Population dynamics of the *Echinomermella matsi* (Nematoda) - *Strongylocentrotus droebachiensis* (Echinoida) system: effects on host fecundity

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ABSTRACT: At high population densities the green sea urchin *Strongylocentrotus droebachiensis* can affect subtidal community structure significantly by grazing down kelp beds to barren grounds. The parasitic nematode *Echinomermella matsi* has been suggested to reduce sea urchin population densities at barren ground localities, thereby giving rise to kelp recovery and possibly a cyclic behaviour between these states. Here, we evaluated the potential of *E. matsi* to affect host population dynamics through effects on host fertility. This was done by estimating the effect of infection on the host population gonad mass at 4 localities, ranging from barren ground to a kelp bed. The relationship between sea urchin gonad wet weight, sea urchin size and worm burden was modelled statistically. From this model we estimated the effect of infection at the host population level. We found a strong negative relationship between gonad wet weight of sea urchins and the wet weight of their nematode infrapopulations. In some animals this reduction in gonad development was estimated to be 100 %, indicating functional castration. At the host population level, the relative reduction in gonad mass due to infection was less than 10 % at all sample sites, and was in the same range both in the kelp forest and on the barren grounds. The main reason for this low population effect of infection is that most sea urchins carry low worm burdens, which will have a small effect on host gonads. Compared to the effect of inter-site differences in sea urchin size on mean gonad sizes, the effect of infection on mean gonad size was found to be small. We therefore suggest that processes that determine sea urchin size distributions, such as survival and growth, are likely to be more important in the determination of local reproductive potential than direct effects of infection on gonad development.

KEY WORDS: Kelp bed ecology · Parasitism · Sea urchin · Reproduction

INTRODUCTION

The green sea urchin *Strongylocentrotus droebachiensis* is a destructive grazer of kelp forests. It has repeatedly been reported to have destroyed former luxuriant kelp forests over extensive coastal areas of the northern hemisphere, both in the Atlantic and the Pacific (Breen & Mann 1976, Duggins 1980, Hagen 1983, Witman 1985, Skadsheim et al. 1995). These bar-

rens may persist for decades, but if the urchin density is reduced sufficiently, algal vegetation soon starts to recover (Duggins 1980, Miller 1985, Scheibling 1986, Johnson & Mann 1988, Christie et al. 1995, Leinaas & Christie 1996). In the North Pacific, predation from sea otters may have such an effect (Estes et al. 1978, Duggins 1980, Estes & Duggins 1995), while mass mortality of *S. droebachiensis* caused by an endoparasitic amoeba has been extensively studied off Nova Scotia in Canada (Jones & Scheibling 1985, Miller 1985, Scheibling 1986, Scheibling & Raymond 1990). In this paper we question the potential of the parasitic nematode *Echinomermella matsi* to limit population densities of *S. droebachiensis* through its effect on host gonad size.

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In Norway, population increases of *Strongylocentrotus droebachiensis* have caused large scale destructions of kelp forests since the 1970s (Skadsheim et al. 1995). More recently several instances of population reduction with subsequent algal regrowth have been documented (Hagen 1987, 1995, Christie et al. 1995, Skadsheim et al. 1995). Many of these populations have been heavily infected by *Echinomermella matsi* (Hagen 1987, 1995, Christie et al. 1995, Stien et al. 1995), and Hagen (1987, 1992, 1995) has suggested that this parasite may regulate infected sea urchin populations and even induce cyclic population dynamics.

