Parasites of the shore crab *Carcinus maenas* (L.): implications for reproductive potential and invasion success

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SUMMARY

The European shore crab, *Carcinus maenas*, is one of the most successful marine invasive species. Its success has been in part attributed to the loss of parasites, rekindling an interest in host-parasite interactions and impacts on host fitness in this crab. In the present study, we investigated *C. maenas* populations from Europe, South Africa and Australia for parasites, and assessed their impact on the fitness of male crabs. For the shore crab, testes weight along with success in mating competition is traded off against other life-history traits. We therefore used this parameter as an indicator both for reproductive fitness and a possible resource trade-off in response to parasite infestation. In the native range, crabs infested with *Sacculina carcini* showed significantly lower testes weight than uninfected crabs. However, helminth parasites did not generally cause reduced testes weights. Crab populations from South Africa and Australia were either parasitized at very low prevalences, or were completely parasite free. However, no population level effect of this parasite release was reflected in testes weight. These findings do not support a severe fitness impact of helminth parasites on *C. maenas*, which questions the role of parasites on its population dynamics, both in the native area and for invasive success.

Key words: *Carcinus maenas*, green crab, invasive species, parasite release, reproductive potential.

INTRODUCTION

Parasites are ubiquitous components of all ecosystems, yet for a long time it was doubted that they have a significant impact on host fitness and population dynamics (Lack, 1954). However, the last three decades have revealed an abundance of theoretical, experimental and field evidence that parasites and pathogens can be important factors for host population dynamics (e.g. Irvine *et al*. 2006). Host fitness revolves around a number of life-history traits: growth, reproduction and survival. These are closely connected, since available resources are limited and should be allocated in a way that optimizes fitness (Agnew *et al*. 2000). Parasites can have a direct or indirect influence on these factors by consuming energy resources, or redirecting them towards defence mechanisms or regenerative activities (Dobson, 1988; Sheldon and Verhulst, 1996).

The European shore crab, *Carcinus maenas*, is one of the most commonly encountered large crustaceans along the coasts of north and west Europe. It is host to

a number of parasites (reviewed by Torchin *et al*. 2001) occurring in varying intensities and prevalences (e.g. Thieltges *et al*. 2008). For decades, the main interest of parasitologists was focused on the cirriped *Sacculina carcini*, which forms conspicuous external brood sacks and castrates the crab host (Høeg, 1995). Other parasites, mainly helminths with sea bird final hosts, are extremely common as well. Microphallid trematodes (*Maritrema subdolum*, *Microphallus claviformis*, *Microphallus similis*) and an acanthocephalan (*Profilicollis botulus*) utilize *C. maenas* as intermediate host. However, reports on their influence on host fitness are scarce and mainly limited to grey literature (Lauckner, 1986; Lauckner and Söhl, 1990).

Recently, interest has focussed on the role of parasite load in determining the success of this species as a marine and estuarine invader. An increase in crab size in invasive populations was linked with the loss or reduction of parasite richness and prevalence (Torchin *et al*. 2001; Grosholz and Ruiz, 2003), suggesting that parasites have a significant impact on host fitness in the native range (Torchin *et al*. 2001). Support for this hypothesis was found for parasitic castrators like *S. carcini*, which reduces spermatogenesis and inhibits moulting and therefore growth (Rubiliani, 1983; Høeg, 1995), resulting in

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Table 1. *Sampling dates, coordinates and methods for different locations*

(Sample sizes for parasitological investigations (N_{total}) and for examinations of testes (N_{testes}) are given, as well as carapace width (CW) ranges and mean CW of sampled crabs ($\pm$ S.D.)).

	Sampling date	Method	Coordinates	N_{total}	N_{testes}	Min CW	Max CW	Mean CW
NS1	10/2008	Dredge	55°01′17″N, 08°27′16″E	49	40	36	64	49·7 ± 7·7
NS2	08/2008	Traps	54°11′03″N, 07°54′11″E	116	68	17	76	41·4 ± 17·1
LF1	06/2006	Dredge	56°38′53″N, 08°41′19″E	129	39	27	73	50 ± 10·6
LF2	09/2007	Traps	56°47′16″N, 08°52′36″E	240	149	31	70	51·8 ± 8·0
LF3	09/2006	Traps	57°01′58″N, 09°38′56″E	115	64	30	64	45·3 ± 8·8
KG1	09/2005	Traps	55°39′26″N, 10°06′45″E	67	21	22	72	44·8 ± 17·1
KG2	06/2008	Traps	54°52′12″N, 09°38′29″E	109	95	34	73	57·6 ± 7·6
KG3	09/2006	Traps	55°09′05″N, 11°34′33″E	179	168	42	77	62·9 ± 5·7
ZA1	03/2007 & 2008	Traps	33°54′29″S, 18°25′08″E	215	86	35	88	61·8 ± 10·2
ZA2	03/2007 & 2008	Traps	34°03′14″S, 18°20′52″E	100	36	21	83	66·3 ± 9·7
AUS	04/2008	Traps	37°52′56″S, 144°50′41″E	107	31	31	73	50·2 ± 7·7

