and northward to the border of Russia (Sivertsen in preparation). High prevalence of *E. matsi* (40 to 88%) was found in all the locations investigated in the Bodø areas and at one location in Troms. Bodø may be the focus of the nematode parasite distribution. Low-prevalence areas ($< 25\%$) were found at Vega, south of Bodø, and in southern and middle Troms, north of Bodø. Skadsheim et al. (1995) also found nematodes in Vikna, North Trøndelag, south of our discovery. They found 2 to 29% prevalence in the area Vikna to Harstad in 1992. The nematode was mainly observed in *S. droebachiensis*, was rare (three individuals observed) in *S. pallidus*, but not found in *Echinus esculentus*.

Fitness

Host fitness, studied here in terms of somatic growth and gonad investment, may be affected by the sea urchins' nematode infection. For this reason, the growth rates of infected and noninfected *Strongylocentrotus droebachiensis* were compared by using the von Bertalanffy growth function (Bertalanffy 1938), but revealed no significant difference. The gonad production in *S. droebachiensis* from dense kelp beds measured about 1 mo before breeding was, however, reduced sharply in infected individuals to about one-sixth (17%) of the level in uninfected sea urchins. As about half the urchins were infected in highly infected areas, the reproductive capacity must have been reduced to about 60% (half population $\times 100\%$ + half population $\times 17\%$) in kelp bed areas as a result of nematode infection. Possible reductions in densities and changes in the size distribution of the sea urchin populations owing to the nematode infection are not taken into account in this calculation because they were not estimated. In barren grounds, however, *S. droebachiensis* densities are high, but the gonad production is low because of food shortage (Sivertsen and Hopkins 1995); the reproductive capacity in barren grounds is therefore low. Infected *S. droebachiensis* had smaller gonads. The reduction in sea urchin gonad investment caused by nematode infection shows that the nematode is a real parasite, and that it is probably a significant inhibitor to reproductive capacity. It is possible that lower reproductive capacity could explain lower densities of urchins.

Prevalence and intensity

The prevalence was high in the age classes 2 to 7 yr in shallow areas, but was low among younger and older individuals. In sea urchin "recruiting" areas at 8 to

12 m depth, infected sea urchins were not found among the 0.8-yr-old sea urchins, but the sharply increased prevalence among the 1.8- and 2.8-yr-old urchins may indicate that in these age classes the transmission rates are high. The sea urchins migrate from the "recruiting" areas to the shallower rocky or stony bottom areas mainly in their third year of life when their tests were approximately 15 to 20 mm in diameter (Sivertsen and Hopkins 1995).

The nematode intensity increased with increasing host test diameter in adults dominating shallow areas. The higher intensities in kelp beds and transition areas than in barren grounds are probably caused by the domination of larger sea urchins in locations where kelp is present. To explain the intensity pattern observed four speculative explanations are considered: (a) the transmission rates may be lower among older individuals in the shallow areas than among younger ones in recruiting areas, (b) the transmission rate may be about the same, but the most heavily infected urchins have greatest probability of dying, keeping the prevalence from increasing with increasing age, (c) older, uninfected sea urchins may be less prone to infection, and (d) the increase in intensity with size may be caused by reproduction of the nematode inside the host. The prevalence, distribution, with few individuals more than 7 yr old, may be speculatively explained by one or more of the following. (1) The nematodes do not live as long (3 to 5 yr) as the host, and they die and retreat from the host after having completed their life-cycle, without causing host mortality. (2) Hosts become immune to the parasite, and the parasite leaves the host. (3) After being infected for some time (3 to 5 yr) the infected hosts die, leaving only uninfected individuals. This leads to an underdispersion of parasites (Anderson and Gordon 1982). (4) The high infection rates may have started and increased sharply some 5 yr previous to our investigations (in the late 1970s, as the increase of the sea urchin population size occurred in the early 1970s), and at that time the infection rates were highest among the young urchins. This seems unlikely in the light of more recent results obtained from the Norwegian coast; Skadsheim et al. (1995) and Stien et al. (1995) showed that areas inhabited by infected sea urchins may maintain large/old individuals for a long time.

Mean intensity may be constant in barren grounds or decrease slowly in kelp bed/transition areas over time, indicating a possible dynamic in the recruitment and mortality rates of the parasite in the host populations. The life span of *Strongylocentrotus droebachiensis* may reach 10 to 15 yr (Sivertsen and Hopkins 1995). The short duration of our studies, however, may not have allowed us to detect long-term cycles. The high prevalence over time shows stability in both nematode and sea urchin populations and, as the host populations are not eradicated, this may indicate that the likelihood of an increase in parasite-induced mortality among sea urchins is not large.

Frequency distribution and nematode-induced mortality

On the basis of model simulation studies, Anderson and Gordon (1982) suggested that changes in the frequency distribution of parasite numbers per host could provide clues concerning causality, but would not necessarily provide clear evidence of parasite-induced host mortality. The ratio of variance/mean abundance of *Echinomermella matsi* showed values much higher than unity, indicating overdispersion of nematodes in the sea urchins (Anderson and Gordon 1982). Anderson and Gordon (1982) also found that overdispersed populations usually showed a negative binomial frequency distribution of parasites. Lester (1984) demonstrated various ways of analyzing the possibility of parasite-induced host mortality. Here three methods are applied.

