



Release from parasites as natural enemies: increased performance of a globally introduced marine crab

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Abstract

Introduced species often seem to perform better than conspecifics in their native range. This is apparent in the high densities they may achieve or the larger individual sizes they attain. A prominent hypothesis explaining the success of introduced terrestrial species is that they are typically free of or are less affected by the natural enemies (competitors, predators, and parasites) they encounter in their introduced range compared to their native range. To test this hypothesis in a marine system, we conducted a global assessment of the effect of parasitism and predation on the ecological performance of European green crab populations. In Europe, where the green crab is native, crab body size and biomass were negatively associated with the prevalence of parasitic castrators. When we compared native crab populations with those from introduced regions, limb loss (an estimator of predation) was not significantly lower in introduced regions, parasites infected introduced populations substantially less and crabs in introduced regions were larger and exhibited a greater biomass. Our results are consistent with the general prediction that introduced species suffer less from parasites compared to populations where they are native. This may partly explain why the green crab is such a successful invader and, subsequently, why it is a pest in so many places.

Introduction

Biological invasions are an increasing threat to marine systems (Carlton and Geller 1993). Much has been done to document the source and impacts of marine exotics, but, surprisingly little attention has focused on why certain invaders do so well. Although most potentially invasive species never become established, those that do may achieve high population densities (Elton 1958; De Bach 1974; Carlton et al. 1990; Buttermore et al. 1994). In addition, introduced species often grow large, suggesting increased growth rates and/or survivorship in their new habitats (Blaustein et al. 1983; Crawley 1987; Blossey and Notzhold 1995). However, others have questioned the generality of this process (Thebaud and Simberloff 2001). Enhanced

performance of a species in a new area may be due to at least three ecological factors: (1) reduced competition (Settle and Wilson 1990; Byers 2000; Callaway and Aschehoug 2000); (2) better environmental conditions, such as increased food resources (Dobson 1988); and (3) an absence of natural enemies such as predators and parasites (Elton 1958; De Bach 1974; Dobson 1988).

Introduced species face three possible outcomes with respect to their parasites. (1) If infected individuals are the source of an introduction, they may bring with them all or a subset of their native parasite fauna (e.g. Delvinquier and Freeland 1988). They may even harbor more parasites than do sympatric native species if parasitized adults invade areas such as islands with few native parasites (Font and Tate 1994). (2) Some of the local parasite fauna may colonize invading hosts

which may or may not have brought parasites from their region of origin (Torchin et al. 1996; Barton 1997). If introduced species achieve high abundance, this could fuel epidemics of those parasites and pathogens able to infect them. (3) Finally, some species may invade without their parasites and remain free of parasites, although some native parasites may colonize over time (Blaustein et al. 1983; Cornell and Hawkins 1994). While all of these scenarios are possible, a lack of natural enemies may be a common benefit afforded by introduced species (Lodge 1993). Introduced plants tend to suffer less damage from insects (Elton 1958; Blaustein et al. 1983). Invading populations of terrestrial vertebrates often carry fewer, or limited subsets of parasites compared to those from native regions (Dobson 1988). For example, twice as many species of ectoparasites infect the house sparrow (several of which are vectors for blood pathogens) in its native range (Europe) than in North America (Dobson 1988). This may explain the low prevalence of blood pathogens of the sparrow in introduced regions (Dobson 1988). Introduced cane toads in Australia lack ectoparasites whose intensities are negatively associated with toad condition index in their native range (Lampo and Bayliss 1996). Further, Lampo and Bayliss (1996) suggest that these ticks may be an important mortality factor and may regulate toad densities in native habitats. Similarly, few parasite species infect mammal populations introduced to islands compared with populations in their native range (Dobson 1988).

There are comparatively few investigations of the natural enemies of exotic marine species and these focus on a taxonomic subset of potential parasites (Calvo-Ugarteburu and McQuaid 1998; Torchin et al. in preparation). In marine systems, introduced species usually arrive as larvae and, therefore, should be free of most parasites (Lafferty and Kuris 1996). If infected adults do invade, their parasites may not find suitable intermediate hosts or vectors. Also, the initial densities of a founding population may be too low to maintain parasite transmission. To investigate the hypothesis that marine introductions experience a release from natural enemies, one can survey introduced populations for parasites and predators and compare them with the types and abundance of such natural enemies where the pest is native (Lafferty and Kuris 1996; Calvo-Ugarteburu and McQuaid 1998).

The European green crab, *Carcinus maenas* (Linnaeus), provides a valuable case study for marine invasions because it is possible to examine the

consequences of invasion in several regions around the world (Lafferty and Kuris 1996; Thresher 1997; Grosholz et al. 2000). It also has usually been a pest where it has invaded with impressive economic and ecological impacts (Glude 1955; MacPhail et al. 1955; LeRoux et al. 1990; Lafferty and Kuris 1996; Thresher 1997; Grosholz et al. 2000).

In Europe, a number of parasites known to affect growth, mortality, and reproduction infect green crabs (see Table 1). Additionally, European birds, mammals, fish, octopus, and other crabs prey on green crabs (Crothers 1968; ap Rheinallt and Hughes 1985; Moreira 1995; Grisley et al. 1996). Although predation is difficult to observe, it is possible to infer the relative risk of predation on crabs because limb autotomy has evolved, at least in part, as an adaptation to predation. When crabs sever an attacked limb and escape, the regeneration process records the event for at least two subsequent molts (Smith and Hines 1991; personal observations).

