

# Parasitic castration of the green echinoid *Strongylocentrotus droebachiensis* by the nematode endoparasite *Echinomermella matsi*: reduced reproductive potential and reproductive death

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**ABSTRACT:** The echinoid *Strongylocentrotus droebachiensis* in the Vestfjorden area of northern Norway is infected by the epizootic nematode endoparasite *Echinomermella matsi*. The incidence of *E. matsi* was 68.8% in a sample taken from Godøystraumen, and 16.4% in a sample from Værøy Island. The high-incidence sample was collected in late February prior to the annual spawning season, when the echinoids have sexually mature gonads, and the low-incidence sample was collected in late August, when the echinoids have sexually immature gonads. Infected echinoids in both samples had smaller gonads than non-infected echinoids. The parasite-related reduction in gonad size for adult echinoids  $\geq 35$  mm in test diameter was approximately 75% in the high-incidence sample, and approximately 63% in the low-incidence sample. Most *S. droebachiensis* in the high-incidence sample were infected before they reached a size of 20 mm test diameter. The infected individuals had parasite loads ranging from approximately 0.01 to  $> 5$  g. However, lightly infected individuals with loads  $< 0.1$  g were most common, comprising 52% of the infected individuals in the high-incidence sample, and 72% of the infected individuals in the low-incidence sample. The abundance of heavily infected echinoids with parasite loads  $\geq 0.1$  g peaked in the [30, 35> mm size group, but dropped abruptly in the next interval of the size-frequency distribution. Although the peak abundance of heavily infected echinoids coincided with the onset of sexual maturity for non-infected echinoids, the majority of the infected echinoids in this size group were still classified as virtual castrates of unknown sex. These results suggest that a large proportion of infected echinoids never reproduce, but are effectively castrated as juveniles and succumb to parasite-related mortality before they reach a size of 35 to 40 mm.

**KEY WORDS:** Sea urchin · Disease outbreak dynamics

## INTRODUCTION

Parasitic castration is not common among the echinoderms (Jangoux 1980, 1987), despite its widespread occurrence in other invertebrate phyla (Kuris 1974, Baudoin 1975, Minchella 1985). Echinoids, in particular, are apparently affected by only 2 macroparasites which may cause castration. One is the gnathostomatid nematode *Echinocephalus pseudouncinatus*, and the other is the mermithid nematode *Echinomermella matsi*. The juveniles of *E. pseudouncinatus* encyst in

the gonadal tubules of the echinoid *Centrostephanus coronatus*, thereby suppressing host gametogenesis in parts of the gonads (Pearse & Timm 1971).

Adults of the other potential echinoid castrator, *Echinomermella matsi*, inhabit the perivisceral coelom of the green echinoid *Strongylocentrotus droebachiensis* (Jones & Hagen 1987). Individuals infected by *E. matsi* tend to have smaller gonads than non-infected echinoids (Hagen 1987, Stien 1993, Sivertsen & Hopkins 1994), and it has been suggested that the nutrient drain associated with the development of the gravid female parasite castrates, and ultimately kills, infected hosts (Hagen 1992).

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*Echinomermella matsi* is an unusually large and conspicuous endoparasite. The gravid females are frequently >60 µm long, the number of parasites per host is often >10, and total parasite load may exceed 10% of the host's wet weight (Hagen 1987, 1992). *E. matsi* is also abundant and may infect >65% of the individuals in an echinoid population (Hagen 1992).

The discovery of *Echinomermella matsi* coincided with a major outbreak of *Strongylocentrotus droebachiensis* in northern Norway in the early 1980s (Hagen 1983). At that time the echinoids decimated much of the benthic macroalgal vegetation, creating extensive echinoid-dominated barren grounds. The epizootic occurrence of *E. matsi* in these barren grounds inspired the hypothesis that macroparasitic epizootic disease may function as a mechanism for the termination of echinoid outbreaks, i.e. that parasite-related mortality may reduce echinoid density sufficiently to permit regrowth of macroalgae (Hagen 1987, 1992). Although localized regrowth of macroalgae has occurred as predicted by the macroparasite hypothesis, a recent surge of recurrent destructive grazing suggests that parasite-related echinoid mortality may have triggered sustainable cyclical fluctuations in echinoid and macroalgal abundance, rather than terminating the echinoid outbreak (Hagen 1995). Nevertheless, this scenario is still largely untested as many aspects of the host-parasite interaction are still unknown or incompletely understood.

This paper examines the effect of *Echinomermella matsi* infection on host reproduction and survival. The hypothesis that *E. matsi* is a castrator of *Strongylocentrotus droebachiensis* is tested by analysing 2 datasets from northern Norway. The gonad size and sexual status of lightly infected, heavily infected and non-infected *S. droebachiensis* are contrasted and related to echinoid size. The prospect of host mortality is also examined, and related to the reproductive success of the parasite.

## MATERIALS AND METHODS

Two datasets from the Vestfjorden area of northern Norway are examined in this study: one consists of 702 echinoids collected at Værøy, an exposed island at the tip of the Lofoten Archipelago, and the other consists of 452 echinoids collected at Godøystraumen, a narrow tidal channel near the mainland town Bodø (see maps in Hagen 1983). The datasets were pooled from subsamples in order to minimize spurious temporal or spatial variation. The dataset for Værøy Island consists of samples from 4 field sites sampled on August 25–27, 1992 (see maps in Hagen 1987), 3 of which were covered with dense kelp forest (sample size: n = 157,

172, 252 echinoids), and 1 of which was an echinoid-dominated barren ground (sample size: n = 121 echinoids). The dataset for Godøystraumen consists of 4 consecutive annual samples, collected on February 25, 1991, February 29, 1992, February 27, 1993, and February 24, 1994 (sample size: n = 125, 61, 149, 117 echinoids). The Godøystraumen field site remained a barren ground during the sampling period. The echinoids were collected, measured, classified and dissected as described in a previous paper (Hagen 1992). Only individuals  $\geq 15$  mm in test diameter are included in the datasets, as smaller echinoids had extremely small gonads,  $\leq 0.01$  g.

The effects of parasite infection (non-infected, infected), parasite load (lightly infected, heavily infected), and location (Værøy, Godøystraumen) were analysed in separate analyses of covariance (ANCOVA), using echinoid diameter as a covariate. Infected echinoids with parasite wet weight (pww) <0.1 g were classified as lightly infected, and echinoids with pww  $\geq 0.1$  g were classified as heavily infected. The dependent variables, gonad wet weight or the combined (parasite + gonad) wet weight, were cube-root transformed prior to analysis. The skewness and kurtosis of the size-frequency distributions were tested for departure from a normal distribution as described by Sokal & Rohlf (1981). In addition, a 2-way contingency table analysis (G-test; Sokal & Rohlf 1981) was used to test the null hypotheses that parasite prevalence, proportion of light infections, and sex ratio were independent of sampling location. Data were analysed using SuperANOVA (Gagnon et al. 1989), StatView (Sager et al. 1992), and Microsoft Excel™ software.