smaller crab mean size and biomass in populations with high prevalences of this parasite (Torchin *et al.* 2001). However, very little is known about the role of helminth parasites, which are much more common than *S. carcini* in many areas (Thieltges *et al.* 2008). It is the aim of this study to investigate a possible effect of helminth parasites on crab fitness. We examined native populations from Europe with varying parasite prevalences as well as invasive populations in South Africa and Australia in which, respectively, no and only non-European parasites were present. Data from the invasive populations provide a broader spectrum of parasite infestation than is available in native populations alone.

By focusing on resource allocation into reproductive effort, we were able to monitor 2 possible outcomes of reduced fitness caused by parasites. Firstly, a reduction in reproductive effort is possible by direct or indirect nutrient competition and resource allocation (Hurd, 2001). Secondly, parasite-induced mortality may lead to increased, or earlier, investment into reproduction to offset the shorter life-span (Agnew *et al.* 2000).

We used male testes weight as an indicator for resource allocation in reproductive effort. This is possible because male testes weight in *C. maenas* is linked to reproductive success: Styrishave *et al.* (2004) showed that the 2 colour morphs encountered in this crab actually represent 2 life-history strategies. Red crabs are stronger, more successful in mating competitions and also have comparatively larger gonads (see Styrishave *et al.* 2004). For this benefit over green colour morph crabs they trade off growth and have an increased susceptibility towards hypoxic and salinity stress (Reid and Aldrich, 1989; Reid *et al.* 1989). These and other studies (Schärer *et al.* 2004) indicate that gonad weight and allocation to reproductive effort are linked, providing us with an easily measured indicator for field samples. In order to determine the potential effect of parasites on predation rate, we examined the crabs for autotomy. The loss of limbs as a method of predator avoidance is a

common phenomenon in *C. maenas* and provides a measure of predation pressure (Smith and Hines, 1991).

MATERIALS AND METHODS

Sampling methods

European *C. maenas* were collected between 2005 and 2008 from 3 populations in the eastern and western range of the Limfjord (LF1-3) and 3 areas in the Kattegat in the western part of the Baltic Sea (KG1-3). In addition, crabs from Helgoland and Sylt in the North Sea were caught in 2008 (NS1-2). Populations from South Africa were sampled in Cape Town and Hout Bay in 2007 and 2008 (ZA1-2). In Australia, crabs were caught in Port Phillip Bay in 2008 (AUS) (see Table 1). The crabs were caught in traps (mesh size max. 10 mm, opening min. 40 mm) and, in 2 cases, by dredge (see Table 1). In the laboratory they were transferred to tanks with filtered sea water in an overflow system and provided with crushed mussels or fish *ad libitum* twice a week. Excess food was removed after 3 h. The animals were kept in the laboratory for no more than 3 weeks. In the case of the North Sea samples, as well as 1 Kattegat sample and the crabs from Australia, no such facilities were available and the crabs were kept in aerated sea water or artificial sea water with the same feeding schedule.

Dissection of crabs

Male crabs were killed prior to dissection by cooling in a freezer (-20 °C) for 15–30 min, depending on size of the individual. We took care not to freeze the tissue, which would have complicated the dissection. During the dissection we removed the testes and carefully examined the visceral cavity, as well as the gills and abdomen, for parasites. The hepatopancreas of the crabs was digested overnight in approx. 0·6 g pepsin (Carl Roth GmbH, Karlsruhe, Germany)
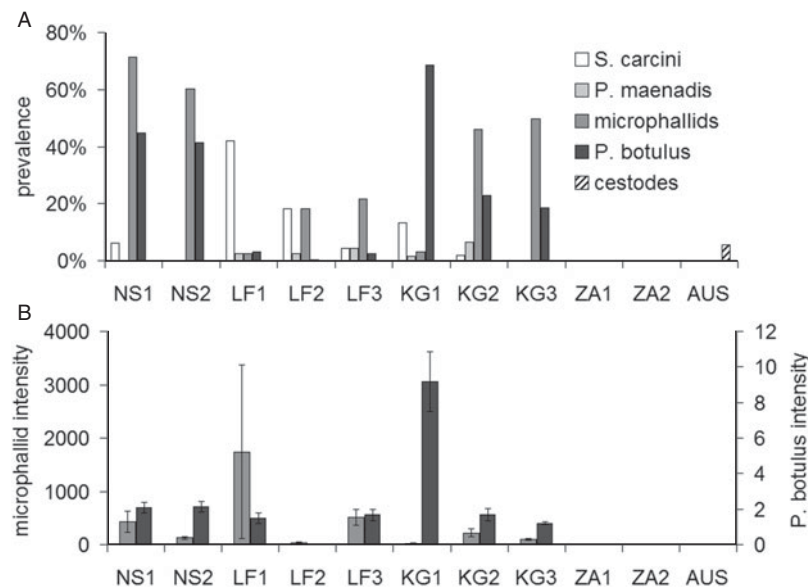
Fig. 1. (A) Prevalence of parasites in Europe, South Africa and Australia. (B) Mean intensity of microphallid and acanthocephalan parasites. All other parasites occurred in intensities of 1 only. Error bars indicate standard error. See Table 1 for sample sizes. Sampling location abbreviations: KG, Kattegat (Denmark); LF, Limfjord (Denmark); NS, North Sea (Germany); ZA, South Africa; AUS, Australia.