We conducted a global comparison of the European green crab to determine if it experienced a release from natural enemies where it is introduced. Although most of our effort focused on examining parasites as natural enemies, we also compared symbiotic egg predators and limb loss (an estimator of predation) between native and introduced regions. We examined the native range of the green crab from Tromsø, Norway, to Gibraltar, as well as every region it has invaded. To understand what regulates green crabs in Europe, we examined how body size (a measure of growth and survivorship) and abundance varied with parasitism and limb loss. To determine if introduced green crabs experienced an increase in performance and suffered less from natural enemies compared to Europe, we compared body size, abundance, limb loss and parasites of the crab where it was exotic and where it was native.

Methods

We sampled exotic *C. maenas* in Tasmania, Australia (TASM); South Africa (SAFR); East Coast, USA (EUSA); and West Coast, USA (WUSA) and from six countries in Europe (EURO) representing its native range (Figure 1). Some supplemental data for Tasmania and Victoria (VICT), Australia were provided by Kuris and Gurney (1997; in preparation). The exact locations of the collection sites will be included in a subsequent

Table 1. Metazoan parasites of the green crab, *C. maenas*.

Parasite	Species	Locality	N or I	Prevalence	Reference
<i>Platyhelminthes</i>					
Trematoda	<i>Microphalus similis</i>	England, Wales	N	+	Crothers (1968)
	<i>M. similis</i>	East Canada	I	42–93%	Bratney et al. (1985)
	<i>M. similis</i>	Massachusetts, USA	I	+	Stunkard (1956)
	<i>Microphalus</i> spp.	France, Netherlands, Norway, Portugal, Spain, Sweden, East Coast, USA	N and I	0–100%	Present study
	<i>M. primas</i>	Portugal	N	+	Castilho and Barandela (1990)
Cestoda	<i>Dolfusiella martini</i>	Australia	N and I	0–89%	Kuris and Gurney (1997)
	<i>Trimacanthus aetobatidis</i> unidentified trypanorynch	Australia Spain			Kuris and Gurney (1997) Present study
Fecampiida	<i>Fecampia erythrocephala</i>	England	N	+	Caullery and Mesnil (1903); Southward (1950); Kuris Torchin and Lafferty, submitted
<i>Acanthocephala</i>	<i>Proflicollis botulus</i>	Scotland	N	35%	Thompson (1985)
	<i>Polymorphus</i> sp.	Netherlands, Norway, Sweden, East Coast, USA	N and I	0–50%	Present study
	<i>Polymorphus</i> sp.	East Canada	I	0–10%	Bratney et al. (1985)
<i>Cirripedia</i>					
Rhizocephala	<i>S. carcini</i>	France, England, Scotland, Wales	N	+	Crothers (1968)
	<i>S. carcini</i>	Denmark	N	0–10%	Rasmussen (1973)
	<i>S. carcini</i>	Ireland	N	0.3–64%	Minchin (1997)
	<i>S. carcini</i>	Scotland	N	6.4–47%	Mathieson et al. (1998)
	<i>S. carcini</i>	France	N	50%	Bourdon (1960)
	<i>S. carcini</i>	France	N	20+%	Bourdon (1963)
	<i>S. carcini</i>	France, Spain, Sweden	N	0–78%	Present study
<i>Isopoda</i>					
Entoniscidae	<i>P. maenadis</i>	England	N	+	Crothers (1968)
	<i>P. maenadis</i>	Denmark	N	0.7–5%	Rasmussen (1973)
	<i>P. maenadis</i>	France	N	+ 'very frequent'	Bourdon (1960)
	<i>P. maenadis</i>	France	N	1–2%	Bourdon (1963)
	<i>P. maenadis</i>	France	N	15%	Bourdon (1964)
	<i>P. maenadis</i>	France, Portugal, Sweden	N	0–5%	Present study
	<i>Nemertea</i>	<i>C. carcinophila</i>	Netherlands, Belgium, England	N	+
	<i>C. carcinophila</i>	Belgium, France, Scotland	N	+	Humes (1942)
	<i>C. carcinophila</i>	Scotland	N	100%	Comely and Ansell (1989)
	<i>Carcinonemertes</i> sp.	Netherlands, Norway, Sweden	N	0–95%	Present study
	<i>C. epialti</i>	California, USA	I	11–79%	Torchin et al. (1996)
<i>Copepoda</i>	<i>Chioniosphaera cancorum</i>	Maine, USA	I	+	Johnson (1957)
	<i>Lecithomyzon menaedis</i>	France	N	+	Gallien and Bloch (1936)

Note: N represents collections from native regions and I represents collections from introduced regions. + indicates presence when prevalence was not available.

paper (Torchin et al., in preparation) and are available from the authors upon request. Ideally, a comparison of the effects of introduction *per se* would consist of an analysis of a large number of introduced species. By focusing on a single species, we lose the ability to compare introduced and native crabs that are interspersed (due to unavoidable confounds of geography).