Histogram intervals are described using the notation  $[x_1, x_2>$ , meaning the interval where the lower limit  $x_1$  is included and the upper limit  $x_2$  is not included.

## RESULTS

### Characteristics of the parasite-host interaction

**Incidence of parasite infection.** The null hypothesis that the incidence of parasite infection was identical in the 2 samples is rejected ( $p < 0.0001$ ,  $G = 332.15$ ), and it is concluded that the observed incidence of 68.8% in the Godøystraumen sample is significantly higher than the observed prevalence of 16.4% in the Værøy sample (Table 1).

**Parasite load.** Parasite load in both samples ranged from ~0.01 g to >5 g wet weight (Fig. 1). Large echinoids,  $\geq 40$  mm in diameter, had the largest loads. However, heteroscedasticity, which could not be alleviated by standard data transformations, precludes the use of echinoid size as a predictor of parasite load. The

Table 1. *Strongylocentrotus droebachiensis* and *Echinomermella matsi*. Analysis of 2 echinoid size-frequency distributions from northern Norway, and their corresponding parasite load-frequency distributions. n: sample size;  $t_{s1}$  and  $t_{s2}$ :  $t$ -values for the skewness ( $g_1$ ) and kurtosis ( $g_2$ ) of the size-frequency distributions when tested for departure from a normal distribution; pww: parasite load (wet weight). Significant test results indicated by asterisks: <sup>ns</sup>not significant,  $p > 0.05$ ; \* $p < 0.1$ ; \*\* $p < 0.01$ ; \*\*\*  $p < 0.001$ . Data for echinoids with test diameter  $\geq 15$  mm

	n	Skewness		Kurtosis	
		$g_1$	$t_{s1}$	$g_2$	$t_{s2}$
Godøystraumen, total echinoids size-frequency	452	0.372	3.243**	-1.065	4.673***
Non-infected	141	-0.448	2.195*	-1.067	2.669**
Infected, subtotal	311	0.764	5.527***	-0.289	1.055 <sup>ns</sup>
Lightly infected, pww < 0.1 g	99	2.214	9.128***	5.699	12.099***
Heavily infected, pww $\geq 0.1$ g	212	0.555	3.322***	-0.543	1.648 <sup>ns</sup>
Værøy, total echinoids size-frequency	702	-0.280	3.035**	-1.247	6.787***
Non-infected	587	-0.474	4.700***	-1.015	5.058***
Infected, subtotal	115	0.692	3.069**	-0.740	1.683 <sup>ns</sup>
Lightly infected, pww < 0.1 g	60	1.073	3.476	-0.245	0.416 <sup>ns</sup>
Heavily infected, pww $\geq 0.1$ g	55	0.432	1.343 <sup>ns</sup>	-0.888	1.454 <sup>ns</sup>
Godøystraumen, parasite load-frequency	311	2.192	15.857***	4.639	16.941***
Værøy, parasite load-frequency	115	2.620	11.667***	6.135	14.010***

plotted data suggest that echinoid size determines the range of possible parasite loads, but is useless as a predictor of parasite load as the observed loads are scattered non-systematically throughout this range (Fig. 1).

**Parasite load-frequency distribution.** The parasite load-frequency distributions are significantly skewed to the right, with lightly infected individuals with parasite load <0.1 g being the dominant group in both

samples (Table 1). The abundance of infected echinoids decreases rapidly with increasing parasite load, and the resulting scarcity of heavily infected individuals indicates that these echinoids had high mortality rates at both sampling locations (Table 1, Fig. 2).

Approximately one-third of the infected echinoids in the Godøystraumen sample, and approximately one-half of the infected echinoids in the Værøy sample, were lightly infected. The discrepancy is sufficiently large to reject the null hypothesis that the abundance of lightly infected individuals is independent of sam-

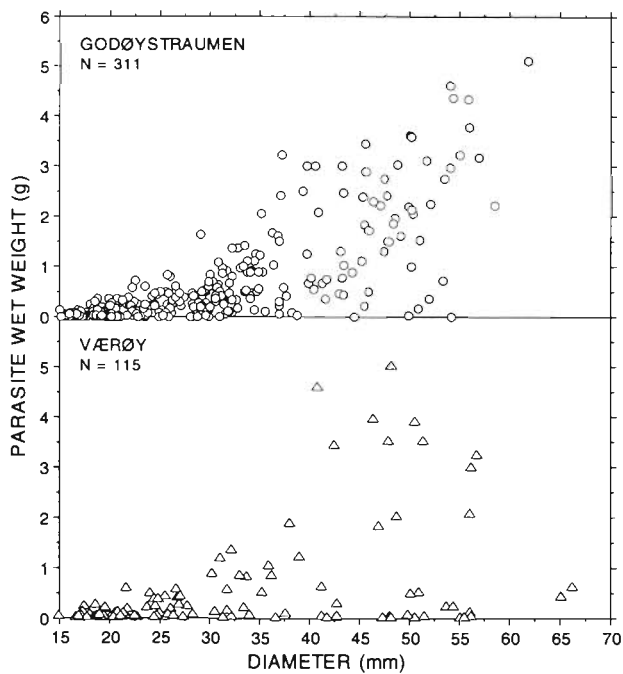


Fig. 1. *Strongylocentrotus droebachiensis* and *Echinomermella matsi*. Parasite load and test diameter of infected echinoids. Data for echinoids with test diameter  $\geq 15$  mm

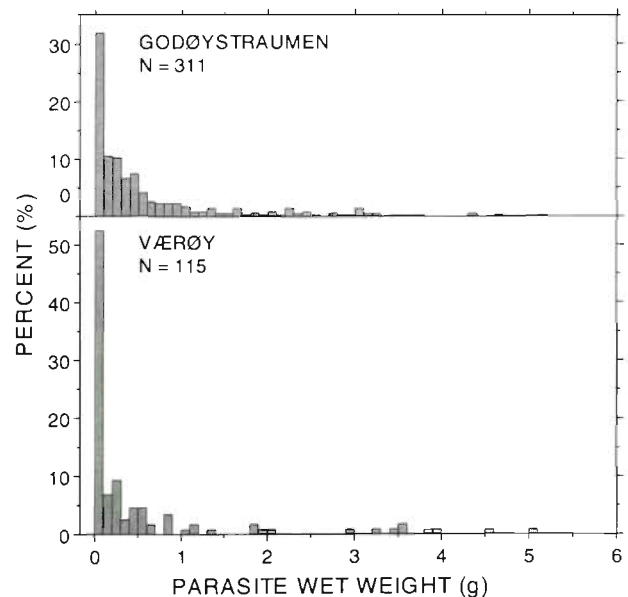


Fig. 2. *Strongylocentrotus droebachiensis* and *Echinomermella matsi*. Parasite load-frequency distribution for infected echinoids. Data for echinoids with test diameter  $\geq 15$  mm

pling location ( $p < 0.0001$ ,  $G = 15.22$ ). This result, as well as the difference in parasite prevalence, suggests that infection pressure or parasite-related mortality rate differs at the 2 locations.