dissolved in 25 ml of filtered seawater and acidified with 6 drops of hydrochloric acid (32%, Carl Roth GmbH, Karlsruhe, Germany). The digested hepatopancreas tissue was filtered through a $200\,\mu$m sieve to retain metacercariae and cystacanths, and the residue examined for the presence and quantity of these parasitic stages. This allowed us to detect even small numbers of metacercariae, which are otherwise easy to miss. *S. carcini* infections are typically single infections. However, we distinguished between 3 intensity stages, ranging from few and translucent internal roots over a medium stage to a fully-grown dense internal root system.

The prepared testes were dried at $60\,°C$ to constant weight. To determine the size of the crab the carapace width (CW) was measured at its widest point. We also recorded the number of missing limbs lost due to autotomy. The incidence of autotomy is considered to be an indicator for predation pressure and can be indicative of higher susceptibility to predation in certain crab populations (Torchin *et al*. 2001). Colour morph was determined visually following the method of McKnight *et al*. (2000). Individuals displaying green, white or yellow colouration of the ventral carapace were categorized as 'green', crabs with a red or orange ventral surface were considered 'red'.

Statistical analysis

The two species of microphallid trematodes found, *Microphallus claviformis* and *Maritrema subdolum*, are difficult to distinguish at the metacercarial stage and were pooled.

Log-testes weight is a log-linear function of crab size. Expected testes weight can then be determined from the linear regression equation of log-testes weight on log-carapace width. We then calculated a reproduction index (RI) as the ratio of observed testes weight to expected testes weight. Styrishave *et al*. (2004) found that testes weight is higher in red coloured morph crabs, and our own preliminary tests showed that sampling site influences testes weight significantly (ANCOVA, F = 32·459, $P < 0·001$). Both factors were eliminated for statistical analysis of parasite effects by calculating RI separately for sample sites and colour morphs. Subgroups with insufficient sample size for this procedure were not included in the statistical analysis. Statistical and graphical analyses of data were conducted with SPSS 17 and MS Excel XP.

RESULTS

Parasite prevalence

In Europe, we found 5 endoparasites: 2 species of microphallid trematodes, *Microphallus claviformis* and *Maritrema subdolum*, cystacanths of the acanthocephalan *Profilicollis botulus*, and 2 species of parasitic castrators, the cirriped *Sacculina carcini* and the isopod *Portunion maenadis*. Parasite prevalence, as well as intensity, varied greatly between sites (Fig. 1). However, trophically transmitted microphallids were typically most prevalent in open sea areas, while showing a lower prevalence within the Limfjord. *P. botulus* showed a similar distribution, but was mostly absent in the Limfjord. Parasitic castrators were found with variable prevalences in several European populations (Fig. 1), although in almost all cases they were less abundant than helminths.

Table 2. Number of crabs with missing limbs (autotomy) in different populations of Europe

