New Zealand Journal of Marine and Freshwater Research, 2006, Vol. 40: 369–378
0028–8330/06/4002–0369

Comparison of the ectosymbionts and parasites of an introduced crab, *Charybdis japonica*, with sympatric and allopatric populations of a native New Zealand crab, *Ovalipes catharus* (Brachyura: Portunidae)

AROHA MILLER[1,2]
GRAEME J. INGLIS[1]
ROBERT POULIN[2]
[1]National Centre for Aquatic Biodiversity and Biosecurity
National Institute of Water and Atmospheric Research Limited
P.O. Box 8602
Christchurch, New Zealand
email: a.miller@niwa.co.nz

[2]Department of Zoology
University of Otago
P.O. Box 56
Dunedin, New Zealand

Abstract The success of biological invaders is often attributed to escape from specialist enemies in their natural range, such as predators and parasites. For enemy escape to have direct consequences in competitive interactions, invaders need to be less vulnerable to enemies than native competitors in the region they invade, but first the presence of these enemies must be established. We investigated the macroparasite and ectosymbiont fauna of the recently introduced portunid crab *Charybdis japonica*, and compared it with sympatric and allopatric populations of the native New Zealand portunid, *Ovalipes catharus*. A total of 468 crabs (350 *O. catharus* and 118 *C. japonica*) were collected from six harbours throughout New Zealand (Whangarei, Waitemata, Nelson, Lyttelton, Dunedin, and Bluff) and the identity, incidence and prevalence of ectosymbionts and parasites were compared among the different populations. *Charybdis japonica* and *O. catharus* harboured different ectosymbionts. Serpulid polychaete tubes occurred on the exoskeleton of 85.4% of *C. japonica* examined, but were absent from *O. catharus*. The bryozoan, *Triticella capsularis* occurred on 97.4% of *O. catharus* but was not found on *C. japonica*. Few endoparasites were present in either species. An unidentified juvenile ascaridoid nematode occurred in the hindgut of 5.9% of *C. japonica*, but was not found in sympatric populations of *O. catharus*. A second, unidentified species of ascaridoid nematode occurred in 7.1% of *O. catharus* from Nelson, but was not present in specimens from the five other harbours sampled. Melanised lesions were observed in the muscle tissue of almost half (46.6%) of the *C. japonica* examined. Histological examination showed these to be of two types: (1) spherical bodies resembling melanised trematode metacercariae; and (2) lesions consistent with wound repair. Lesions were not observed in *O. catharus*. Although the identity of parasites and epibionts carried by each species differed, both *C. japonica* and *O. catharus* had relatively low parasite species richness. We could not test whether the introduced portunid, *C. japonica*, is any less vulnerable to parasite enemies than the New Zealand portunid, *O. catharus*.

Keywords *Charybdis japonica*; *Ovalipes catharus*; parasites; ectosymbionts; introduced species; Portunidae

INTRODUCTION

The impacts of marine biological invasions are now recognised as a global threat to native ecosystems and human economies (Cohen & Carlton 1998). The success of invaders has often been attributed to escape from specialist enemies in their native regions (Shea & Chesson 2002). Several recent studies have related the larger individual size, greater reproductive output and higher population densities achieved by invasive species to lower parasite burdens experienced in the regions they invade (Torchin et al. 2001, 2003). Introduced species lose parasites through several mechanisms. Small founding populations may bring with them only a subset of the parasites present in the natural range

M05074; Online publication date 12 May 2006
Received 28 November 2005; accepted 20 April 2006

of the invader (Aliabadi & Juliano 2002). Specialist parasites with complex life cycles (e.g., trematodes) may not be able to establish in the new environment because suitable alternative hosts for particular life stages are not present (Barton 1997). In marine environments, planktonic larvae that are free of adult parasites may also establish founding populations (Lafferty & Kuris 1996; Torchin et al. 2002).

Although the enemy release hypothesis (ERH) has some support at biogeographical scales, evidence for it is weak or absent at the community level (Colautti et al. 2004). Comparative studies of the ERH often confound the richness of parasites in introduced populations with that present throughout the invader's entire natural range. This type of comparison overlooks variation in the richness and prevalence of parasites between host populations that could have been the source of the invader (Colautti et al. 2004). Similarly, comparisons of the parasite burdens between invasive species and native species in the introduced range need to account for variation in infection rates within populations of the native species. According to the ERH, introduced species are less vulnerable to enemies in the invaded region than comparable native species. Evidence for reduced vulnerability is equivocal, with some studies showing lower or equal incidence, prevalence or virulence of enemies within native species (Poulin & Mouillot 2003; Colautti et al. 2004). Before the ERH can be tested though, the identity, prevalence and intensity of the parasite fauna already present in the native species need to be established.