Other factors than the parasite *Echinomermella matsi* may cause population decline. Skadsheim et al. (1995) found severe density reductions in uninfected areas, and Stien et al. (1995) concluded that a local mass mortality observed within an infected area was unlikely to have been caused by the parasite. However, along the coast of central and northern Norway, populations of *Strongylocentrotus droebachiensis* are generally infected by the parasite (Skadsheim et al. 1995, Sivertsen 1996) which potentially may be an important factor in host population dynamics. *E. matsi* is found in the coelom of *S. droebachiensis* and infrapopulations (parasite populations in individual hosts) can in extreme cases fill up almost the entire volume available (Jones & Hagen 1987, Stien 1993). Negative effects of infection on host gonads at the individual level have been demonstrated (Hagen 1987, 1996, Sivertsen 1996), and effects on host survival have been indicated (Hagen 1987, 1995, 1996, Sivertsen 1996). However, conclusions concerning parasite reduction of host density need to be based on population studies and not just on effects on individual hosts. Hagen (1992) and Sivertsen (1996) attempted to estimate the population effect of infection, but calculated only the grand mean reduction in the gonad mass without taking into account that large sea urchins carry most of the gonad mass in the population and were, at least in Sivertsen's (1996) study, less often infected and less affected than smaller sea urchins. In this paper we approach this problem by estimating the effects of infection on the weight of host gonads and sum these effects at the individual level to estimate the effect on gonad mass at the local host population level.

Due to the long lasting pelagic larvae stage of *Strongylocentrotus droebachiensis* (Emlet et al. 1987), local effects on fecundity will normally have little effect on larval supply to the same sites, and thus are a weak determinant of local population dynamics (Caley et al. 1996). However, along the coast of central Norway, the effect of infection on host fecundity may be important, because of the presence of infection on regional scales (Hagen 1987, Christie et al. 1995, Skadsheim et al. 1995, Sivertsen 1996).

To estimate the effect of infection, we modelled statistically the expected gonad wet weights of uninfected sea urchins and the effect of observed worm burdens on predicted gonad wet weights. The gonad size of uninfected hosts depends on the quality as well as the quantity of food available (Gonor 1972, Vadas 1977, Larson et al. 1980, Lawrence & Lane 1982, Thompson 1982, Keats et al. 1984, Rawley 1990, Pearse & Cameron 1991). Moreover, gonad size varies seasonally due to annual spawning cycles (Himmelmann 1978, Falk-Pedersen & Lønning 1983, Keats et al. 1984). In order to evaluate whether the effect of infection varies with food availability and season, we analysed data collected over 3 yr from 4 *Strongylocentrotus droebachiensis* populations located close to the island of Vega in central Norway. The sampling sites differed with respect to algal cover, ranging from barren grounds to mature kelp forest.

MATERIALS AND METHODS

Sea urchins were collected at 4 skerries off the island of Vega, central Norway, from July 1990 to October 1993 (Table 1). Three sites were located within a former extensive barren ground area where differential population decline led to the growth of patchy vegetation after 1991 (Leinaas & Christie 1996). Site 1 was barren until autumn 1991, and sampling from this site was then terminated as very few urchins had survived a mass mortality a few months earlier. At site 2 the population decline was less pronounced, and the site remained largely barren throughout the study period, but with a limited growth of annual algae during the summer months. At site 3 the urchin density was reduced experimentally between October 1988 and June 1989, which initiated a succession of kelp vegetation (Leinaas & Christie 1996). The last site (4) was a reef near the border of the barren area. Here a mature kelp forest was inhabited by a high density of *Strongylocentrotus droebachiensis*. This was in contrast to most mature kelp forests along the coast of Norway, where *S. droebachiensis* was rare. Consequently, the material represents 3 primarily barren ground populations, one of them (site 3) with greatly improved foraging conditions during the last few years, and 1 kelp bed population (site 4), easily recognisable by the larger urchins composing it.

Sea urchins were collected by divers at 5 m depth. One sampling scheme involved sampling from within 0.5 × 0.5 m frames repeatedly placed on the bottom to attain a representative sample of the sea urchin size distribution. After the mass mortality at site 1 in May–June 1991 (Christie et al. 1995), the sampling scheme was redesigned to incorporate sampling over

larger areas, in order to obtain sufficient numbers of urchins. The other sampling scheme involved selective sampling of large urchins (>30 mm). For the analysis of the effects of infection at the individual host level we used both selective and representative samples, while only the representative samples were used for the evaluation of differences in mean gonad wet weights between populations. Only data on urchins with a test diameter of 25 mm or more have been analysed. Smaller urchins contribute little to the population gonad mass because they have very small gonads (predicted values <0.2 g; authors' pers. obs. and Fig. 1). Test diameter, wet weight and gonad wet weight of sea urchins and the wet weight of their parasite infrapopulations were measured.