**Echinoid size-frequency distribution.** The overall echinoid size-frequency distribution of both samples is significantly leptokurtic, but the 2 distributions are skewed in opposite directions (Table 1): the sample from Godøystraumen is significantly skewed to the right, whereas that from Værøy Island is significantly skewed to the left. The sample from Godøystraumen is dominated by small individuals, and has a smaller mode in the larger size classes, indicating high mortality and high recruitment (Fig. 3). The sample from Værøy Island is dominated by large individuals and has a secondary mode composed of small echinoids, indicating low mortality and regular recruitment. Non-infected echinoids from both samples follow the same pattern as the overall size-frequency distribution from Værøy Island, being significantly skewed to the left and having a secondary mode of smaller individuals (Fig. 3, Table 1).

The abundance of infected echinoids is highest in the smallest size class (Fig. 3). The abundance of lightly infected echinoids is also highest in the smallest size class, indicating that most initial infections occur before the echinoids reach a size of 20 mm in test diameter. The abundance of lightly infected echinoids decreases rapidly with increasing size, and this increase is initially offset by an increase in the abundance of heavily infected individuals. However, the abundance of heavily infected echinoids peaks in the [30, 35> mm size interval and then plummets to its initial level, before it continues to decline after a small secondary peak in the [45, 50> mm size interval (Fig. 3).

The proportional change in abundance from one interval of the size-frequency distribution to the next is similar for infected and non-infected echinoids in the upper and lower part of the size range, but differs for echinoids of intermediate size (Fig. 4). The difference is most pronounced in the Godøystraumen sample, where the transition into the [35, 40> mm size interval is marked by a >50% decrease in the abundance of infected echinoids, and a >80% increase in the abundance of non-infected echinoids. There is a similar discrepancy of a smaller magnitude in the next

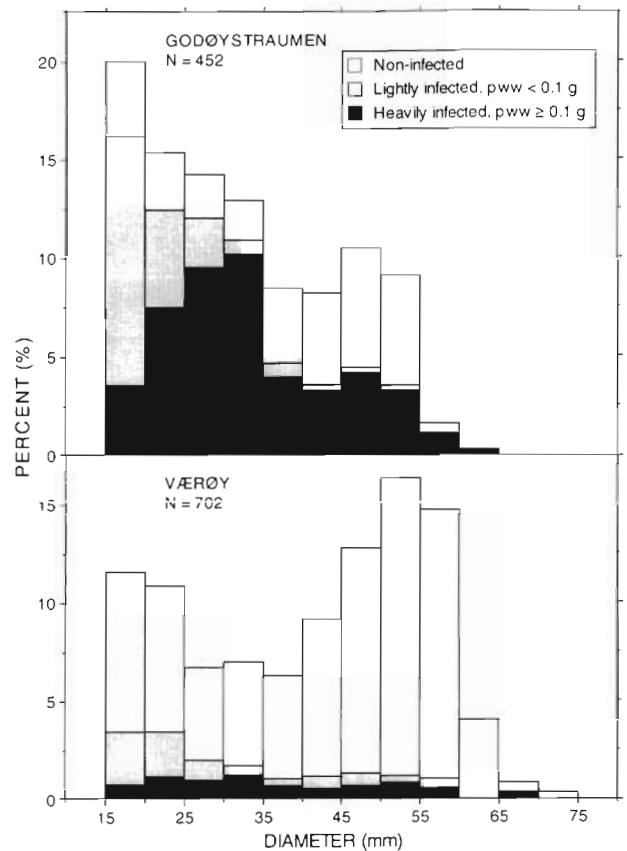


Fig. 3. *Strongylocentrotus droebachiensis* and *Echinomermella matsi*. Echinoid size-frequency distribution subdivided by degree of infection. pww: parasite wet weight. Data for echinoids with test diameter  $\geq 15$  mm

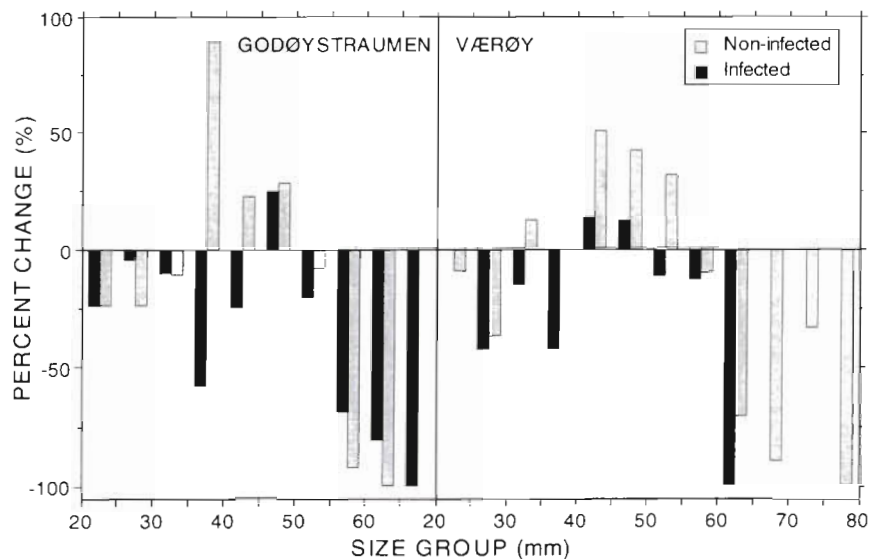


Fig. 4. *Strongylocentrotus droebachiensis* and *Echinomermella matsi*. Percent change in the abundance of infected and non-infected echinoids from one interval of the size-frequency distribution to the next. Data for echinoids with test diameter  $\geq 15$  mm

transition, and a corresponding discrepancy is also evident in the Værøy sample. The conspicuous decrease in the abundance of infected echinoids of intermediate size, and the equally conspicuous increase in the abundance of non-infected echinoids of a similar size, is consistent with a hypothesis of heavy parasite-related mortality.