In this study we compared the macroparasites and ectosymbionts of a spatially restricted population of the introduced Asian paddle crab, *Charybdis japonica* (A. Milne-Edwards, 1861), with sympatric and allopatric populations of the native New Zealand portunid, *Ovalipes catharus* (White, 1843). *Charybdis japonica* is a relatively recent arrival in New Zealand. A native of coastal regions of China, Malaysia, Korea, Taiwan, and Japan, it was first reported in New Zealand in 2000, when fishers caught several specimens in Waitemata Harbour and Rangitoto Channel, near the city of Auckland (Webber 2001). Subsequent surveys revealed a substantial population within Waitemata Harbour, but its overall distribution appears to be restricted to estuaries of the inner Hauraki Gulf (Gust & Inglis 2006). The population is thought to have established following accidental introduction of one or more individuals by vessels entering the port of Auckland (Smith et al. 2003). Only limited information is available about the ecology and parasite fauna of *C. japonica* in its native range, although it is a known host for the sacculinid barnacle *Heterosaccus papillosus* (Kim 2001) and is a potential carrier of white-spot syndrome (Maeda et al. 1998).

The native swimming crab, *Ovalipes catharus*, is generally found in shallow, sandy coastal habitats throughout New Zealand in waters <10 m depth (McLay 1988). During winter (June–August) it migrates into harbours and estuaries to breed (Wear 1984). In Waitemata Harbour, the distribution of *O. catharus* overlaps with *C. japonica*, although *C. japonica* is more abundant in muddy estuarine habitats where *O. catharus* is uncommon (Gust & Inglis 2006). Both *C. japonica* and *O. catharus* are generalist scavengers and predators that feed mainly on bivalves, gastropods, and occasionally polychaetes and fish (Wear & Haddon 1987; Haddon & Wear 1993; Haddon 1994; Jiang et al. 1998). Both are large crabs with a maximum size >100 mm carapace width (McLay 1988; Gust & Inglis 2006). Although *O. catharus* is commercially fished in New Zealand and its general biology has been described (Osborne 1987; Wear & Haddon 1987; Armstrong 1988; Haddon & Wear 1993; Haddon 1994), there are no published accounts of its parasite fauna. Our aim in this paper was to determine the prevalence and intensity of infestation of parasites and ectosymbionts, and where possible their identity, within the introduced population of *C. japonica* and in the native species, *O. catharus*, and to compare these findings within sympatric populations of the two species, and across the biogeographic range of the native species.

MATERIALS AND METHODS

Specimens of *C. japonica* and *O. catharus* were collected from within Waitemata Harbour during three separate surveys in April, August, and October 2003. Collections of *O. catharus* were also made from five other locations distributed throughout New Zealand: Bluff Harbour (August 2003), Dunedin/Otago Harbour (August 2003), Lyttelton Harbour (July 2003), Nelson (July/August 2003), and Whangarei Harbour (October 2003) (Fig. 1). In each location crabs were caught using small collapsible box traps (62 cm long × 42 cm wide × 20 cm high) baited with pilchards. Up to 50 trap lines, each containing three baited traps, were deployed throughout each harbour at water depths ranging from 1.5 m to 15 m. Traps were generally left overnight before being retrieved.