When comparing the gonad sizes of sea urchins of different sizes, a gonad index, measuring the gonad weight as a percentage of the animal's weight, has traditionally been used. Gonor (1972) noted that the gonad index had to be independent of animal size in the sea urchin size range considered for its use to be justified when comparing animals of unequal size. In preliminary analyses we found that the value of the gonad index depended non-linearly on sea urchin diameter (Fig. 1B). We therefore chose to use gonad wet weight directly due to its easier interpretation.

The expected gonad size of *Strongylocentrotus* sp. generally increases non-linearly with increasing sea urchin size (Fig. 1A; Gonor 1972, Hagen 1996). Preliminary analyses also suggested that the effect of infection varied non-linearly with worm burden, and that the variability in observed gonad sizes increased with increasing expected values of sea urchin gonad size (Fig. 1A). Such non-linearities and the heterogeneous variance may have hindered earlier attempts at analyses using linear regression. Here we approached this problem by using non-linear, non-parametric regression to model gonad size as a function of explanatory variables, and by using a parsimonious variance function for the random component of the model.

In the statistical analyses we use generalised additive models (GAM) with identity link functions (Hastie & Tibshirani 1990). These models are extensions of the ordinary linear models where the expected value of the response variable is assumed to be a linear function of the *p* predictor variables x_i:

Table 1. Summary of *Strongylocentrotus droebachiensis* sampling. Year and month of sampling, sampling site and size (N), prevalence of infection and mean sea urchin diameter are given. The sampling schemes used were selective sampling (S) of large sea urchins, or representative sampling (R). When both selective and representative samples were collected, prevalence and mean diameter are given for the representative samples

Year	Month	Site	N	Prevalence (%)	Mean diameter (mm)	Sampling scheme
1990	7	1	16	65	46.7	S
1990	10	1	35	63	42.9	S
1991	3	1	109	45	36.6	R
1991	4	1	95	31	33.3	R, S
1991	6	1	51	25	29.1	R, S
1991	7	1	29	31	32.2	R
1991	9	1	100	52	36.1	R
1991	11	1	78	45	36.5	R
1991	11	2	41	32	50.3	S
1992	3	2	104	35	32.0	R, S
1992	4	2	28	29	52.3	S
1992	5	2	41	21	45.9	S
1992	6	2	117	32	36.3	R, S
1992	9	2	124	18	34.7	R, S
1993	5	2	197	17	42.0	S
1993	10	2	64	25	34.8	R
1990	7	3	12	48	55.0	S
1990	10	3	39	50	45.1	S
1991	4	3	99	25	36.1	R, S
1991	6	3	60	11	34.9	R
1991	9	3	52	33	38.7	R
1991	11	3	93	30	38.5	R
1992	3	3	53	30	46.8	S
1992	9	3	53	23	35.8	R
1990	7	4	20	27	63.5	S
1990	10	4	44	14	61.2	S
1991	3	4	127	29	48.5	R
1991	4	4	107	31	57.8	R
1991	6	4	196	26	52.9	R
1991	9	4	86	40	52.6	R
1991	11	4	82	27	53.0	R
1992	3	4	94	36	50.9	R
1992	4	4	30	13	60.7	S
1992	5	4	39	15	63.7	S
1992	6	4	96	34	53.5	R
1992	9	4	85	21	55.7	R
1993	5	4	85	30	55.9	R
1993	10	4	90	21	52.4	R

$$E(Y) = \alpha + \sum_{i=1}^{p} \beta_i \times x_i \qquad (1)$$

in that the linearity assumption is relaxed and replaced by a smoothing function $f_i(x_i)$, estimated by a data-driven scatter plot smoother:

$$E(Y) = \alpha + \sum_{i=1}^{p} f_i(x_i) \qquad (2)$$

Combinations of smooth and linear functions of the predictor variables can also be modelled within this framework:

$$E(Y) = \alpha + \sum_{i=1}^{m} f_i(x_i) + \sum_{j=m+1}^{p} \beta_j \times x_j \qquad (3)$$