Because there is only one native range and Europe cannot be replicated, we limited our analysis to two approaches. The first was a comparison of native crabs at sites throughout their European range, controlling for latitude and habitat type. The second approach was to compare European sites with introduced sites, with the prediction that differences among sites would

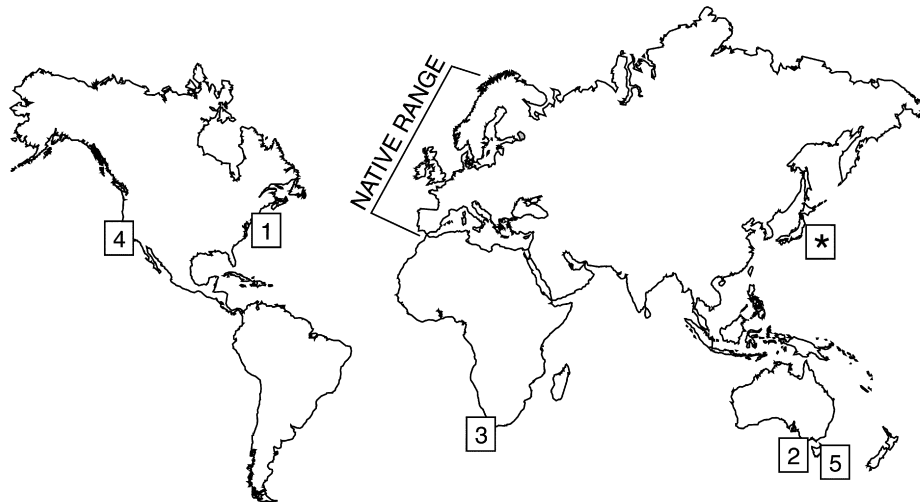


Figure 1. World map showing the native range of the green crab and regions where it has been introduced (numbers are in chronological order). 1 – East Coast, USA (early 1800s), 2 – Australia (early 1900s), 3 – South Africa (1983), 4 – West Coast, USA (1989), and 5 – Tasmania (1992). * Indicates invasion of the very similar Mediterranean species (*C. aestuarii*) to Japan (1984).

reflect differences between native and introduced crabs. We acknowledge the alternative hypothesis that such comparison could be influenced by intrinsic geographical differences between Europe and the introduced sites.

We collected the crabs on muddy substrates in estuaries or on rocky shores using baited minnow traps with enlarged openings that we usually set out overnight. At a few locations, logistics required us to collect crabs by hand at low tide. We measured crab size as carapace width (CW), defined as the distance between the notches anterior to the fifth (widest) lateral spines of the carapace to avoid variation in carapace spine length. We also recorded sex, female reproductive condition, abdomen width, and limb loss.

From each size-frequency distribution, we calculated two measures of performance: crab body size (populations with larger crabs have, on average, faster growth and/or greater survivorship) and abundance, as catch per unit effort (CPUE). Because there are several ways to describe the average body size of a population, for each population, we recorded the mean, median, mode, actual maximum, and projected maximum CW. For projected maximum CW, we constructed a cumulative frequency curve (0–100%) of CWs, arcsin transformed the curve to approach linearity and then used linear regression to estimate the theoretical widest carapace in the population (analogous to estimating L-infinity from life history data). This provided a

standardized measure of the projected maximum CW for each site within a region (because this estimate can be smaller than the maximum size encountered in the sample, the estimate is more appropriately termed a measure of the size of ‘large crabs’ in a population, not the maximum size *per se*). We limited our analyses of body size to include only trapped samples (the bulk of our data) at those sites where $N \geq 20$.

We used biomass as a measure of CPUE because we felt that it was the most appropriate indicator of invasion success and accordingly the impacts of the invader (Torchin et al. 2002). We calculated CPUE by measuring the biomass (kg) of crabs caught in our traps, adjusting for the number of traps set at each location. We calculated crab weight by determining the allometric relationship between CW and weight ($\log \text{weight} = 2.88 \log \text{CW} - 3.41$, $r^2 = 0.99$, $P < 0.0001$, $N = 24$). This relationship is representative because green crabs vary little in body shape metrics (Clark et al. 2001). This very highly correlated size-weight ratio is also common among other decapod crustaceans (see Kuris et al. 1987).

We examined all ovigerous females and the first 50 other green crabs collected at each site for symbionts and external evidence of parasitism. We then dissected a subsample ($N \geq 20$) of crabs from each site by removing the carapace and carefully examining the general body cavity, digestive tract, gonads, digestive gland, abdomen, and gill chambers for parasites. As an

indirect measure of predation pressure, we quantified the proportion of crabs missing and regenerating limbs (distinguishing between claws and walking legs) at each site, as well as the mean number of limbs missing per crab.

We separated trophically transmitted parasites and parasitic castrators in our analyses because they have different effects on host fitness (Kuris and Lafferty 2000). For our measure of the degree of parasitism of a population ($\text{prevalence}_{\text{all species}}$), we summed the prevalences (Bush et al. 1997) of all trophically transmitted parasite species at each location. We did the same for the parasitic castrator species. We did not include nemertean worm prevalences in our analysis for crab size as they are external symbiotic egg predators that cannot affect growth of their host.

We transformed all frequency data ($p' = \arcsin \sqrt{p}$) and used a stepwise linear model to examine the extent to which latitude, environmental quality (qualitatively described as degraded or not degraded habitat), mean limb loss, and parasitism at each location explained the variation in body size and CPUE within Europe. For these analyses, we used the mean body size and mean CPUE for each location. We used a non-parametric Kruskal–Wallis chi-square approximation to compare the number of parasite species found in Europe to the number found in introduced regions. We used 95% confidence intervals to identify differences in mean biomass, crab size, limb loss and parasitism between Europe and introduced regions.