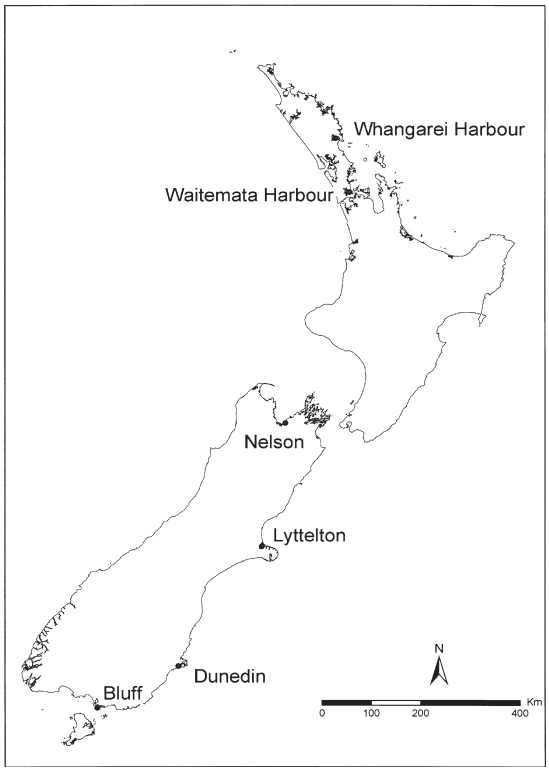

Fig. 1 Sampling locations of *Charybdis japonica* (Waitemata Harbour) and *Ovalipes catharus* (Waitemata Harbour and all other sites shown) within New Zealand.

Specimens recovered from the traps were frozen and transported to the laboratory for dissection. Carapace width (CW) (mm) was recorded to one decimal point, and sex was noted for all specimens. The exoskeleton of each animal was examined for epibionts and ectoparasites before dissection. Patterns of association between the bryozoan *Triticella capsularis* and *O. catharus* were explored in more detail, by scoring the relative abundance of the bryozoan on each crab using a four-point scale (0 = no *Triticella*, 1 = thin covering, 2 = moderate covering, 3 = thick fur).

The carapace was removed from each specimen and the muscles, body cavity, digestive tract, gonads, digestive gland, abdomen, and gill chambers were examined under a binocular microscope (6.3–40× magnification) for the presence of macro-parasites. Each appendage was also inspected for parasites. As an indirect measure of predation pressure and/or intraspecific aggression, we also measured the proportion of crabs from each population that was missing and regenerating limbs and the mean number of limbs missing per crab (*sensu* Torchin et al. 2001). We calculated the prevalence of parasitism (percentage of infected crabs in a sample) for each population and the mean intensity of infection (mean number of parasites or symbionts per infected crab) by each parasite. Samples of muscle tissue containing lesions found in *C. japonica* were fixed in 10% formalin in sea water. Subsequently, samples were processed for wax histopathology, cut into 4-μm sections and stained with haematoxylin and eosin using standard techniques (Bell & Lightner 1988). The sections were cut to obtain transverse sections of the lesions and examined under a compound microscope for identification. The number of individuals harbouring lesions and the number of lesions per crab were determined.

Statistical analysis

Chi-squared tests and generalised linear models (GLM) were used to examine relationships between the prevalence and intensity of infection by parasites and the size, sex, and geographic source of the crabs within New Zealand (SYSTAT 2000). Backward stepwise GLMs were fitted to explore the relationships between the source population, gender, and size (CW) of *O. catharus* and the relative abundance scores of *T. capsularis*. GLMs were fitted using the backward elimination procedures in SYSTAT v.10, with $P > 0.15$ for removal of terms. A t test on means with unequal variance was used to examine differences in limb loss between the two species, using individual crabs as the unit of replication (SYSTAT 2000). The only known report of a parasite from *C. japonica* in its native area details the presence of a rhizocephalan barnacle *Heterosaccus papillosus* (Kim 2001). We used a binomial detection probability stratified by sex (*sensu* McArdle 1990) with rates of prevalence indicated in Kim (2001) to estimate chances of detecting at least one individual infected with a rhizocephalan parasite in this study.

RESULTS

In total, 350 *O. catharus* and 118 *C. japonica* were dissected. The sex ratio of the trapped samples was highly male-biased, with females comprising 11.0% of the *C. japonica* sample and 34.5% of *O. catharus* (Table 1). Only a single ovigerous female was caught. No ovigerous *C. japonica* were recovered. The sample of *C. japonica* from Waitemata Harbour comprised a single, broad size-class of relatively

large individuals, between 66.4 and 104.2 mm CW (Table 1). In comparison, trapped populations of *O. catharus* from Waitemata Harbour and the five other locations throughout New Zealand exhibited a much broader range of sizes (46.9–128.2 mm CW) and greater variation in sex ratio (Table 1), with female crabs outnumbering males in some samples (i.e., Bluff and Lyttelton).