|	NS1		NS2		LF1		LF2		LF3		KG1		KG2		KG3	
Sacculina carcini																
	No	Yes	No	Yes	No	Yes	No	Yes	No	Yes	No	Yes	No	Yes	No	Yes
No autot.	31	2	77	0	50	33	26	23	77	4	21	5	70	2	113	0
Autotomy	15	1	81	0	25	21	20	7	33	1	37	4	37	0	66	0
Microphallids																
	No	Yes	No	Yes	No	Yes	No	Yes	No	Yes	No	Yes	No	Yes	No	Yes
No autot.	10	23	32	45	80	3	48	1	65	15	26	0	37	35	56	57
Autotomy	4	12	38	43	46	0	26	1	15	5	39	2	22	15	34	32
Profilicollis botulus																
	No	Yes	No	Yes	No	Yes	No	Yes	No	Yes	No	Yes	No	Yes	No	Yes
No autot.	19	19	44	33	81	2	49	0	80	1	7	19	30	0	131	0
Autotomy	8	8	39	42	44	2	27	0	32	2	14	27	5	0	49	0
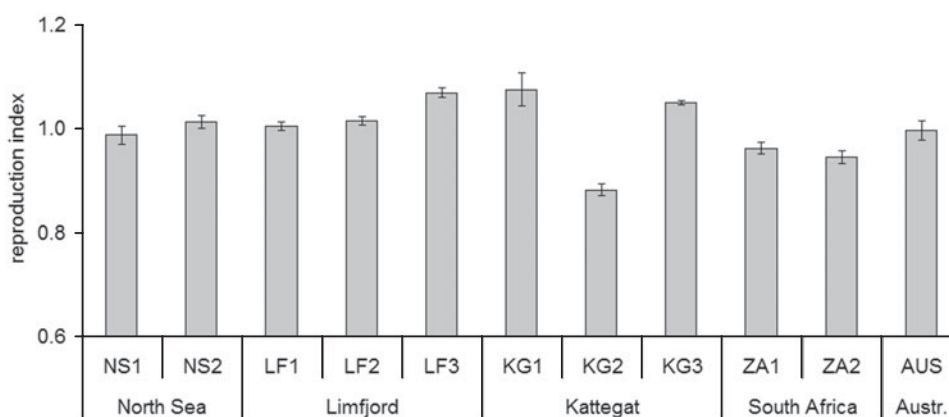
Fig. 2. Reproduction index in different populations of *Carcinus maenas*. Error bars indicate standard error. See Table 1 for sample sizes. Sampling location abbreviations: KG, Kattegat (Denmark); LF, Limfjord (Denmark); NS, North Sea (Germany); ZA, South Africa; AUS, Australia.

Both parasitic castrators occur as single infections only (Høeg, 1995). The intensities of microphallids could range as high as several thousand metacercariae in a single crab, whereas the larger cystacanths of *P. botulus* were only once found in intensities of over 50. High helminth intensities were not consistently connected with high prevalences (Fig. 1).

Invasive crab populations in South Africa, where we could sample 200 individuals, appeared to be completely parasite free. More than 100 crabs examined in Australia revealed low prevalences (under 5%) of 2 parasites that were previously described for the area (Gurney *et al*. 2004; Gurney, 2006): the trypanorhynch *Trimacracanthus aetobatidis* and a nematode of the genus *Proleptus*. Both were found in intensities of only 1 parasite per crab.

Autotomy

We found that autotomy is highly variable between populations, ranging from under 5% to 38% (see Table 2). In Europe there were significant differences between the 8 examined populations (Chi-square test: $\chi^2_7 = 12.391$, $P = 0.006$). There was no significant difference between the 2 South African populations, but a trend was present as well (Chi-square test: $\chi^2 = 5.546$, $P = 0.062$). Due to these differences, the role of parasites for autotomy was analysed for individual populations. Neither helminth parasites nor the castrator *S. carcini* had any significant influence on the frequency of autotomy in their host (see Table 2).

Analysis of testes dry weight

The reproduction index (RI) over all sampled crabs confirmed that both sampling site and parasite infection have a significant effect on testes weight (Kruskal-Wallis test: $\chi^2 = 229.157$, $P < 0.001$). A ranking of the different locations shows that the invasive sites are situated at the lower end of the testes weight spectrum, with only one North Sea and one Kattegat population on a similar or lower level (see Fig. 2).

When testing unparasitized crabs and crabs with varying parasite infections, we found a significant difference (Kruskal-Wallis-test: $\chi^2 = 74.341$, $P < 0.001$).
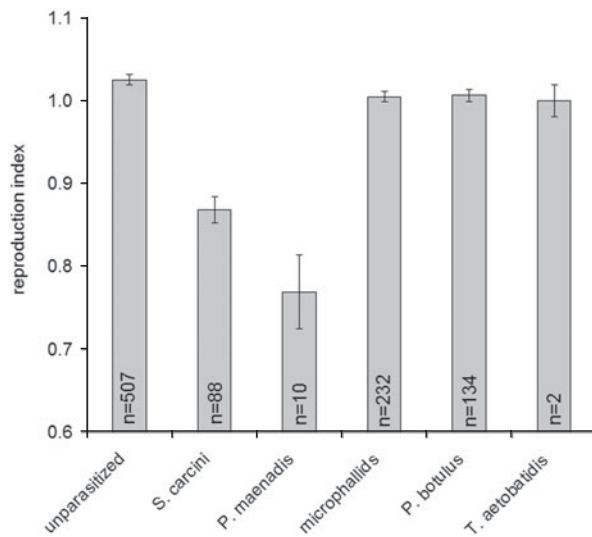
Fig. 3. Reproduction index in crabs infected by different parasites. Sample size is given in individual columns. Error bars indicate standard error.