Results

Latitude, environmental quality, mean limb loss, and trophically transmitted parasites ($\text{prevalence}_{\text{all species}}$) were not significantly associated with mean CW (stepwise linear model, $P > 0.05$ for all, $N = 11$) within Europe. Parasitic castrator prevalence ($\text{prevalence}_{\text{all species}}$) was significantly negatively associated with, and explained 64% of the variance in, mean CW (stepwise linear model, $P = 0.004$, $r^2 = 0.64$, $N = 11$, Figure 2a, Table 2). To determine if the association between size and parasitism was due to the stunting effect of parasitic castrators on host growth (Høeg and Lützen 1985; O'Brien and van Wyk 1985; Takahashi and Matsuura 1994; Høeg 1995), we separated parasitized and unparasitized individuals within populations and ran similar analyses using castrator prevalence as a covariate. We found no significant

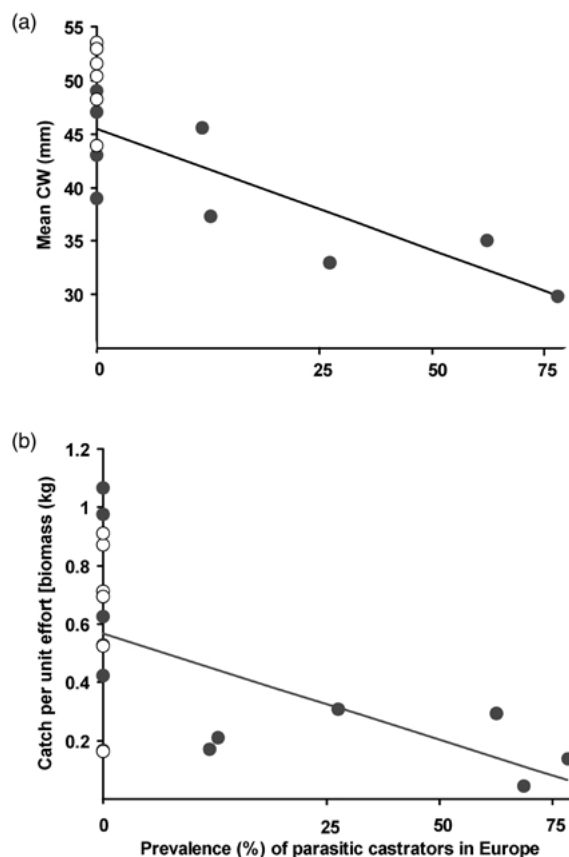


Figure 2. (a) Association between mean CW (mm) and parasitic castrator prevalence (arcsine transformed $\text{prevalence}_{\text{all species}}$) for sites in native region ($R^2 = 0.64$, $P = 0.0032$, mean CW = $45.5 - 14.4 * \arcsin \sqrt{\text{prevalence}}$). Regression is based on transformed prevalence data ($p' = \arcsin \sqrt{p}$). ● is Europe and ○ is introduced regions (not used in analysis) including East Coast of USA, South Africa, West Coast of USA and Tasmania. Mean size estimates are based on crabs collected from similar habitats (protected bays) and by the same technique (traps). Identical analyses using the median, mode and projected maximum CW (measured at each site) yielded the same significant negative association with parasitism. (b) Association between CPUE as biomass (kg/trap) and parasitic castrator prevalence (arcsine transformed $\text{prevalence}_{\text{all species}}$) for sites in native region ($R^2 = 0.36$, $P = 0.039$, CPUE = $565 - 462 * \arcsin \sqrt{\text{prevalence}}$). Regression is based on transformed prevalence data ($p' = \arcsin \sqrt{p}$). ● is Europe and ○ is introduced regions (not used in analysis) including East Coast of USA, South Africa, and West Coast of USA. CPUE estimates are based on crabs trapped in similar habitats (protected bays).

difference between infected and uninfected crabs with respect to mean size ($P = 0.93$, $N = 10$). However, the effect of castrator prevalence was still significant ($P = 0.01$, $r^2 = 0.61$, $N = 10$, Figure 5b). Because these were paired observations and not independent

Table 2. Stepwise linear model of the effect of parasites on mean CW and biomass for crabs from sites within Europe.

Model	Mean CW				Biomass			
	ss	df	F	P	ss	df	F	P
Castrator prevalence	58.90	1	24.22	0.0012	43 3420	1	5.65	0.0389
Trophic prevalence	391.16	1	3.65	0.0926	—	—	—	—
Error	129.20	8	—	—	76 7686	10	—	—

samples, we also analyzed the data using a paired *t*-test. The difference in size between infected and uninfected individuals (-0.2 mm) was not significantly different from zero ($t = -0.27$, $P = 0.6$, $N = 5$, one-tailed).

An analogous analysis of CPUE within Europe was consistent with the results for crab body size. Latitude, environmental quality, limb loss, prevalence of trophically transmitted parasites, and symbiotic egg predators were not significantly associated with CPUE (stepwise linear model, $P > 0.05$ for all, $N = 12$). The prevalence of parasitic castrators was significantly negatively associated with CPUE and explained 36% of the variation in CPUE (stepwise linear model, $P = 0.039$, $r^2 = 0.36$, $N = 12$, Figure 2b, Table 2).