Almost a third (23.7%) of the trapped *C. japonica* had lost limbs (Mean no. missing limbs ± SE = 2.3 ± 0.3 per crab) (Table 2). Although this was significantly lower than the overall rate of limb loss for *O. catharus* (46% of all individuals captured nationwide; $\chi^2 = 14.20$, d.f. = 1, $P < 0.001$), there was significant variation in the prevalence of limb loss among populations of the native species. The Waitemata Harbour samples of *O. catharus* had the lowest rate of limb loss (33.3%) of all the native populations sampled (Table 2). There was no difference in the proportions of *C. japonica* and *O. catharus* captured in Waitemata Harbour that had lost limbs ($\chi^2 = 1.38$, d.f. = 1, $P > 0.100$), but individual *C. japonica* from Waitemata Harbour lost more limbs on average than *O. catharus* from the same area (*t* test on means with unequal variance: $t = 2.89$, d.f. = 44.7, $P < 0.01$).

Exoskeletons of *C. japonica* and *O. catharus* were fouled by several species of epibiont, but the types of organisms encountered on each crab species were distinct. In the August and October 2003 samples, most *C. japonica* (85.4%) (Table 2) were fouled by large numbers of serpulid polychaete tubes (24.7 ± 3.6 tubes per crab). Because no intact worms were recovered from the tubes it was not possible to identify the serpulid species. In general, the serpulids were much more abundant on male (23.2 ± 2.5 tubes per crab, $n = 105$) than female *C. japonica* (2.3 ± 1.0 tubes per crab, $n = 13$; $F = 3.759$, d.f. = 1, 82, $P = 0.057$), and variation in their abundance was not significantly related to either the size ($F = 0.015$, d.f. = 1, 82, $P = 0.904$) or date of capture of the crabs ($F = 0.028$, d.f. = 2, 82, $P = 0.867$). Serpulid tubes were not encountered on *O. catharus*.

Balanomorph barnacles were the only other fouling organisms encountered on *C. japonica*. They occurred on 8.5% of individuals and were found on only one of the 350 *O. catharus* examined (117 mm CW, Dunedin/Otago Harbour) (Table 2).

The ctenosome bryozoan *T. capsularis* occurred on almost all *O. catharus* (97.4%) examined and was present in each of the populations surveyed (Table 2). It was not found on *C. japonica*. *Triticella capsularis* appears to be an obligate symbiont of *O. catharus* that forms thick furs predominantly on the ventral anterior surfaces of the crabs (Gordon & Wear 1999). The size ($F = 38.513$, d.f. = 1,343, $P < 0.001$) and source population of the crabs ($F = 2.144$, d.f. = 5, 343,= $P = 0.060$) explained significant proportions of the variation in bryozoan abundance ($r^2 = 0.142$). In general, the relative abundance of the bryozoan increased with the size of the crab, but *Triticella* was equally abundant on male and female *O. catharus* of similar size ($F = 1.122$, d.f. = 1, 343, $P = 0.290$).

Juvenile stages of two previously undescribed (Robin Overstreet pers. comm.) species of ascaridoid nematode were recovered from the crabs. In *C. japonica*,

Table 1 Number (*n*), size (CW, carapace width), sampling date, and sex-ratio of *Charybdis japonica* and *Ovalipes catharus* collected from each harbour.

Species	Location	Date sampled	*n*	Range CW (mm)	Mean CW (mm)	Percentage female (%)
C. japonica	Waitemata	1–8 April 2003	56	66.4–92.4	81.48	12.5
	Waitemata	25–27 August 2003	14	76.4–97.2	84.41	0
	Waitemata	13–17 October 2003	48	70.1–104.2	85.86	12.5
Overall			118		83.61	11
O. catharus	Waitemata	1–8 April 2003	15	75.8–123.1	102.60	0
	Waitemata	25–27 August 2003	92	46.9–126.9	92.65	21.7
	Waitemata	13–17 October 2003	7	72.7–106.4	92.36	0
	Whangarei	29 September–10 October 2003	11	69.5–128.2	102.68	18.2
	Nelson	15 July/5 August 2003	60	91.2–108.8	98.61	11.7
	Lyttleton	7–14 July 2003	17	51.2–83.5	63.86	58.8
	Dunedin	4–8 August 2003	104	53.2–117.2	75.39	46.2
	Bluff	18–21 August 2003	44	53.3–88.4	69.95	70.5
Overall			350		85.03	34.5

the nematodes occurred in the mid- to hind-gut region of seven individuals (5.9%, 1.3 ± 0.2 nematodes per crab); two from the April sample, and five individuals from the October collection. None of the *C. japonica* caught in August 2003 contained nematodes.