Pair-wise comparisons showed that both *S. carcini* (Mann-Whitney test: $Z = -9.389$, $P < 0.001$) and *P. maenadis* (Mann-Whitney test: $Z = -4.854$, $P < 0.001$) infected crabs had considerably smaller testes than uninfected crabs (see Fig. 3). There was no difference between crabs with and without either helminth infection (Fig. 3).

When investigating the effect of different parasite intensities on testes dry weight we found no correlation between cystacanth intensity and RI. However, there was a significant positive correlation between microphallid intensity and RI (Fig. 4), although at an extremely low level (Pearson: $R = 0.097$, $P = 0.006$), explaining less than 1% of the variance ($R^2 = 0.009$). If the single extreme value is removed, the correlation is not significant. However, we examined metacercarial intensity more closely and found a highly significant correlation at intensities over a threshold of 1000 metacercariae per crab (Pearson: $R = 0.945$, $P < 0.001$). At such high intensities, number of metacercariae explained almost 90% of the variance in testes weight, but the sample size was considerably smaller than for other groups ($R^2 = 0.89$, $N = 9$). Although the castrator *S. carcini* only occurs as single infections, we distinguished between 3 different stages of internal infection from weak to strong. Crabs with stronger and older infections had significantly smaller testes (Pearson: $R = -0.371$, $P = 0.009$) (Fig. 4).

DISCUSSION

Our study shows that the distribution and abundance of parasites differed highly between the sampled populations of *C. maenas* in Europe. *P. botulus* was mainly found in the North and Baltic Sea where the final host, the eider duck *Somateria molissima*, is

common (Petersen *et al.* 2006). Microphallid trematodes were more patchily distributed. Their abundance appeared to be connected to occurrence of their final hosts (a number of seabirds) and also the first intermediate host, the mud snail *Hydrobia ulvae* (Mouritsen *et al.* 1997). *H. ulvae* is known to have a scattered distribution, depending partly on the floating migration of juveniles (Armonies and Hartke, 1995), as well as habitat characteristics and competition (Fenchel, 1975). Parasitic castrators, despite being attributed an important role in parasite release (Torchin *et al.* 2001), were not highly prevalent in the populations we investigated, and completely absent in 2 of them. The more common *S. carcini* is monecious with planktonic larvae, allowing for possibly high distribution rates, however, larval development may be limited by salinity and other environmental factors leading to a patchy distribution between host populations (Kashenko and Korn, 2002; Tolley *et al.* 2006).

In the South African and Australian populations investigated, none of the European parasites were present, but very low prevalences of 2 native parasites were found in Australia. The lack of parasites in these invasive areas can easily lead to the conclusion that parasite release may play an important role for invasion success. However, the highly variable prevalences and intensities of parasites even within Europe indicates that the origin of the invading crab populations has to be taken into account to confirm that they were indeed released from parasites in a relevant way.

The significant effect of sampling area on testes weight indicates that environmental factors do have an impact on the testes weight of *C. maenas*. However, our findings show that neither parasite prevalence nor intensity is one of these factors. There were no indicators for population level effects of parasite pressure on testes weight that might be caused indirectly by resource allocation towards defence mechanisms. On the individual level, parasite infection was indeed connected to altered testes weight. However, reduced weight was only caused in crabs infected with the parasitic castrators *S. carcini* and *P. maenadis*.

The effect of *S. carcini* on testes weight has not previously been studied. It is known that this parasitic castrator causes degeneration of the androgenic gland, as well as inhibition of spermatogenesis (Rubiliani-Durozoi *et al.* 1980; Rubiliani, 1983) and general feminization of male crabs (Høeg, 1995). It is often assumed that *S. carcini* infections lead to smaller or even completely reduced testes; however, this has never been quantified before. Our results show that testes weight is only reduced by an average of 12% in infested crabs, demonstrating that 'parasitic sterilization' is a more appropriate term than the more commonly used 'parasitic castration' (Høeg, 1995). *P. maenadis* showed a similar effect on
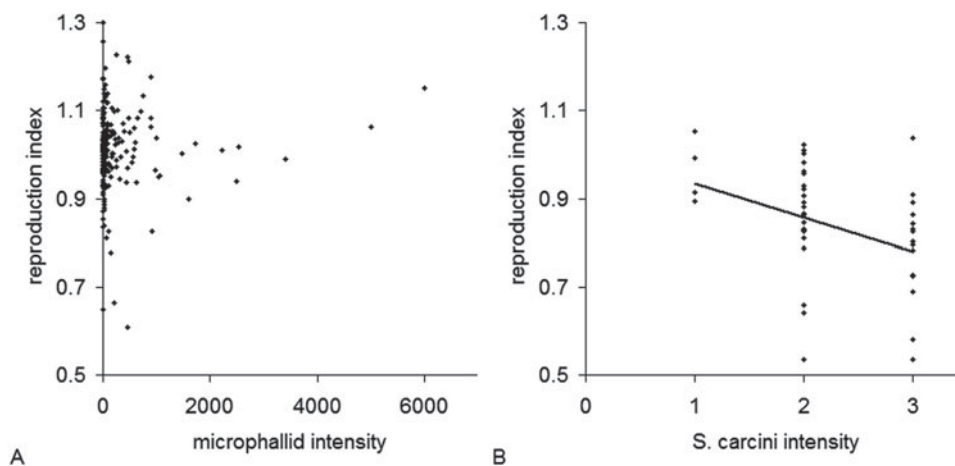
Fig. 4. (A) Influence of metacercarial intensity on the reproduction index. (B) Influence of the 'intensity' of a *Saccolina carcini* infection (stages 1 to 3) on reproduction index.