Rates of parasitism were much lower where crabs were introduced compared to Europe where they were native. Introduced crabs were never infected by parasitic castrators, while in Europe, on an average, 16% of the crabs were so parasitized (primarily with the rhizocephalan barnacle, *Sacculina carcini*) (Figure 3a). Trophically transmitted parasites were also more prevalent in Europe (96%) compared to introduced regions (8%) (Figure 3b). Crabs in Europe were also parasitized by more species, despite the greater sampling effort in introduced regions (Kruskal–Wallis $\chi^2 = 14.9$, $df = 1$, $N = 25$, $P = 0.0001$, Table 3). The proportion of crabs missing limbs was not significantly lower in introduced regions (32%) compared to Europe (24%) (Figure 3c). On an average, green crabs were 1.3 times larger and CPUE was 1.6 times greater in regions where crabs were introduced compared to populations in Europe (Figure 4).

Discussion

Our results are consistent with the prediction that parasites suppress green crabs in many areas of Europe, and that the release from these natural enemies increases the crab's performance where it has invaded. An alternative explanation for the remarkably similar negative association between prevalence and crab size for both

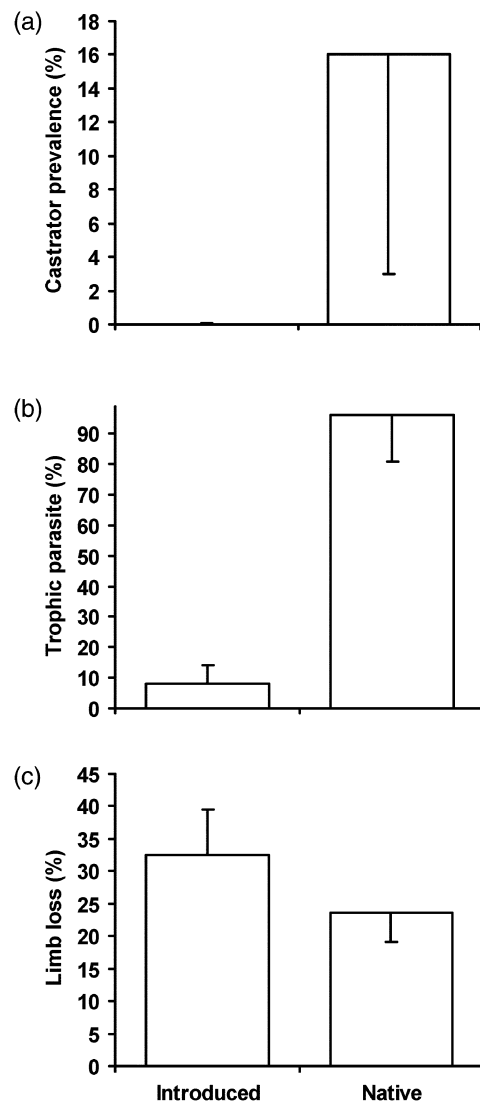


Figure 3. (a) Comparison of the prevalence (%) of parasitic castrators in introduced and native regions. Error bars represent the one-tailed 95% confidence intervals. (b) Comparison of the prevalence (%) of trophically transmitted parasites in introduced and native regions. Error bars represent the one-tailed 95% confidence intervals. (c) Comparison of the percent limb loss (both claws and walking legs) in introduced and native regions. Error bars represent the one-tailed 95% confidence intervals.

Table 3. Prevalence (%) or presence (+) of parasites infecting green crabs in native and introduced regions.

	Native region	Introduced region					
	EURO	EUSA	WUSA	JAPAN*	VICT	TASM	SAFR
N(N*)	372 (284)	242 (39)	102 (89)	31 (23)	103 (0)	120 (75)	39 (39)
N ^a N ^b	2221 ^a (550 ^a)	685 ^a	495 ^a , 259 ^b				
Trematodes	81 (80)	40 (3)	0	0	0	0	0
Cestodes	10 (14)	0	+	0	67	6 (3)	0
Nematodes	0 (0)	1	0	0	1	0	0
Acanthocephalans	8 (8)	2	0	0	0	0	0
Rhizocephalans	19 (20)	0	0	0	0	0	0
Entoniscid isopods	1 (0)	0	0	0	0	0	0
Nemerteans	13 (17)	0	15 (14)	0	0	0	0

* Indicates prevalences for the closely related Mediterranean green crab, *C. aestuarii* (not used in our comparative analyses).

Notes: Prevalences (%) are for parasites collected from all habitats and by all collection methods. Prevalences in parentheses are for similar habitats (protected bays) and by the same technique (traps). + indicates parasites present in samples collected by other means. Parasitic castrators and egg predators in boldface. *N* is sample size, *N** is sample size for crabs trapped in bays or estuaries. *N*^a is sample size examined for rhizocephalans, and *N*^b is sample size examined for nemerteans.