This choice of method allows statistical modelling of non-linear relationships and also statistical inference when the variance varies with the mean. In the present analysis, we have assumed that the variance is proportional to the squared mean. Residual plots showed this to be acceptable. For non-linear relationships we used a locally weighted scatter plot smoother (lowess) (Hastie & Tibshirani 1990, Chambers & Hastie 1992; see Fig. 1). The neighbourhood parameter, which determines the degree of smoothness of the fitted line, was adjusted by graphical analyses. Separate smooth lines were fitted for the relationship between gonad wet weight and the continuous predictor variables sea urchin diameter and and infrapopulation wet weight, within the levels of the factor predictors month of sampling, year of sampling, and sample site. This was done using as many dummy variables for the continuous variables as factor levels in the factor predictor variables. These dummy variables were assigned the observed value of the continuous variable when the observation had the given level of the factor and were coded zero when the observation did not have the given level of the factor.

An important decision when analysing data is to choose a model for the data that is neither too complex,

giving low precision of the estimates, nor too simple, giving heavily biased estimates (Burnham & Anderson 1992). To find a reasonable model that fitted the data, we used F-tests to compare models that were nested, and the AIC statistic to compare models that were not nested (McCullagh & Nelder 1989, Hastie & Tibshirani 1990). The identity link function was chosen because we considered the effect of infection on gonad weights to be additive to the effect of sea urchin size. In combination with a model of variance as a power function of the mean, this choice induced problems in the estimation procedure, because expected values of zero mean and thereby zero variance could be obtained. To overcome this problem the response variable was transformed to gonad wet weight + 2.

In a preliminary analysis of the relationship between gonad wet weight and sea urchin diameter in the uninfected sea urchins sampled, this relationship was found to differ significantly with respect to both time and site of sampling. We therefore used separate lowess fits for each sample when we modeled the expected gonad wet weight in uninfected sea urchins. The importance of the effect of parasitism on gonad development was evaluated by comparing the effect of different mean sea urchin sizes in the host populations. All analyses were done using S-PLUS (Anonymous 1995).
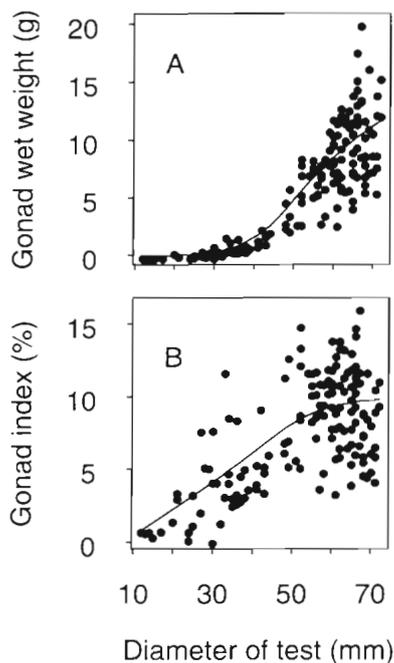

Fig. 1. Gonad sizes of *Strongylocentrotus droebachiensis* not infected by the nematode *Echinomermella matsi*, plotted against the diameter of the sea urchins. A locally weighted regression line is drawn through the data. The sea urchins were collected at site 4 on 15 March 1991. (A) Gonad wet weight vs gonad size. (B) The gonad index vs gonad size