### Gonad size

Gonad size increases with increasing echinoid size, but the degree of increase varies with location and parasite load (Table 2). As there is no significant difference between the regression coefficients for heavily and lightly infected echinoids in the Godøystraumen

sample, the data for infected echinoids have been pooled and fitted with a common regression line (Fig. 5a). Both the interaction term between parasite infection and covariate, and the single factor effects of infection and covariate, are highly significant, indicating that gonad size increases with increasing echinoid diameter, but that the rate of increase (the slope of the regression lines in Fig. 5a) differs for infected and non-infected echinoids. The regression line for non-infected echinoids has the greater rate of increase ( $\beta_{\text{non-infected}} = 0.060$ ,  $\beta_{\text{infected}} = 0.036$ ; Table 3), and rises above the regression line for infected echinoids when test diameter exceeds 16.1 mm (Fig. 5a).

In the Værøy sample, parasite load does interact significantly with echinoid diameter (Table 2), and the effects of light and heavy infection were therefore

Table 2. *Strongylocentrotus droebachiensis* and *Echinomermella matsi*. Single-factor analyses of covariance for the effect of parasite load and sampling location on the transformed gonad size (wet weight)<sup>1/3</sup> of echinoids from northern Norway. Covariate: echinoid test diameter (mm). pww: parasite wet weight (g). Significant test results indicated by asterisks: <sup>ns</sup>not significant,  $p > 0.05$ ; \* $p < 0.05$ , \*\*\* $p < 0.001$ . Data for echinoids with test diameter  $\geq 15$  mm

Source	df	MS	F-value
<b>Godøystraumen</b>			
Parasite load (pww < 0.1 g; pww $\geq$ 0.1 g)	1	0.037	0.797 <sup>ns</sup>
Diameter (Covariate)	1	28.474	619.320***
Parasite load $\times$ Diameter ( $H_0$ : regression lines parallel)	1	0.057	1.240 <sup>ns</sup>
Residual	307	0.046	
Infection (infected; non-infected)	1	1.448	26.782***
Diameter (Covariate)	1	125.564	2323.213***
Infection $\times$ Diameter ( $H_0$ : regression lines parallel)	1	7.730	143.024***
Residual	448		
<b>Værøy</b>			
Parasite load (pww < 0.1 g; pww $\geq$ 0.1 g)	1	0.059	1.986 <sup>ns</sup>
Diameter (Covariate)	1	24.813	837.496***
Parasite load $\times$ Diameter ( $H_0$ : regression lines parallel)	1	0.556	18.765***
Residual	111	0.030	
Light infection (pww < 0.1 g; non-infected)	1	0.022	0.554 <sup>ns</sup>
Diameter (Covariate)	1	61.382	1579.125***
Light infection $\times$ Diameter ( $H_0$ : regression lines parallel)	1	0.030	0.765 <sup>ns</sup>
Residual	643	0.039	
Heavy infection (pww $\geq$ 0.1 g; non-infected)	1	0.177	4.218*
Diameter (Covariate)	1	50.366	1203.188***
Heavy infection $\times$ Diameter ( $H_0$ : regression lines parallel)	1	1.475	35.240***
Residual	638	0.042	
<b>Infected</b>			
Location 1 (Værøy pww < 0.1 g; Godøystraumen infected)	1	0.025	0.569 <sup>ns</sup>
Diameter (Covariate)	1	44.086	993.967***
Location 1 $\times$ Diameter ( $H_0$ : regression lines parallel)	1	0.276	6.224*
Residual	367	0.044	
Location 2 (Værøy pww $\geq$ 0.1 g; Godøystraumen infected)	1	0.024	0.492 <sup>ns</sup>
Diameter (Covariate)	1	34.753	699.272***
Location 2 $\times$ Diameter ( $H_0$ : regression lines parallel)	1	0.177	3.565 <sup>ns</sup>
Residual	362	0.050	
<b>Non-infected</b>			
Location (Værøy; Godøystraumen)	1	0.813	17.880***
Diameter (Covariate)	1	193.803	4261.805***
Location $\times$ Diameter ( $H_0$ : regression lines parallel)	1	4.420	97.205***
Residual	724	0.045	

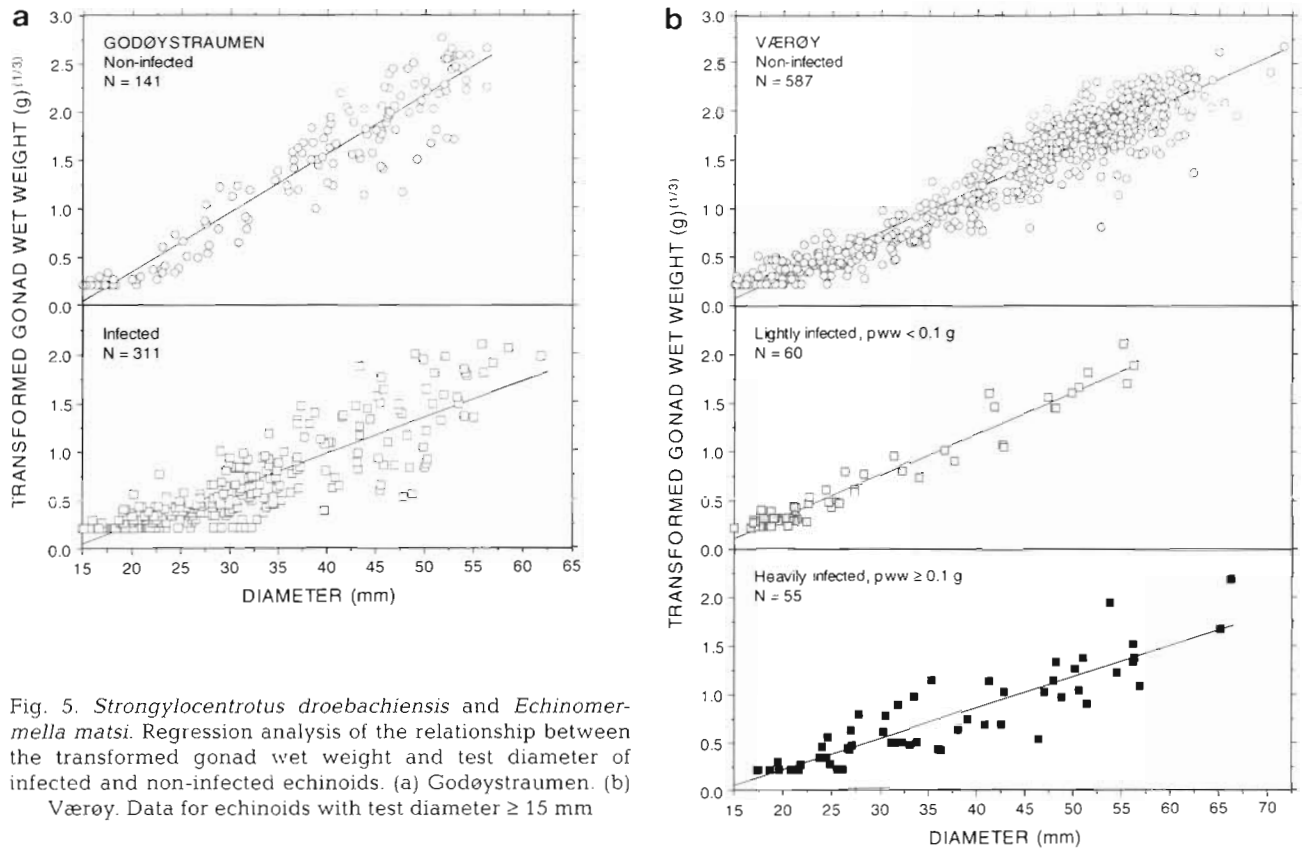


Fig. 5. *Strongylocentrotus droebachiensis* and *Echinomermella matsi*. Regression analysis of the relationship between the transformed gonad wet weight and test diameter of infected and non-infected echinoids. (a) Godøystraumen. (b) Værøy. Data for echinoids with test diameter  $\geq 15$  mm