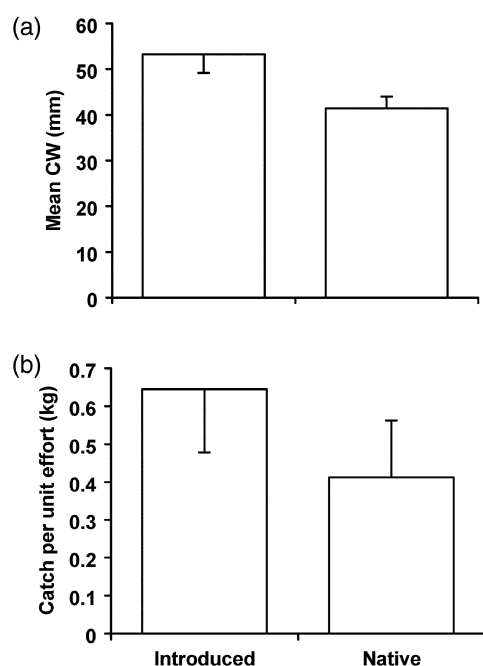


Figure 4. (a) Comparison of mean CW in introduced and native regions. Error bars represent the one-tailed 95% confidence intervals for the mean. (b) Comparison of CPUE as biomass (kilograms per trap) in introduced and native regions. Error bars represent the one-tailed 95% confidence intervals.

infected and uninfected crabs, is that both vary with another measure of environmental quality that we did not test for. However, careful consideration of the parasitological evidence permits that hypothesis to be rejected. (1) The literature on the development of

S. carcini in *C. maenas* thoroughly documents a marked reduction in the growth rate of infected crabs leading to cessation of further ecdysis upon emergence of the externa of the parasite (parasite maturation) (reviewed by Høeg 1995). Additionally, we molt staged all crabs in our study. Postmolt and premolt crabs were frequently included among the uninfected crabs and crabs with virgin externas (indicating recent emergence of the maturing parasite externa). In contrast, crabs with mature externas were always in intermolt (C4) molt stage. This confirms that crabs with externas cease molting. (2) If this was the only factor affecting crab size, then we should expect to see mean crab size decrease in a linear fashion with prevalence (solely due to a proportional change in infected versus uninfected crabs). However, the size of either the (small) parasitized crabs or the size of the (large) uninfected crabs would be unaffected (modeled in Figure 5a). But, as in Figure 5b, there is no significant difference between the size of infected and uninfected crabs. This indicates that the effect of parasitism was not solely an effect of stunting. Several hypotheses can explain this counter-intuitive observation. We will analyze most of these hypotheses elsewhere (Lafferty et al., in preparation) but here we can show that the environmental covariate hypothesis cannot explain the pattern of observations. Autocorrelation would occur if parasitism and crab growth react in opposite ways to environmental quality. If host stress in poor quality environments decreases growth and increases susceptibility, then in good environments, prevalence would be low and crabs would be large. However, the cessation of molting induced

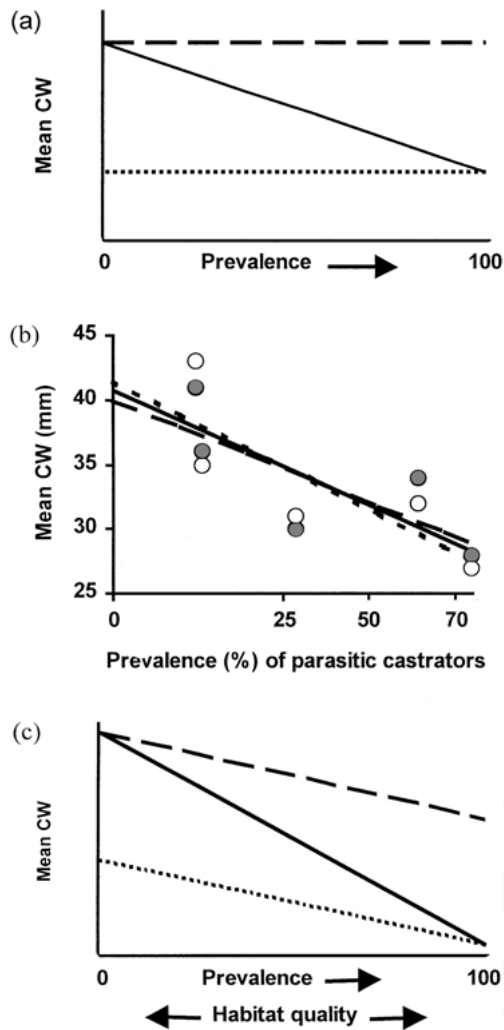


Figure 5. (a) Association between mean CW (mm) and parasitic castrator prevalence ($\text{prevalence}_{\text{all species}}$) for a hypothetical scenario, where the overall negative association between mean CW and prevalence (—) is solely due to the change in proportion of parasitized (\cdots) and non-parasitized crabs (---). (b) Association between mean CW (mm) and parasitic castrator prevalence (arcsine transformed $\text{prevalence}_{\text{all species}}$) for sites in native region (—). Each site is separated into the mean for non-parasitized (O, ---) and parasitized (\bullet , \cdots) individuals. (c) Association between mean CW (mm) and parasitic castrator prevalence ($\text{prevalence}_{\text{all species}}$) for a hypothetical scenario, where the overall negative association between mean CW and prevalence (—) is due to a combination of the change in proportion of parasitized (\cdots) and non-parasitized crabs (---) and negatively or positively affected by a third factor such as environmental stress.