Four *O. catharus* were also hosts for ascaridoid nematodes (prevalence 1.1%, intensity 15.7 ± 9.5 nematodes per crab). The specimens obtained from *O. catharus* appear to be a different species of nematode to those found in *C. japonica* (Robin Overstreet pers. comm.) and occurred in the cardiac stomach of affected individuals. The four *O. catharus* with nematode larvae were all from the Nelson sample. Nematodes were not present in any other *O. catharus* populations in this study.

Melanised lesions (Fig. 2A) occurred throughout the body tissues of almost half (prevalence 46.6%) of the *C. japonica* captured. They were not present in *O. catharus*. The lesions were generally small (800–1000 μm), round or irregularly shaped, brown, and occurred in a variety of body tissues, including body muscle, muscle in the chelipeds, around the nerve ring, in the digestive gland and, occasionally, in the walking legs. Histological examination revealed two types of lesion. Type I lesions (800–900 μm diam.) resembled fluke (trematode) metacercarial cysts or another type of parasite (Ben Diggles pers. comm.), encapsulated by the crab's immune response. Type II lesions were smaller (200–1000 μm diam.), multifocal melanised nodules and granulomas interspersed between larger necrotic lesions which had a centre consisting of a mixture of bacterial cells and granular debris surrounded by a melanised layer of host haemocytes (Fig. 2B). This type of lesion is

Table 2 Prevalence (%) and mean values ± SE (in parenthesis) of lost limbs, epibionts, and endoparasites in samples of *Charybdis japonica* and *Ovalipes catharus*. (n.d. no data collected).

			Epibionts			Endoparasites	
Species	Sample	Limb loss	Serpulid tubes	Balanomorph barnacles	Ctenosome[1] bryozoans	Ascaridoid nematodes	Melanised lesions
C. japonica	Waitemata (April)	16.1 (1.9±0.5)	n.d.	0	0	3.5[2] (1.0±0)	23.2 (30.7±7.7)
	Waitemata (August)	0	100 (24.1±5.5)	28.6 (1±0)	0	0	7.1 (53±0)
	Waitemata (October)	39.6 (61.9±12.5)	81.2 (2.4±0.3)	12.5 (24.9±4.5)	0	10.2[2] (1.4±0.3)	85.4
	Total *C. japonica*	23.7 (2.3±0.3)	85.4 (24.7±3.6)	8.5 (3.2±1.4)	0	5.9 (1.3±0.2)	46.6 (54.4±9.6)
O. catharus	Waitemata (April)	0	0	0	40.0 (3.0±0)	0	0
	Waitemata (August)	33.7 (1.3±0.1)	0	0	100.0 (2.1±0.1)	0	0
	Waitemata (October)	100.0 (2.4±0.6)	0	0	100.0 (2.1±0.1)	0	0
	Total Waitemata	33.3 (1.5±0.1)	0	0	92.1 (2.2±0.1)	0	0
O. catharus	Whangarei	81.8 (3.2±0.5)	0	0	100.0 (2.5±0.2)	0	0
	Nelson	35.0 (1.4±0.1)	0	0	100.0 (1.9±0.1)	7.1[3] (15.7±9.5)	0
	Lyttleton	64.7 (2.1±0.4)	0	0	100.0 (1.8±0.2)	0	0
	Dunedin	51.9 (2.1±0.2)	0	1.0 (1.0±0)	100.0 (1.8±0.1)	0	0
	Bluff	63.6 (1.8±0.2)	0	0	100.0 (1.6±0.1)	0	0
	Total *O. catharus*	46.0 (1.9±0.1)	0	0.3 (1.0±0)	97.4 (2.0±0.0)	1.1 (15.7±9.5)	0

[1] Abundance area based on an index of the relative thickness of bryozoan growth (1 = thin, 2 = medium, 3 = thick).
[2] Located in the digestive tract.
[3] Located in the cardiac stomach.