C. maenas to that of *S. carcini*. These findings show that parasite influence on host spermatogenesis, and therefore invested energy resources, is indeed reflected in male gonad weight.

Generally, microphallid and acanthocephalan larvae using the crab as an intermediate host did not significantly influence testes weight. However, microphallid infestation appears to lead to increased testes weight when it reached extreme intensities of over 1000 metacercariae per crab. Although the sample size for such highly infested crabs is low and additional samples should be made to check this result, this is a potentially interesting finding and suggests that the crabs might compensate for a potentially shorter life span by increased resource allocation towards reproduction. While this can indicate mortality, intensities of over 1000 metacercariae only occurred in less than 5% of all crabs infected with microphallids, making it unlikely that this potential effect has a serious impact on the population dynamics of *C. maenas*.

Parasite-induced fitness losses can also be caused by behavioural modifications of the host, making them more vulnerable or visible to predators (Thomas *et al*. 2005). So far, there is some evidence that this is also caused by helminth larvae in large decapod crabs (Haye and Ojeda, 1998; Latham and Poulin, 2002*b*). But our results on the frequency of autotomy in parasitized crabs suggest that behavioural modification is not an issue for *C. maenas*. If this occurred, we would predict that the proportion of crabs showing autotomy would increase with the level of infestation. This is not the case. We cannot conclude, however, that parasites are a trivial problem for the shore crab in its natural range or elsewhere.

It is possible that negative effects on fitness may not be reflected in such an easily accessible feature as testes weight. For example, they could be more apparent in female reproduction, as is the case in *Gammarus* (Plaistow *et al*. 2001). Female shore crabs

care for the eggs until the larvae hatch, so they have a higher reproductive energy expenditure than males. This may make them more vulnerable to parasites if there is a trade-off in energy partitioning between brood care and immune defence (Zuk and Stoehr, 2002). Unfortunately, in our study, the sample size of parasitized female crabs with the correct ovarial stage for dissection was too small for statistical analysis.

Lauckner (1986) considered how juvenile *C. maenas* in the Wadden Sea seem to have a higher mortality and grow more slowly when they are highly infected with microphallids and *P. botulus*. Yet, reliable data are sadly lacking and it is unclear if these effects extend to adult crabs and more common parasite loads. Other crab species do show an increased mortality of individuals infected with acanthocephalans (Latham and Poulin, 2002*a*).

Our findings are in contrast with the general experience that intermediate hosts of trophically transmitted parasites suffer negative effects on fitness (Ewald, 1995). A number of studies on crustaceans have confirmed this for various host traits. They are often found to increase the general metabolic rate or decrease growth, but relatively little is known about their consequences for reproductive fitness (Vivarès and Cuq, 1981; Haye and Ojeda, 1998). In *Gammarus pulex*, gravid females are known to suffer from reduced lipid reserves under the influence of the acanthocephalan *Pomphorhynchus laevis* (Plaistow *et al*. 2001). Also, an investigation on different lines of the snail *Biomphalaria glabrata* found an association between increased parasite resistance and decreased fertility (Webster and Woolhouse, 1999). In *C. maenas*, however, no such mechanism is evident.

Overall, the results of our study do not hint at a relevant effect of helminth parasites on the reproductive fitness of the European shore crab, either at the population level, or for individual crabs. However, our study mostly focused on a single aspect of fitness. It is entirely possible that helminths influence

C. maenas in other ways not covered by this study. In any case we found that parasite prevalence is highly diverse between different locations. Parasitic castrators – the lack of which is a suggested cause for invasion success of the host – are not at all omnipresent. We should therefore be careful when making generalizations about the effect of parasites in both native and invasive populations of the shore crab. Additionally, there are few empirical data on the density of *C. maenas* in its native and invasive habitats, and none relating parasite prevalence to crab density. A careful survey of green crab populations in relation to parasite pressure in their home range would help our understanding of their population dynamics and might also be crucial for the development of control measures in invaded areas.

REFERENCES

Agnew, P., Koella, J. C. and Michalakis, Y. (2000). Host life history responses to parasitism. *Microbes and Infection* **2**, 891–896. doi: 10.1016/S1286-4579(00) 00389-0.