The first method is based on the theory that the decrease in both abundance and variance/mean abundance ratios among older individuals in a population indicate parasite-induced host mortality (Anderson and Gordon 1982; Lester 1984). The host age/parasite abundance curves (parasite burden) for *Strongylocentrotus droebachiensis* and *Echinomermella matsi* showed peaked curves for high nematode prevalence areas (with the highest values among 4- to 7-yr-old sea urchins), and the variance/mean abundance curves decreased among cohorts older than 8 yr of age. This indicates reduced abundance in old/large individuals. In low-prevalence areas the abundance and variance/mean abundance curves increased with increasing age/size of the host. The decrease in both abundance and variance/mean abundance ratios among older individuals in high-prevalence areas may indicate parasite-induced host mortality among sea urchins. Peaked curves may also be explained by factors other than parasite-induced host mortality (Anderson and Gordon 1982; Pacala and Dobson 1988).

In the second method Anderson and Gordon (1982) showed that in parasites, as in free-living nematodes, plots on a log scale of observed variance against abundance tend to produce highly significant linear relationships. Specifically, where the frequency distribution of the parasites is overdispersed and can be described by the negative binomial distribution, the relationship should be approximately linear with a slope of roughly 2.0 if no parasite-induced mortality occurred. However, when the rate of parasite-induced host mortality is high, the slope might be lower. The slope of log scales of variance against abundance showed values of 1.69 and 1.35 for high- and low-prevalence areas, respectively. This may indicate that parasite-induced mortality occurs in high-prevalence areas in our sea urchin populations, while the evidence for parasites as a cause of death in low-prevalence areas is weaker. Thus, consideration of the relationship between variance and mean

parasite abundance with age provides an indication of parasite-induced host mortality.

The third method is based on increasing mortality with increasing number of parasites present in an individual (Crofton 1971; Lester 1984). Measurements of the frequency distribution of nematodes in sea urchins and the corresponding estimates of the negative binomial distribution of parasites showed a significant difference among populations in areas with a high but not with low prevalence. There were significantly higher counts in estimated than observed subpopulations exceeding 20 nematodes per sea urchin. This indicates that individuals with high intensity may have died. This method, therefore, may support the hypothesis of nematode-induced mortality. This hypothesis can be complicated, as the effect of a given number of nematodes may be weaker in larger individual hosts than in smaller ones. Anderson and Gordon (1982) also rejected the idea of a lethal level at which hosts who harbour less than a specific number of parasites survive, while those who harbour more die. They simply assumed, in accordance with the available empirical evidence, that the probability of a host dying during a given time interval is a function of its parasite burden (Anderson 1978, 1979; Anderson and Gordon 1982).

In our studies the nematode intensity and host density correlated negatively with each other, while cyclic dependence would have meant that they correlated positively with each other (Scott and Dobson 1989). This probably indicates that host–nematode interaction is not cyclic; although long-term studies may provide other results. Our relatively short time scale (Fig. 4B) showed slow or no decreases in intensity, and the low *Strongylocentrotus droebachiensis* densities may be caused by other effects than the nematode infection, for instance a result of high densities of *Echinus esculentus*. In interspecific competition between *S. droebachiensis* and *E. esculentus*, however, *S. droebachiensis* is probably more successful (Sivertsen in preparation). In this study host density/nematode abundance, intensity and prevalence relationships at many locations were examined. To answer questions of mortality clearly a long-term series of investigations at specific sites is required.

There was no significant difference in prevalence between kelp bed and barren ground areas. Of the randomly distributed barren ground locations in Helgeland and Salten investigated in 1981 and in Troms in 1990, only the heavily infected Bodø area, investigated in 1982 to 1984, showed significantly lower *Strongylocentrotus droebachiensis* densities than the surrounding locations. This may indicate that a restricted geographic area rather than the type of habitat is important for the infection rate, and in heavily infected areas a lower host density may be found. Sivertsen (in preparation) used a canonical correspondent analysis (CCA) to discriminate between different biota and environmental parameters among locations consisting of

kelp beds, transition and barren ground areas. The CCA showed that nematode infection makes a significant contribution to explaining the variability, and infected areas showed low *S. droebachiensis* densities. An agent important for the spread of the nematode may be present, and this agent may be more common in the Bodø area than other areas, independent of kelp and sea urchin densities. If the peaked age/parasite burden curve is caused by the nematode burden on the host, the conclusion would be that nematodes cause increased mortality among older sea urchins. Low host densities in highly infected barren ground areas could also be caused by reduced reproduction rates, owing to the nematode infection. Other reasons why the *S. droebachiensis* densities in Bodø area are low may be that this area does not support higher densities, or that these are reduced by interspecific competition with *Echinus esculentus*.

Regrowth of kelp beds has been observed in Trøndelag and Helgeland, the southern part of the overgrazed area (Skadsheim et al. 1995; Sivertsen in preparation), and at Værøy (Hagen 1995). *Echinomermella matsi* was not found in South Trøndelag, but had low prevalence in North Trøndelag, Helgeland and Værøy (prevalence ranged from 7.5 to 21.6% with one location at 41.9%). Kelp regrowth was not observed in Bodø during the present investigations. Reasons other than nematode infection in *Strongylocentrotus droebachiensis* may have caused the kelp regrowth in Trøndelag and Helgeland. Skadsheim et al. (1995) and Stien et al. (1995) came to the same conclusion.

In order to be able to determine whether *Echinomermella matsi* cause increased mortality rates in *Strongylocentrotus droebachiensis* populations, one must know the life cycle of the nematode, and have access to long-term host density and nematode intensity/prevalence data. However, it is likely that low prevalence among older individuals is caused by higher host mortality rates.

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