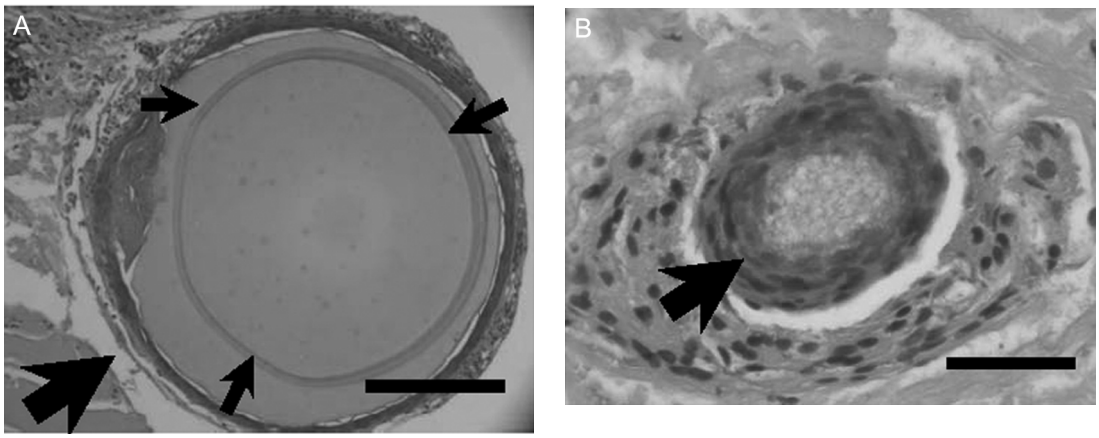

Fig. 2 **A**, Histology of a Type I lesion from *Charybdis japonica,* showing spherical amorphous area surrounded by a thin melanised capsule of host inflammatory tissue (large arrow). Note the inner spherical body within the amorphous area, surrounded by a double walled capsule (small arrows). Scale bar = 200 μm at 4× magnification. **B**, Type 2 lesion from *Charybdis japonica,* with a grainy central area surrounded by a melanised capsule (arrow) and another granulomatous outer layer in the host muscle. Scale bar = 20 μm at 400× magnification.

consistent with wound repair in decapod crustaceans in response to cellular trauma (Ben Diggles pers. comm.). No lesions were recorded from the body tissues of *O. catharus*.

As the distinction between the two types of lesions was not obvious under binocular magnification and could only be made by histological analysis, we combined data for both types of lesions in the following analysis. Lesions increased in prevalence within the *C. japonica* population between April and October 2003 (χ^2 = 40.1, d.f. = 2, P < 0.001). Most (85.4%) crabs in the October sample were affected (Table 2). The mean density of lesions within affected crabs did not change during the study (F = 1.89, d.f. = 2, 113, P = 0.175) and lesions were similarly abundant in crabs of different sex (F = 0.101, d.f. = 1, 113, P = 0.752) and size (F = 0.022, d.f. = 1, 113, P = 0.884).

Kim (2001) reported the presence of a rhizocephalan barnacle, *Heterosaccus papillosus* in populations of *C. japonica* in Korea. This parasite was not recovered from the New Zealand population of *C. japonica*. Our calculations determined a 79% chance of detecting at least one individual infected with a rhizocephalan, if it was present in the New Zealand population of *C. japonica*.

DISCUSSION

Because of their economic importance and key trophic position in coastal environments, portunids are among the most studied of all crab families (Shields 1992; Sumpton et al. 1994; Boone et al. 2004; Gaddes & Sumpton 2004). However, to our knowledge, this is the first investigation of the parasites of New Zealand portunids. Compared to estuarine portunids of similar size from Australia (*Portunus pelagicus*; Shields 1992; Brockerhoff 1993; Shields & Wood 1993), the United States (*Callinectes sapidus*; Overstreet 1978), and Europe (*Carcinus maenas*; Torchin et al. 2001), the two species we investigated had relatively low parasite species richness and levels of infestation in relation to size. Shields (1992) reported 15 parasites and symbionts from the tissues, branchial chambers, and external surfaces of the sand crab *Portunus pelagicus* from Moreton Bay, Australia, including tapeworms, trematodes, crustacean gill parasites, nemertean and copepod egg predators. Diverse parasite assemblages have also been recorded from the blue crab, *Callinectes sapidus* from Chesapeake Bay (Messick 1998) and from native populations of the European shore crab, *Carcinus maenas* (Torchin et al. 2001).