Armonies, W. and Hartke, D. (1995). Floating of mud snails *Hydrobia ulvae* in tidal waters of the Wadden Sea, and its implications in distribution patterns. *Helgoländer Meeresuntersuchungen* **49**, 529–538. doi: 10.1007/ BF02368380.

Dobson, A. P. (1988). Restoring island ecosystems: the potential of parasites to control introduced mammals. *Conservation Biology* **2**, 31–39. doi: 10.1111/ j.1523-1739.1988.tb00333.x.

Ewald, P. W. (1995). The evolution of virulence: a unifying link between parasitology and ecology. *The Journal of Parasitology* **81**, 659–669.

Fenchel, T. (1975). Factors determining the distribution patterns of the mud snails (Hydrobiidae). *Oecologia* **20**, 1–17. doi: 10.1007/BF00364318.

Grosholz, E. D. & Ruiz, G. M. (2003). Biological invasions drive size increases in marine and estuarine invertebrates. *Ecology Letters* **6**, 700–705. doi: 10.1046/ j.1461-0248.2003.00495.x.

Gurney, R. H. (2006). Potential biological control agents for the European green crab, *Carcinus maenas*, in Australian waters. Ph.D. thesis, University of Tasmania.

Gurney, R. H., Nowak, B. F., Dykova, I. and Kuris, A. M. (2004). Histopathological effects of trypanorhynch metacestodes in the digestive gland of a novel host, *Carcinus maenas* (Decapoda). *Diseases of Aquatic Organisms* **58**, 63–69. doi: 10.3354/dao058063.

Haye, P. A. and Ojeda, F. P. (1998). Metabolic and behavioral alterations in the crab *Hemigrapsus crenulatus* (Milne-Edwards 1837) induced by its acanthocephalan parasite *Profilicollis antarcticus* (Zdzitowiecki 1985). *Journal of Experimental Marine Biology and Ecology* **228**, 73–82. doi: 10.1016/S0022-0981(98)00007-0.

Høeg, J. T. (1995). The biology and life cycle of the rhizocephala (cirripedia). *Journal of the Marine Biological Association of the United Kingdom* **75**, 517–550. doi: 10.1017/S0025315400038996.

Hurd, H. (2001). Host fecundity reduction: a strategy for damage limitation? *Trends in Parasitology* **17**, 363–368. doi: 10.1016/S1471-4922(01)01927-4.

Irvine, R. J., Corbishley, H., Pilkington, J. G. and Albon, S. D. (2006). Low-level parasitic worm burdens may reduce body condition in free-ranging red deer (*Cervus elaphus*). *Parasitology* **133**, 465–475. doi: 10.1017/S0031182006000606.

Kashenko, S. D. and Korn, O. M. (2002). Effects of temperature and salinity on the larvae of two species of rhizocephalan (Crustacea: Cirripedia). *Invertebrate Reproduction and Development* **41**, 179–184.

Lack, D. (1954). *The Natural Regulation of Animal Number.* Clarendon Press, Oxford, UK.

Latham, A. D. M. and Poulin, R. (2002*a*). Field evidence of the impact of two acanthocephalan parasites on the mortality of three species of New Zealand shore crabs (Brachyura). *Marine Biology* **141**, 1131–1139. doi: 10.1007/s00227-002-0913-7.

Latham, A. D. M. and Poulin, R. (2002*b*). Effect of acanthocephalan parasites on hiding behaviour in two species of shore crabs. *Journal of Helminthology* **76**, 323–326. doi: 10.1079/JOH2002139.

Lauckner, G. (1986). Einfluss von Trematodeninfestationen auf Überleben und Wachstum der Strandkrabbe *Carcinus maenas*. *Jahresbericht der Biologischen Anstalt Helgolands*, 11–12.

Lauckner, G. and Söhl, M. (1990). Populationsdynamik parasitengeschädigter Strandkrabben (*Carcinus maenas*) im Nordsylter Wattenmeer. *Jahresbericht der Biologischen Anstalt Helgolands*, 19–22.

McKnight, A., Mathews, L. M., Avery, R. and Lee, K. T. (2000). Distribution is correlated with color phase in green crabs, *Carcinus maenas* (Linnaeus, 1758) in Southern New England. *Crustaceana* **73**, 763–768. doi: 10.1163/156854000504787.

Mouritsen, K. T., Jensen, T. and Jensen, K. T. (1997). Parasites on an intertidal *Corophium*-bed: factors determining the phenology of microphallid trematodes in the intermediate host populations of the mud-snail *Hydrobia ulvae* and the amphipod *Corphium volutator*. *Hydrobiologia* **355**, 61–70. doi: 10.1023/ A:1003067104516.