analysed separately. There is no significant difference between the gonad size of non-infected and lightly infected echinoids in the Værøy sample. However, the interaction term for non-infected and heavily infected echinoids is significant, indicating that the regression lines for these subsamples have different slopes (Fig. 5b). The regression line for non-infected echinoids has the greater rate of increase ( $\beta_{\text{non-infected}} = 0.045$ ,  $\beta_{\text{heavily infected}} = 0.032$ ; Table 3), and lies above the regression line for infected echinoids throughout the range of the plotted data (Fig. 5b).

There is no significant difference between the regression lines for heavily infected echinoids from Værøy and infected echinoids from Godøystraumen

(Fig. 5a, b, Table 2). However, significant interaction terms indicate that the regression lines for non-infected echinoids from the 2 sampling locations have different slopes, and that the slope of the line for lightly infected echinoids from Værøy differs from the slope of the line for infected echinoids from Godøystraumen. The regression line for non-infected echinoids from Godøystraumen has the greater rate of increase (Table 3), and rises above the regression line for non-infected echinoids from Værøy when test diameter exceeds 18.5 mm (Fig. 5a, b).

Fig. 6 shows gonad size, as estimated by the back-transformed regression equations (Table 3), plotted as a function of echinoid size. It is evident from the plots

Table 3. *Strongylocentrotus droebachiensis* and *Echinomermella matsi*. Regression coefficients for the linear regression equation  $y = \alpha + \beta$  (Echinoid diameter). Data for echinoids with test diameter  $\geq 15$  mm

Location	Parasite status	y	$\alpha$	$\beta$	R <sup>2</sup>
Godøystraumen	Non-infected	(Gonad wet weight) <sup>1/3</sup>	-0.857	0.060	0.896
	Infected		-0.471	0.036	0.764
Værøy	Non-infected		-0.580	0.045	0.906
	Lightly infected		-0.529	0.043	0.952
	Heavily infected		-0.403	0.032	0.789
Godøystraumen		(Parasite + gonad wet weight) <sup>1/3</sup>	-0.347	0.041	0.897
Værøy			-0.270	0.037	0.898

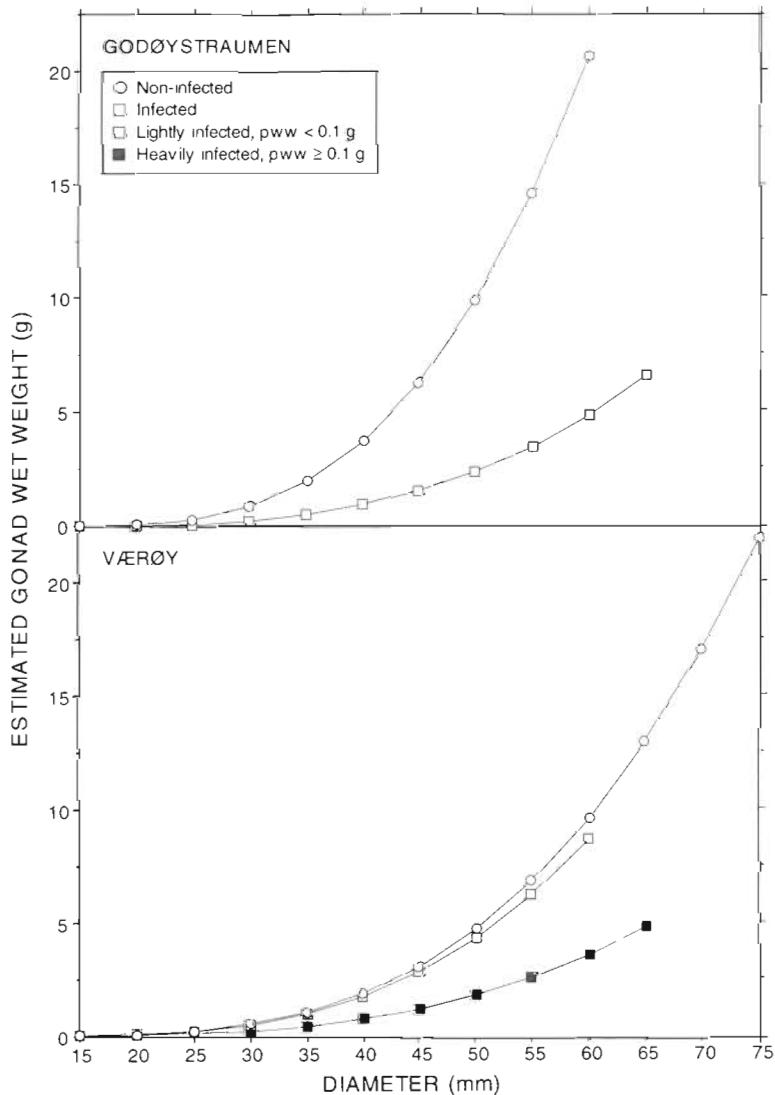


Fig. 6. *Strongylocentrotus droebachiensis* and *Echinomermella matsi*. Back-transformed regression estimates of gonad wet weight for infected and non-infected echinoids. Data for echinoids with test diameter  $\geq 15$  mm

that infected echinoids, with the exception of lightly infected echinoids from Værøy, have smaller gonads than non-infected echinoids. It is also evident that the magnitude of the difference increases rapidly as gonad size increases with increasing echinoid size. The difference is largest in the Godøystraumen sample where the non-infected echinoids have the largest gonads. Echinoids  $< 25$  mm in diameter have small gonads irrespective of infection status.