RESULTS

Modelling the effect of infection on the gonad size of individual hosts showed a significant effect of the parasite infrapopulation wet weight on gonad wet weights (Table 2). There was also a significant interaction between parasite wet weight and sea urchin diameter (Table 2). The statistical model that best described the effect of infection (lowest AIC) had a linear term for parasite wet weight and a non-linear term describing the interaction (Model 6 in Table 2). We did not find this effect of infection to vary significantly with site, month or year of sampling (Table 3). Thus, in equal sized sea urchins the same worm burden appears to give approximately the same reduction in gonad wet weights independent of site and time of sampling. To estimate the effect of infection we therefore used the model that did not include site and time of sampling (Model 6 in Table 2). This model describes a surface with increasingly negative absolute effects of infection with increasing sea urchin size (Fig. 2). This implies that the reduction in gonad wet weight caused by an infrapopulation of a specific mass increases with increasing size of the sea urchin. However, the gonad mass reduction measured relatively, i.e. as a percentage of the expected gonad mass of an uninfected sea

Table 2. Analysis of deviance table to detect effects of *Echinomermella matsi* infrapopulation wet weight on gonad wet weight (g) + 2 for sea urchins *Strongylocentrotus droebachiensis* with a test diameter of more than 24 mm. Deviance, residual degrees of freedom, the AIC statistic, and results from approximate *F*-tests evaluating the significance of nested terms are given. The models were estimated assuming a variance equal to the second power of the mean. In the Model column, 'lo(D)$_{Sample}$' implies that the effect of sea urchin diameter on gonad wet weights was modelled using non-parametric, locally weighted (lowess) regression within each sample. 'P' implies addition of a linear term for effects of infrapopulation wet weight. 'PD' and 'P^{2}D' refer to linear terms describing the interaction between infrapopulation wet weight and sea urchin diameter, and between P^2 and D. 'lo( )' refers to non-linear terms. The numbers in the model column give the number of the model to which the term is added

Model number	Model	Deviance	Residual df	AIC	Comparison of model no.	F	p-value
0	Intercept	1645.98	2870				
1	0 + lo(D)$_{Sample}$	251.43	2714.81	276.04	1 vs 0	97.03	<0.0001
2	1 + P	220.54	2714.01	245.27	2 vs 1	470.04	<0.0001
3	2 + PD	216.70	2713.00	241.61	3 vs 2	47.50	<0.0001
4	1 + lo(P)	220.24	2710.89	245.48	4 vs 2	1.19	0.31
5	4 + PD	214.07	2709.93	239.46	5 vs 4	81.36	<0.0001
6	2 + lo(PD)	213.14	2709.36	238.61	6 vs 3	12.50	<0.0001
7	4 + lo(PD)	213.13	2706.28	239.09	7 vs 6	0.007	0.99
8	6 + lo(P^{2}D)	212.97	2702.61	239.51	8 vs 6	0.16	0.95

Table 3. Analysis of deviance table to detect whether the effect of *Echinomermella matsi* infrapopulation wet weight on *Strongylocentrotus droebachiensis* gonad wet weight + 2 differs between sample sites ('S'), month of sampling ('M') or year of sampling ('Y'). Deviance, residual degrees of freedom and results from approximate *F*-tests evaluating the significance of nested terms are given. Interaction terms are symbolised by combinations of the letters 'S', 'M' and 'Y'. 'lo(X)$_Z$' implies that non-parametric regression fits for the relationship between sea urchin gonad wet weight and the covariate X were performed for each level of variable Z. The '/' operator symbolises that the expression to the right of the operator is nested within the expression to the left of the operator

Model number	Model	Deviance	Residual df	Comparison of model no.	F	p-value
1	Intercept + lo(D)$_{SMY}$	251.43	2714.81			
2	1 + P + lo(PD)	213.14	2709.36			
3	1 + S / P + lo(PD)$_S$	211.88	2688.83	3 vs 2	0.77	0.75
4	1 + Y / P + lo(PD)$_Y$	211.75	2687.74	4 vs 2	0.81	0.71
5	1 + M / P + lo(PD)$_M$	208.97	2658.34	5 vs 2	1.03	0.40
6	1 + SY / P + lo(PD)$_{SY}$	208.95	2637.50	6 vs 2	0.74	0.95
7	1 + MY / P + lo(PD)$_{MY}$	203.63	2609.20	7 vs 2	1.22	0.07
8	1 + SM / P + lo(PD)$_{SM}$	200.63	2533.70	8 vs 2	0.90	0.82
9	1 + SMY / P + lo(PD)$_{SMY}$	199.11	2506.02	9 vs 2	0.87	0.91

urchin of the same size, decreases with increasing sea urchin size. The effect of infection is, therefore, a complex function of both the worm burden and the size of the host. Several other models had values of AIC almost as low as model 6 (Table 2). These showed qualitatively the same relationships as the selected model.