by maturation of *S. carcini* would still cause infected crabs to be significantly smaller than infected crabs. In poor environments uninfected crabs would be smaller than uninfected crabs from good quality environments,

but sacculinized crabs would be smaller still in such environments as modeled in Figure 5c. The analogous pattern would hold true if parasites flourished in good environments but crabs grew larger in poor quality environments. There is no trace of such a pattern in our data, so we must reject the hypothesis that crab size and parasite prevalence co-vary with an environmental quality factor such as pollution. Another consideration also makes this hypothesis untenable. The environmental quality co-variate hypothesis requires that the samples from introduced populations were taken from either all good or all poor environments because introduced crabs are always rather large. Actually, our samples from both Europe and the introduced regions come from locations with a wide range of environmental quality. These include degraded locations (e.g. Bay of Cadiz, Spain; Table Bay, Cape Town Harbor, South Africa and San Francisco Bay, California) and locations with good environmental quality (e.g. Fiskebäckskil, Sweden; Bodega Bay, California and Barn Island Marsh, Stonington, Connecticut). We are currently exploring the three viable hypotheses which could explain this size-prevalence pattern (Lafferty et al., in preparation). These are that (1) there is a cost of resistance to *S. carcini* which is proportional to exposure, (2) that the *Sacculina-Carcinus* infection dynamics influence demographics of green crabs and (3) that the life histories of uninfected crabs are altered by *S. carcini* prevalence.

To standardize our analyses, we used data from crabs trapped in bays and estuaries, and for the analysis of body size we used mean CW. To evaluate the robustness of these analyses, we also conducted comparable statistical analyses using all of our data, which includes hand-collected crabs and crabs caught in different habitats. This did not change the direction nor the significance of the results. For body size, we also analyzed median, mode, actual maximum, and projected maximum CW. All were negatively associated with parasitic castrator prevalence. Actual maximum CW also had negative relationship with castrator prevalence but it was not significant.

In addition to the effect of castrator prevalence on size, there was also a negative association between CPUE and the prevalence of parasitic castrators. Further, CPUE was higher in introduced populations, suggesting that biomass was greater than in European populations.

Our limb loss data, which provided an indirect measure of the intensity of predation pressure, suggest that

green crabs were not released from predation pressure where they were introduced. This is not entirely unexpected given that the suite of crab predators in intertidal habitats in Europe (Crothers 1968; ap Rheinallt and Hughes 1985; Moreira 1995; Grisley et al. 1996) is similar to the suite of potential predators in at least some of the introduced locations (Edwards et al. 1982; Dumas and Whitman 1993). Additionally, there is substantial local variation in limb loss in both native and introduced regions (McVean and Findlay 1979; Abello et al. 1997; Mathews et al. 1999; present study), making it difficult to detect differences between native and introduced regions.

Introduced populations of green crabs were less parasitized compared to native European populations. Parasitic castrators did not infect green crabs in introduced regions and green crabs were larger in introduced regions indicating that they were either surviving longer and/or growing faster than were crabs in Europe. Green crabs in Europe were substantially more parasitized both by parasitic castrators and by trophically transmitted parasites compared to introduced regions. Although our data do not allow a direct comparison of growth rates, we do know that parasitism of crustaceans often slows growth (O'Brien and van Wyk 1985; Takahashi and Matsuura 1994). More importantly, all of the parasites we quantified have the potential to decrease crab fitness. Rhizocephalan barnacles cause growth to cease and completely block reproduction (O'Brien and van Wyk 1985; Høeg and Lützen 1985; Høeg 1995). Entoniscid isopods slow growth and block reproduction (O'Brien and van Wyk 1985). Our analysis of another data set (Minchin 1997) reveals a negative association between the prevalence of a parasitic castrator, the rhizocephalan barnacle, *S. carcini*, and the biomass of green crabs trapped in Ireland ($r = -0.39$, $N = 15$). However, this association was not significant ($P > 0.05$), likely due to a lack of statistical power. While a release from parasitic castrators can lead to an increase in host biomass, an introduction of a parasitic castrator may lead to reductions in host biomass. In the early 1960s, oysters were brought from the Gulf of Mexico to the Chesapeake Bay in Virginia, USA. These shipments contained live xanthid crabs (*Rithropanopeus harrisi*) infected with the sacculinid barnacle, *Loxothylacus panopaei* (Van Engel et al. 1966). In Virginia, the crab host was abundant and the parasite unknown. The barnacle successfully infected this host along with another abundant xanthid, *Eurypanopeus depressus*. Soon after, both species

became rare (Andrews 1980). A third, formerly rare xanthid, *Dyspanopeus sayi* (= *Neopanope texana sayi*), was not susceptible to the barnacle and became the dominant mud crab in the Chesapeake Bay (Andrews 1980).

Although our study examined the combined contribution of all the parasite species recovered, we only detected an effect of parasitic castrators. It seems reasonable, however, that the high prevalence of other parasites in Europe should also handicap green crabs to some extent. Nemertean worms eat crab eggs and can cause substantial brood mortality, including complete brood failure (Wickham 1979; Kuris et al. 1991). The larval worms we encountered (trematode metacercariae, acanthocephalan cystacanths, cestode plerocercoids and larval nematodes) are trophically transmitted. Such parasites often alter host behavior to increase susceptibility to predation (Lafferty 1999).