#### Parasite load and gonad size

There was no direct relationship between gonad size and parasite load (Fig. 7). However, the combined vari-

able (parasite + gonad wet weight) was successfully transformed, and analysed with echinoid diameter as a covariate (Table 4). The significant interaction term, between location and covariate, indicates that the 2 regression lines have significantly different slopes, Godøystraumen being the steeper ( $\beta_{\text{Godøystraumen}} = 0.041$ ,  $\beta_{\text{Værøy}} = 0.037$ ; Table 3, Fig. 8). Furthermore, in both samples the slope of the regression line for the infected echinoids' combined (parasite + gonad) variable is significantly steeper than the slope of the regression line for the gonad size of the non-infected echinoids (Tables 3 & 4). The estimated (parasite + gonad) wet weight of an infected individual, and the estimated gonad wet weight of a similarly sized non-infected individual, is similar at intermediate echinoid size (diameter<sub>Godøystraumen</sub>  $\approx 26.8$  mm, diameter<sub>Værøy</sub>  $\approx 38.8$ ), higher at smaller sizes, and lower at larger sizes (Table 3, Figs. 5a, b & 8).

Parasite load (wet weight) exceeded gonad wet weight in 72% of the infected echinoids from Godøystraumen, and 52% of the infected echinoids from Værøy (Fig. 7). The proportion of infected echinoids with parasite load  $\geq$  gonad wet weight was significantly higher in the Godøystraumen sample than in the Værøy sample ( $H_0$ : proportion independent of location;  $G = 15.17$ ,  $p < 0.0001$ ). This difference may, in light of the difference in parasite prevalence (see 'Incidence of parasite infection' above), be an indication of higher infection pressure in Godøystraumen.

#### Sex

The null hypothesis that sex ratio (female:male:unknown sex) is independent of parasite status (infected, non-infected) is rejected with  $p < 0.0001$  ( $G = 73.23$ ). The proportion of non-infected females is nearly 3 times higher, and the proportion of non-infected males nearly 2.5 times higher, than the corresponding proportions of infected individuals (Fig. 9). In isolation, this result suggests that approximately two-thirds of the infected females, and more than half of the infected males, have been castrated.

The most abundant group in the sample is infected echinoids of unknown sex, which comprise 50.7% of

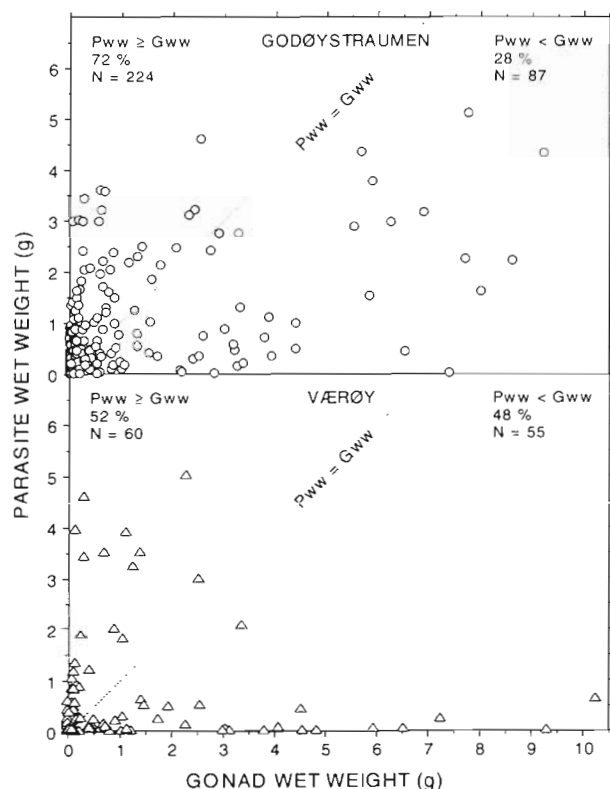


Fig. 7. *Strongylocentrotus droebachiensis* and *Echinomermella matsi*. Parasite and gonad wet weight of infected echinoids. Pww: parasite wet weight; Gww: gonad wet weight. Data for echinoids with test diameter  $\geq 15$  mm

the total sample, and 73.6% of the infected portion of the sample (Fig. 9). Echinoids of unknown sex are most numerous in the smaller size classes of the size-

frequency distribution (Fig. 10), suggesting that many infected echinoids are sexually immature juveniles.

The proportion of non-infected echinoids of unknown sex drops abruptly in the [30, 35> mm size interval, and reaches zero in the next interval (Fig. 10), indicating that most non-infected echinoids  $\geq 30$  mm have reached sexual maturity. In contrast, the proportion of infected echinoids of unknown sex remains high, approximately 70% in the [30, 35> mm size interval and approximately 40% in the [35, 40> mm size interval (Fig. 10), indicating that the sexual maturity of infected echinoids is inhibited or delayed. Furthermore, as noted above, the transition into the [35, 40> mm size interval is marked by a >50% decrease in the abundance of infected echinoids (Figs. 3 & 4). These results suggest that a large proportion of the infected echinoids are already reproductively dead when they succumb to parasite-related mortality.

#### Autopsy

Dead echinoids were abundant in Godøystraumen in August 1993. Most were reduced to empty skeletons, but some moribund or recently dead specimens were still covered with spines and had intact peristomial membranes. Autopsies revealed that all echinoids in a sample of 27 recently dead specimens were heavily infected with live nematodes. However, several of these echinoids contained neither nematode larvae nor mature egg-bearing female nematodes. This observation would suggest that parasite-related host mortality may occur prior to parasite reproduction.

Table 4. *Strongylocentrotus droebachiensis* and *Echinomermella matsi*. Single-factor analyses of covariance for the effect of sampling location on the transformed variable (parasite + gonad wet weight)<sup>1/3</sup>. Covariate: echinoid test diameter (mm). Significant test results indicated by asterisks: <sup>ns</sup>not significant,  $p > 0.05$ ; \*\*\* $p < 0.001$ . Data for echinoids with test diameter  $\geq 15$  mm

Source	df	MS	F-value
<b>Infected</b>			
Location (Værøy; Godøystraumen)	1	0.068	2.715 <sup>ns</sup>
Diameter (Covariate)	1	80.450	3200.492***
Location $\times$ Diameter ( $H_0$ : regression lines parallel)	1	0.291	11.595***
Residual	422	0.025	
<b>Godøystraumen</b>			
Infection (infected; non-infected)	1	2.530	69.867***
Diameter (Covariate)	1	138.872	3834.552***
Infection $\times$ Diameter ( $H_0$ : regression lines parallel)	1	4.836	133.546***
Residual	448	0.036	
<b>Værøy</b>			
Infection (infected; non-infected)	1	1.252	31.998***
Diameter (Covariate)	1	113.729	2906.754***
Infection $\times$ Diameter ( $H_0$ : regression lines parallel)	1	1.062	27.131***
Residual	698	0.039	