Using model 6 (Table 2) we estimated the gonad wet weights of the sea urchins with the observed distribution of infrapopulation wet weights, and the predicted gonad wet weights assuming that all urchins were uninfected. The discrepancy between these values was interpreted as the effect of infection. Most of the infected sea urchins had small estimated reduc-

tions in gonad wet weight due to infection (Fig. 3A), because most urchins had low worm burdens (Fig. 3B), but for some individuals the predicted reduction in gonad wet weight due to infection was close to 100%. This agrees with our visual observations of the most heavily infected hosts, and shows that some urchins are functionally castrated by the parasite. Estimated mean gonad wet weight loss in representative samples was less than 10% due to infection at all sites (Fig. 4), and the estimated reductions were not higher on the barren grounds than in the kelp beds (Fig. 4). In comparison, the estimated mean gonad wet weight increased fairly monotonically more than 3-fold, from 2.5 g to around 9 g, with increasing mean
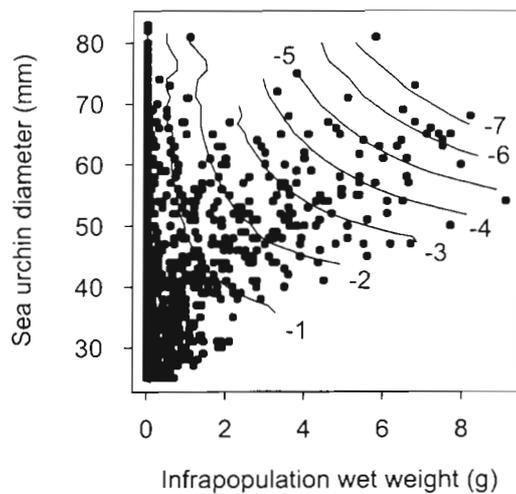
Fig. 2. Diameters of *Strongylocentrotus droebachiensis* plotted against the wet weight of their *Echinomermella matsi* infrapopulations. The contour lines give the estimated effect (g) of parasite infrapopulation wet weights on sea urchin gonad wet weights given by model 6 in Table 2

sea urchin diameter (Fig. 5). The samples with high mean diameter values were from the kelp bed while the low ones were from the barren grounds. The estimated <10% reduction in mean gonad size due to infection is therefore of relatively little importance relative to sea urchin size for between-site differences in mean gonad size.

DISCUSSION

Effects on the individual host

Our finding of a negative effect of the parasitic nematode *Echinomermella matsi* on the reproductive potential of infected sea urchins agrees with earlier reports (Hagen 1987, 1992, 1996, Stien 1993, Sivertsen 1996). The gonads of sea urchins produce and store gametes, and function as a storage organ for nutrients that are used for gametogenesis (Lawrence & Lane 1982). A reduction in gonad size caused by the parasite is therefore likely to reduce host fecundity.