Those few parasites we did find in introduced green crabs could have expanded their host range from native crabs to include green crabs. This has already been shown for *Carcinonemertes epialti*, a nemertean egg predator of the shore crab, *Hemigrapsus oregonensis* (Torchin et al. 1996). We suspect this was also the case for the larval trematodes, a larval acanthocephalan, and a larval nematode we encountered in our combined hand-collected and trapped samples along the East Coast, USA (the oldest introduction). In Australia, trypanorhynch tapeworms and a nematode have successfully shifted from native shore crabs to introduced green crabs (Kuris and Gurney 1997; in preparation). However, other parasites in these groups have clearly not been able to expand their host range to include green crabs. A nemertean that is abundant on the congeneric (Portunidae) lady crab, *Ovalipes ocellatus*, in New England has never been found infesting the green crab (Coe 1902; present study). Two species of acanthocephalan that are abundant in a variety of crab hosts in Tasmania and Victoria have not been recovered from green crabs from either region (Pichelin et al. 1998).

Some parasite groups apparently cannot infect introduced green crabs at all. Rhizocephalan barnacles have never made such a host shift despite their sometimes abundant presence in ecologically similar and/or related (portunid) hosts along the east coast of North America and Victoria (Kuris and Gurney 1997; in preparation). In California, a congener of the entoniscid isopod, *Portunion maenadis*, which infects the green crab in Europe, is common in the native shore

crabs *H. oregonensis* and *H. nudus* (Kuris et al. 1980; Torchin, unpublished data), but has never been recovered from West Coast green crabs.

Similar, although less well documented, patterns of parasite prevalence occur among other introduced crab species, suggesting that a release from parasites appears to be a general phenomenon among introduced marine species. We sampled an introduced population of the European green crab's sibling species (*C. aestuarii*) in Japan and found no parasites (Kuris and Lafferty, unpublished data), while on the Mediterranean coast of France they are commonly parasitized by trematodes, rhizocephalan barnacles, and entoniscid isopods (Kuris, unpublished data). We found that rhizocephalans (6%) and trematode metacercariae (55%) infected the native *H. sanguineus* in Japan (Kuris and Lafferty, unpublished data). Further, rhizocephalan prevalences are reported to reach up to 64% in native *H. sanguineus* populations (Yamaguchi et al. 1994). However, along the East Coast of North America, where *H. sanguineus* is introduced, we only found 1 of 27 crabs with any parasites (a larval nematode which also infected introduced green crabs). In New Jersey, McDermott (1998) did not find any parasites in over 1000 *H. sanguineus* sampled. Interestingly, Lohrer et al. (2000) have found that where they are introduced, *H. sanguineus* are often larger and more abundant than where they are native. A comparison of the pie crust crab, *Cancer novaezelandiae* in Tasmania, where it is introduced, with a population from New Zealand, where it is native, found abundant trematode metacercariae at some sites in New Zealand, while no parasites were recovered from several locations in Tasmania (Kuris and Gurney 1997). Trematodes infected nearly all individuals of the native *H. penicillatus* in Japan (Kuris and Lafferty, unpublished data). These crabs have not been examined for parasites where they are introduced in Europe, but we predict that they will be relatively free of parasites.

An informative exception to the generalization that introduced crabs are released from natural enemies occurs in Victoria, Australia, where green crabs are commonly parasitized by two species of larval trypanorhynch tapeworms (Kuris and Gurney 1997; in preparation). Crabs from these Victoria populations are not considered pests, as they are neither large nor abundant (Thresher 1997). They are, however, still less often parasitized than are sympatric populations of the related (subfamily Carcininae) native portunid, *Nectocarcinus integrifrons*. Prevalences of

trophically transmitted parasites (tapeworms) and CW from our hand-collected sample from Victoria are similar to those from Europe. These relatively heavily parasitized crabs are also very small compared to all other introduced populations. The tapeworms in these crabs use elasmobranchs (sharks and rays) as final hosts and the analysis by Kuris and Gurney (1997 and in preparation) strongly suggests that infection by these parasites makes crabs more susceptible to predation. In this region, the ray, *Trigonorhina fasciata*, is abundant (Last and Stevens 1994) and commonly harbors adult trypanorhynchs (Beveridge 1990). The geographic range of this ray does not extend south of the Bass Strait, to the east coast of Tasmania, where the green crabs are large, abundant, and rarely parasitized by tapeworms. This suggests that the interaction between parasites and predators may control both size and abundance of green crabs in this region. We note that including this hand-collected sample in our analysis did not change our result that introduced populations are less parasitized and introduced crabs are larger in body size than are crabs from native populations. Consistent with this pattern, the smallest crabs we encountered in our entire sampling effort were from the one location in Europe (Vigo, Spain) where a related species of larval trypanorhynch tapeworm was common. CPUE from this location was also among the lowest we encountered. However, the prevalence of the parasitic castrator, *S. carcini*, was also extremely high at this location.

Release from parasites may give invaders an advantage over their competitors. Native crabs in regions where green crabs have invaded harbor several pathogenic parasites. For example, in California, the native shore crab, *H. oregonensis*, is host to a suite of pathogenic parasites including a parasitic castrator (Poinar and Kuris 1975; Kuris et al. 1980; Ching 1991; Torchin, unpublished data). In contrast, green crabs in California lack internal parasites and parasitic castrators. We postulate that the absence of parasites as natural enemies of the green crab is a substantial advantage in their interactions with the heavily parasitized native crabs.

In conclusion, the faster growth and/or greater longevity and the greater biomass of crabs from introduced populations is associated with and may be caused by reduced parasitism. Our results are consistent with the general prediction that introduced species suffer less from parasites compared to populations where they are native. This may partly explain why the green crab

is such a successful invader and, subsequently, why it is a pest in so many places.

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