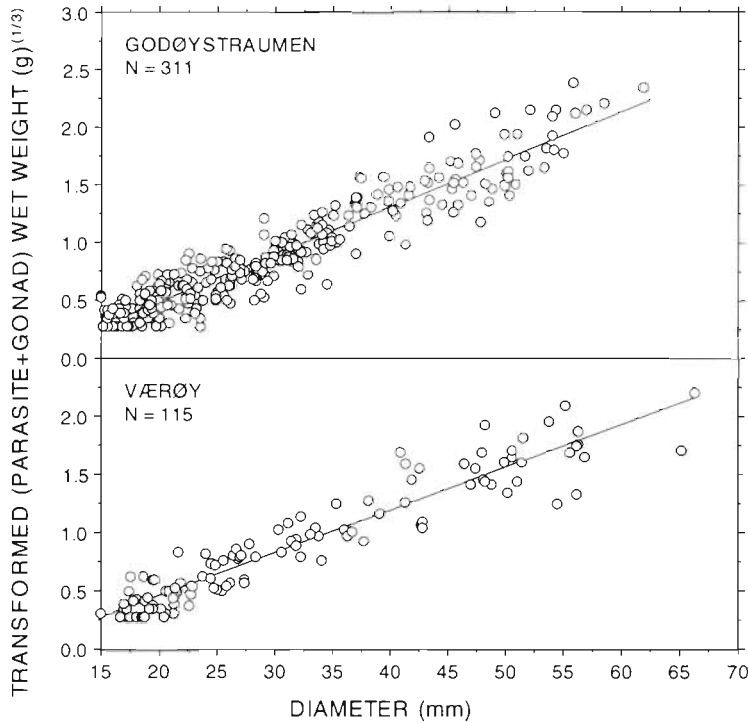


Fig. 8. *Strongylocentrotus droebachiensis* and *Echinomermella matsi*. Regression analysis of the relationship between the transformed variable (parasite + gonad wet weight)<sup>1/3</sup> for infected echinoids. Data for echinoids with test diameter ≥ 15 mm

DISCUSSION

Parasitic castration, per definition, involves a curtailment of the reproductive effort of the host, ranging from

permanent sterility to drastically reduced fecundity (Baudoin 1975). Both the qualitative and quantitative effects of *Echinomermella matsi* on the reproduction of *Strongylocentrotus droebachiensis* appear to be consistent with this definition. Most echinoids in the sample with highest parasite prevalence were infected before they reached a size of 20 mm in diameter. The abundance of heavily infected echinoids with parasite loads ≥ 0.1 g peaked in the [30, 35> mm size group, and dropped abruptly in the next interval of the size-frequency distribution. Furthermore, although the peak abundance of heavily infected echinoids coincided with the onset of sexual maturity for non-infected echinoids, most infected echinoids in this size group were still classified as virtual castrates of unknown sex. It would seem, therefore, that a large portion of the infected echinoids are castrated as juveniles and succumb to parasite-related mortality before they reach a size of 35 to 40 mm. Such echinoids never reproduce. They are reproductively dead prior to their actual death, and their fitness is, by definition, equal to zero.

It has been inferred on morphological grounds that parasite-related host mortality is caused by parasite reproduction, which involves the synchronous release of several hundred thousand nematode larvae into the coelom of the host (Jones & Hagen 1987). A minimum estimate for the time from infection to completion of the parasite life

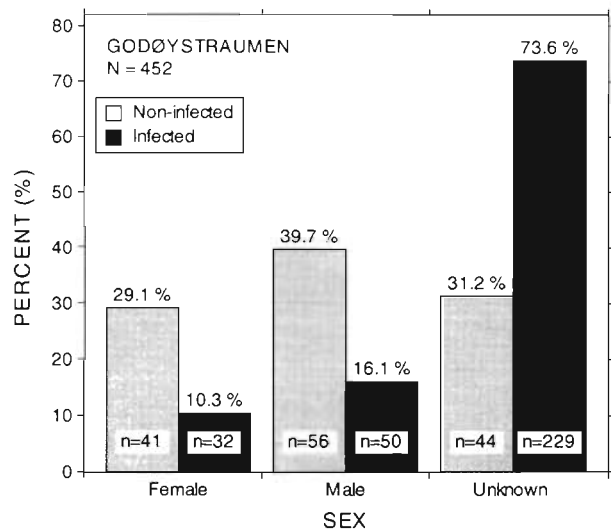


Fig. 9. *Strongylocentrotus droebachiensis* and *Echinomermella matsi*. Sex-frequency distribution for infected and non-infected echinoids. Data for echinoids with test diameter ≥ 15 mm

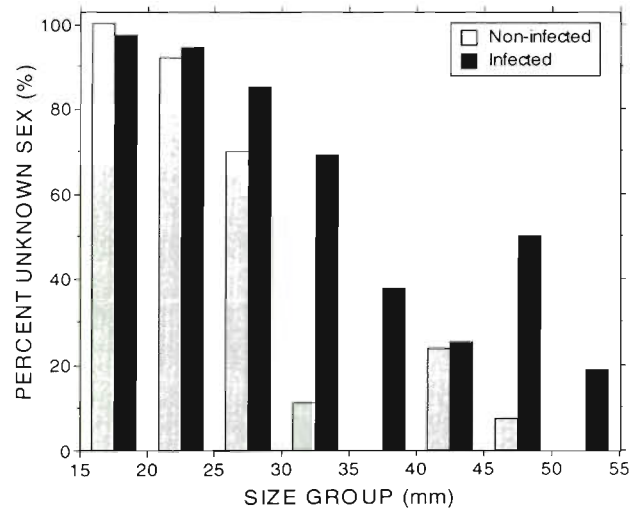


Fig. 10. *Strongylocentrotus droebachiensis* and *Echinomermella matsi*. Percent infected and non-infected echinoids of unknown sex in intervals of the size-frequency distribution. Data for echinoids with test diameter ≥ 15 mm

cycle can be obtained by noting that most echinoids were infected by the time they had reached a size of 20 mm in diameter, and that the heaviest mortality of infected echinoids occurred as echinoid size increased beyond 30 mm. Growth studies suggest that it takes at least 2 yr for *Strongylocentrotus droebachiensis* to reach [15, 20> mm size, and at least 3 yr to reach 30 mm size (Miller & Mann 1973, Ebert 1975, Raymond & Scheibling 1987, Hagen 1996). The completion of the echinoid-resident portion of the parasite's life cycle would therefore take at least 1 yr, if the growth rate of infected and non-infected echinoids is comparable.

It has been argued that completely castrated hosts, which are already reproductively dead, may increase the inclusive fitness of their relatives by dying prematurely before the parasite has completed its life cycle (Smith Trail 1980). Autopsies of moribund and recently dead echinoids from Godøystraumen suggest that some heavily infected echinoids do die prior to parasite reproduction, and this observation is consistent with a hypothesis of premature host mortality in response to parasitic castration.