The numerical relationship between the wet weight of the parasite infrapopulation and the effect of parasitism on gonad sizes has not been described before The increasing effect of infection with increasing infrapopulation wet weights indicates that the pathogenic effect of *Echinomermella matsi* may be caused by competition with the host for available nutrients, but also influence on hormones that regulate gonad growth and gametogenesis may be of importance (Pearse & Timm 1971). The effect of infection depends on the size of the host. The gonad mass of larger sea
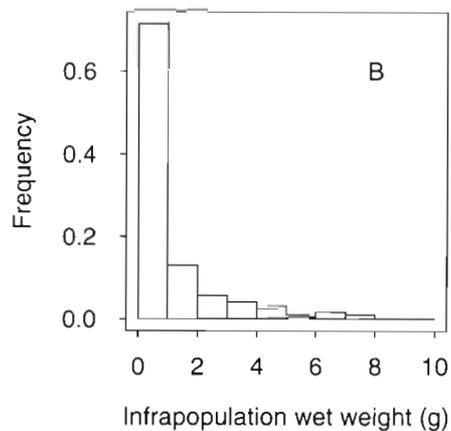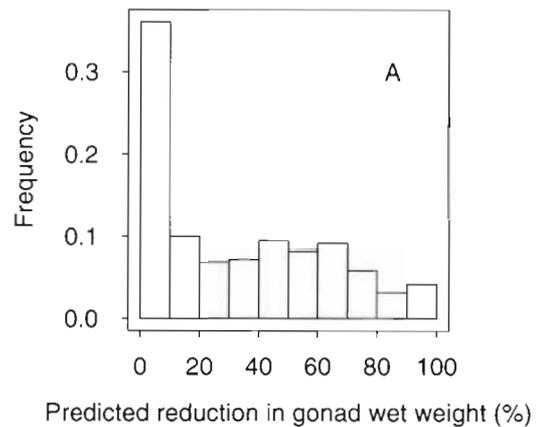

Fig. 3. (A) Frequency distribution of predicted reduction in gonad wet weight for *Strongylocentrotus droebachiensis* due to infection by *Echinomermella matsi*, and (B) frequency distribution of nematode infrapopulation wet weights in infected sea urchins from the 4 sample sites

urchins was reduced more by an infrapopulation of a given size than that of smaller sea urchins. This may be due to nonlinearities caused by an effect of infection on hormone levels, but could also be due to nematodes in larger hosts extracting their nutrients at a higher rate, and suggests that nematodes may develop faster in larger hosts. The observed complex relationship between gonad wet weight, sea urchin size and worm burden implies that the effect of infection cannot easily be calculated from data on prevalence of infection or mean worm burden. The actual distribution of worm burden with respect to sea urchin size needs to be incorporated in the estimates as in our modelling approach, to obtain relevant estimates.

Population effects

Although *Echinomermella matsi* can have a dramatic effect on the fecundity of individual hosts, the esti-
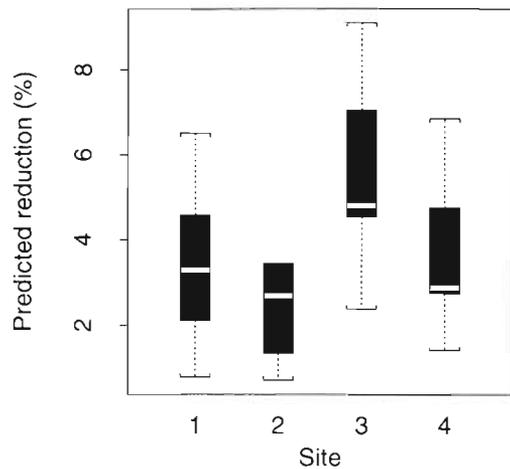
Fig. 4. Box plots of predicted reduction in mean gonad wet weight of *Strongylocentrotus droebachiensis* due to infection by *Echinomermella matsi* in samples from each of the sampling sites. In the plot the boxes cover the central quartiles divided by the line giving the median. The whiskers cover the extremes of the data
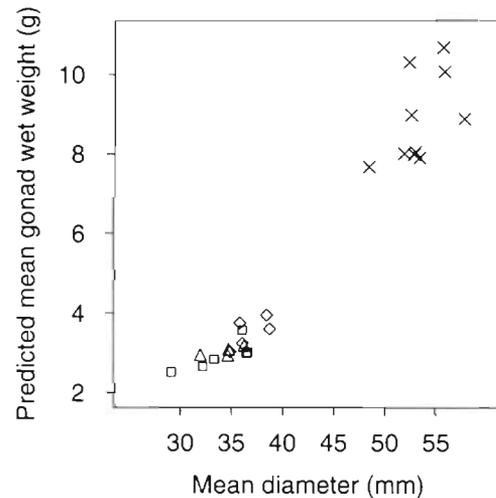