Petersen, I. K., Pihl, S., Hounisen, J. P., Holm, T. E., Clausen, P., Therkildsen, O. and Christensen, T. K. (2006). Landsdækkende optaellinger af vandfugle, januar og februar 2004. Danmarks Miljøundersøgelser,

76 s. Faglig rapport fra DMU nr. 606. http://www2. dmu.dk/Pub/FR606.pdf.

Plaistow, S. J., Troussard, J. P. and Cézilly, F. (2001). The effect of the acanthocephalan parasite *Pomphorhynchus laevis* on the lipid and glycogen content of its intermediate host *Gammarus pulex*. *International Journal for Parasitology* **31**, 346–351. doi: 10.1016/ S0020-7519(01)00115-1.

Reid, D. G. and Aldrich, J. C. (1989). Variations in responses to environmental hypoxia of different colour forms of the shore crab *Carcinus maenas* (L.). *Comparative Biochemistry and Physiology* **92A**, 535–539. doi: 10.1016/0300-9629(89)90361-7.

Reid, D. G., Abelló, P., McGaw, I. J. and Naylor, E. (1989). Phenotypic variation in sympatric crab populations. In *Phenotypic Responses and Individuality in Aquatic Ectotherms* (ed. Aldrich, J. C.), pp. 89–96. JAPAGA, Dublin, Eire.

Rubiliani, C. (1983). Action of a rhizocephalan on the genital activity of host male crabs: characterization of a parasitic secretion inhibiting spermatogenesis. *International Journal of Invertebrate Reproduction* **6**, 137–147.

Rubiliani-Durozoi, M., Rubiliani, C. and Payen, G. G. (1980). Déroulement des gamétogenèses chez les crabes *Carcinus maenas* (L.) et *C. mediterraneus* Czerniavsky parasités par la Sacculine. *International Journal of Invertebrate Reproduction* **2**, 107–120.

Schärer, L., Ladurner, P. and Rieger, R. M. (2004). Bigger testes do work more: experimental evidence that testis size reflects testicular cell proliferation activity in the marine invertebrate, the free-living flatworm *Macrostomum* sp. *Behavioral Ecology and Sociobiology* **56**, 420–425. doi: 10.1007/ s00265-004-0802-9.

Sheldon, B. C. and Verhulst, S. (1996). Ecological immunology: costly parasite defences and trade-offs in evolutionary ecology. *Trends in Ecology and Evolution* **11**, 317–321. doi: 10.1016/0169-5347(96)10039-2.

Smith, L. D. and Hines, A. H. (1991). Autotomy in blue crab (*Callinectes sapidus* Rathbun) populations: geographic, temporal, and ontogenetic variation. *Biological Bulletin* **180**, 416–431.

Styrishave, B., Rewitz, K. and Andersen, O. (2004). Frequency of moulting by shore crabs *Carcinus maenas* (L.) changes their colour and their success in mating and physiological performance. *Journal of Experimental Marine Biology and Ecology* **313**, 317–336. doi: 10.1016/j.jembe.2004.08.013.

Thieltges, D. W., Hussel, B., Herrmann, J., Jensen, K. T., Krakau, M., Taraschewski, H. and Reise, K. (2008). Parasites in the northern Wadden Sea: a conservative ecosystem component over 4 decades. *Helgoland Marine Research* **62**, 37–47. doi: 10.1007/ s10152-007-0091-6.

Thomas, F., Adamo, S. and Moore, J. (2005). Parasitic manipulation: where are we and where should we go? *Behavioural Processes* **68**, 185–199. doi: 10.1016/ j.beproc.2004.06.010.

Tolley, S. G., Winstead, J. T., Haynes, L. and Volety, A. K. (2006). Influence of salinity on prevalence of the parasite *Loxothylacus panopaei* in the xanthid *Panopeus obesus* in SW Florida. *Diseases of Aquatic Organisms* **70**, 243–250. doi: 10.1016/0169-5347(96) 10039-2.

Torchin, M. E., Lafferty, K. D. and Kuris, A. M. (2001). Release from parasites as natural enemies: increased performance of a globally introduced marine crab. *Biological Invasions* **3**, 333–345. doi: 10.1023/ A:1015855019360.

Vivarès, C. P. and Cuq, J. L. (1981). Physiological and metabolic variations in *Carcinus mediterraneus* (Crustacea: Decapoda) parasitized by *Thelohania maenadis* (Microspora: Microsporida): an ecophysiopathological approach. *Journal of Invertebrate Pathology* **37**, 38–46.

Webster, J. P. and Woolhouse, M. E. J. (1999). Cost of resistance: relationship between reduced fertility and increased resistance in a snail-schistosome host-parasite system. *Proceedings of the Royal Society of London, B* **266**, 391–396. doi: 10.1098/rspb.1999.0650.

Zuk, M. and Stoehr, A. M. (2002). Immune defense and host life history. *The American Naturalist* **160**, 9–22. doi: 10.1086/342131.