The reproductive output of infected and non-infected echinoids was estimated by comparing the pre-spawning gonad sizes of the Godøystraumen sample, and the post-spawning gonad sizes of an independent sample from another barren ground location in Nordland County (Stien 1993). Fig 11 shows the resulting estimates of reproductive output and post-spawning nutrient reserve. As echinoids have little muscle tissue, their gonads serve the dual purpose of reproduction and nutrient storage (Andrew 1989), and a certain portion of the gonad is retained as a post-spawning nutrient reserve (Keats et al. 1984). The figure suggests that infected echinoids have a lower nutrient reserve as well as a greatly reduced reproductive output. The possibility of a parasite-related reduction in nutrient reserve is interesting, but remains tentative, due to a geographical bias of unknown magnitude.

The effect of parasite infection on host fecundity is quantified in Fig. 12, which shows the estimated reduction in gonad size and reproductive output for echinoids infected by *Echinomermella matsi*. The estimated reduction in reproductive output increases with increasing echinoid size, surpassing the estimated reduction in gonad size for echinoids >35 mm in test diameter. The estimated reduction for these adult individuals, which normally would carry most of the reproductive capacity of the echinoid population, is approximately 75 to 85%, but the estimate is tentative due to the possibility of geographical bias. The estimated reduction in gonad size also increases with echinoid size and is, for echinoids >35 mm, approximately 75% in the Godøystraumen sample and approximately

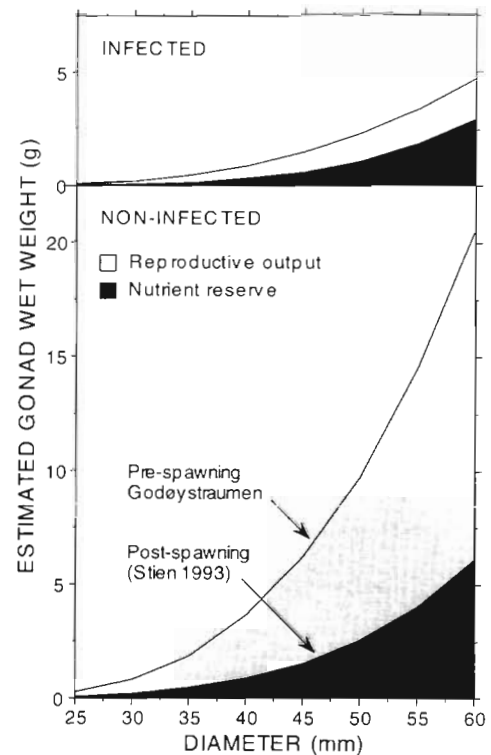


Fig. 11. *Strongylocentrotus droebachiensis* and *Echinomermella matsi*. Estimated reproductive output and post-spawning nutrient reserve of echinoids from barren grounds in Northern Norway. Pre-spawning gonad wet weight was estimated by pooling data from 4 consecutive annual samples of an echinoid population in Godøystraumen, near Bodø. Post-spawning gonad wet weight is based on an estimate by Stien (1993) from an echinoid population at Kontrollskjær, near Vega Island

63% in the Værøy sample. The estimated reduction is higher in the Godøystraumen sample because non-infected echinoids from Godøystraumen had larger gonads than non-infected echinoids from Værøy. Godøystraumen, a barren ground, was sampled in late February, just prior to the annual spawning season of *Strongylocentrotus droebachiensis* in northern Norway (Falk-Pettersen & Lønning 1983), and Værøy, a kelp-dominated area (Hagen 1995), was sampled in August, halfway between 2 spawning events. The observed difference in gonad size is not consistent with differences in food availability, but correlates well with the echinoid's annual reproductive cycle.

There are 2 previous estimates of parasite-related reduction in the gonad size of *Strongylocentrotus droebachiensis* infected by *Echinomermella matsi*. Hagen (1992) arrived at a tentative estimate of 48.7% reduction by comparing the average gonad indices of infected and non-infected female echinoids. This estimate is not adjusted for size dependency of the gonad index (Gonor 1972, Stien 1993), and appears

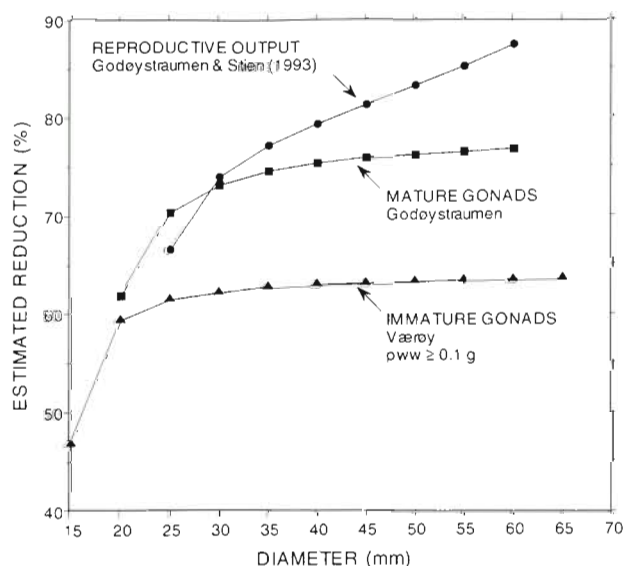


Fig. 12. *Strongylocentrotus droebachiensis* and *Echinomermella matsi*. Estimated reduction in gonad size and reproductive output of infected echinoids from Northern Norway. Immature gonad estimates from Værøy are based on comparison of back-transformed regression equations for non-infected and heavily infected echinoids. Reproductive output estimates are based on comparison of back-transformed regression equations for mature, pre-spawning gonad size of echinoids from Godøystraumen, and post-spawning gonad size of echinoids from Kontrollskjær (Stien 1993). pww: parasite wet weight

too low in light of the present results. The other estimate is by Stien (1993), who suggests that the parasite-related reduction in gonad size decreases with increasing echinoid size, and ranges from 80% for 25 mm echinoids to 50% for 55 mm echinoids. This estimate is based on data from a post-spawning sample, taken at a time when the gonad size of *S. droebachiensis* is at its annual minimum, and on an analysis which did not include an interaction term between echinoid size and parasite status (infected, non-infected). Results of the present study, however, suggest that the parasite-related reduction in gonad size is largest prior to the spawning season, when the gonad size is at its annual maximum, and that it increases with increasing echinoid size when the interaction term between echinoid size and parasite status is included in the analysis.

In conclusion, it would appear that infection by *Echinomermella matsi* reduces the maximum gonad size and reproductive output of adult echinoids by approximately 75%. It would also appear that infection by *E. matsi* inhibits the sexual maturation of juvenile echinoids, and that a large proportion of the infected juveniles die before reaching a size of 35 to 40 mm, without ever having reproduced.

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