Fig. 5. Predicted mean gonad wet weight of *Strongylocentrotus droebachiensis*, assuming all sea urchins uninfected by *Echinomermella matsi*, plotted against the mean test diameter in the different samples. (□) Samples from Site 1, (△) samples from Site 2, (◇) samples from Site 3, (×) samples from Site 4

mated population effect on gonad mass was relatively small. This result differs from Hagen's (1992) estimate of a 47% reduction and Sivertsen's (1996) estimate of a 40% reduction. The higher estimates presented by Hagen and Sivertsen may be due to higher worm burden in their study areas, but the prevalences of infection they found were not much higher than the highest presented here (65 and 50% respectively compared to 52% this study; Table 1). The difference may also appear because their estimation procedure did not take into account that the effect of infection depends both on sea urchin size and worm burden, and that larger sea urchins carry a high proportion of the population gonad mass. If smaller sea urchins were more affected by infection than in larger ones, this would have biased their estimates upwards. The main reason for our low estimates is that few hosts carried heavy worm burdens. Hagen (1996) also found that most hosts harboured infrapopulations of low wet weights, while only a few carried heavy worm burdens in an area with a higher prevalence of infection. We believe that this is typical of the *E. matsi - Strongylocentrotus droebachiensis* relationship. High infrapopulation weight appears when one or a few female nematodes manage to develop to sexual maturity (Stien et al. 1996). The development rate of the nematodes is low—time to maturity is estimated to be in the same order of magnitude as the life expectancy of the host when an age-independent host mortality rate is assumed (Stien & Halvorsen unpubl.). This means that female nematodes in a considerable number of infrapopulations do not reach a large size before the host dies, leading to a low fraction of infected urchins with high worm mass (Anderson & May 1991).

Increased parasite mortality, due to natural parasite mortality, host immune responses and parasite-induced host mortality, can further reduce the fraction of infected hosts with high worm burdens. We believe that all these causes of parasite mortality may be of importance in the *E. matsi - S. droebachiensis* system, but at present we find the uncertainties associated with the growth of *E. matsi* to be too high to allow the infrapopulation wet weight development to be modelled. This hinders a quantitative analysis of the importance of these processes relative to parasite-independent host mortality in producing the low frequency of high worm burdens. The general implication of the pattern of low frequencies of hosts with high worm burdens, however, is that the parasite has a limited potential to reduce the gonad mass at the host population level through direct effects on host gonad development.

At the urchin population level, the effect of infection on fecundity was small compared to the large effect of mean host size. The generally low reproductive potential of individuals at the barren ground sites appears therefore to be mainly due to the small size of individuals at these sites, and not due to direct effects of *Echinomermella matsi* on host gonads. The positive relationship between kelp availability and mean sea urchin size as found earlier (Vadas 1977, Sivertsen & Hopkins 1995) is likely to be due to food limited sea urchin growth and survival rates on barren grounds. The very large effect of host size compared to the effect of parasite infection on mean gonad sizes suggests that processes that determine sea urchin size distributions are more likely than *E. matsi* to affect mean gonad weights significantly at regional scales.

Concluding remarks

As *Strongylocentrotus droebachiensis* has a long-lasting pelagial stage, a weak relationship between local fecundity and local recruitment is expected. Only factors that significantly reduce fecundity on a regional scale should significantly affect recruitment. In the populations investigated in our study, fecundity was not strongly affected by *Echinomermella matsi*. The effect on regional recruitment is therefore likely to be small. This indicates that if *E. matsi* has a significant effect on the population dynamics of *S. droebachiensis* in our study area, this is more likely to be caused by effects on host survival and growth than by direct effects on gonad development. Survival and growth appear to be the major determinants of the reproductive potential in host populations. Moreover, effects on host survival affect host population densities directly.

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