All but one of the six populations of *O. catharus* in this study were free of endoparasites. The sixth population (from Nelson) hosted an undescribed ascaridoid nematode that was present in 7.1% of individuals examined. Only a single endoparasite—a second species of ascaridoid—was recovered from the introduced population of *C. japonica*, although 85.4% of the October 2003 sample showed lesions symptomatic of cellular trauma and/or an unknown infection. The lesions remained prevalent in a

subsequent sample of 21 *C. japonica* taken in September 2004 (Miller unpubl. data).

The high prevalence of melanised tissue lesions in later samples of *C. japonica* from Waitemata Harbour warrants further study, particularly as their appearance corresponds with what appears to be a decline in abundance of the introduced crab population (G. Inglis, unpubl. data). Crustaceans typically produce melanised nodules as a haemocytic response to foreign bodies (Sparks 1980). For example, crustaceans in general can produce melanised capsules around parasites such as trematode metacercariae that penetrate their cuticle and encyst within their tissues (Johansson & Söderhäll 1989). Our preliminary examinations did not reveal a pathology associated with the lesions, but many appear typical of response to an infection process. Sparks (1980) described two types of melanised nodules in the mid-gut of the Dungeness crab, *Cancer magister*, that were similar to those described here. Although he found no direct evidence of their cause, Sparks (1980) concluded that both types of lesions were biotic in origin and initiated in response to potentially different organisms. Although the nodules were prevalent in the *C. japonica* population they did not occur in sympatric *O. catharus*. It is possible that they are a response to an unknown pathogen, but further work is needed to determine their true cause, and effects they may have on *C. japonica*.

Our sample was dominated by male crabs and, although the surveys overlapped the main reproductive period of *O. catharus* (July–May; McLay 1988), contained only a single ovigerous female *O. catharus*. We were, therefore, unlikely to find egg parasites and predators if they are present in the populations. Nemertean egg parasites have not yet been reported from *O. catharus* in New Zealand (McLay 1988), despite intensive study of its reproduction (Osborne 1987; Armstrong 1988; Haddon & Wear 1993; Haddon 1994).

The relatively small numbers of parasites recorded in our study meant that we could not test whether the introduced population of *C. japonica* was less vulnerable to parasites than native *O. catharus*. The New Zealand coastline is home to only 87 known species of crab (McLay 1988). This limited host diversity may also be reflected in New Zealand's native fauna of decapod parasites, although too few parasitological studies have yet been done to test this hypothesis (Poulin 2004). Recent investigations of parasites in New Zealand grapsid, cancrid and ocypodid crabs have revealed relatively high levels of infestation by acanthocephalan, trematode, nematode, and nematomorph parasites, some of which have strong influences on behaviour and survival of their hosts (Kuris & Gurney 1997; Latham & Poulin 2001, 2002a,b; Poinar & Brockerhoff 2001; Moravec et al. 2003; Poulin et al. 2003).

Most evidence for the enemy release hypothesis (ERH) in decapods comes from introduced populations that have escaped comparatively high levels of infection (10–20% of the population) by parasitic castrators (Torchin et al. 2001). Rhizocephalan barnacles can cause varying degrees of parasitic castration, feminisation of males (Høeg 1995), and decreased growth rates (Hawkes et al. 1987) in infected individuals. As a result, release from these parasites can lead to an increase in average host biomass and fertility (Torchin et al. 2001). Rhizocephalan barnacles are common parasites of portunids and afflict some species of *Charybdis* (Walker & Lester 2000; Innocenti et al. 2003). In part of its native range, *C. japonica* is host to the rhizocephalan *H. papillosus* (Kim 2001). Rates of infection in the Korean population studied by Kim (2001) were c. 3.8% of female crabs and 1% of males. Given the relatively low prevalence of infestation it is unclear what effect the rhizocephalan barnacles may have on overall population dynamics. At those levels of prevalence, we estimated that our study had a 79% chance of detecting at least one individual infected with a rhizocephalan. The chance of an infected individual reaching New Zealand would depend on the vector of transport for *C. japonica* into New Zealand, as it is thought that the most likely methods for its arrival would have been via larvae in ballast water or as juveniles or adults in the sea chests of ships (Smith et al. 2003). Larvae arriving in ballast water are generally free of natural enemies, including parasites (Lafferty & Kuris 1996), thus reducing the chances of parasites being present and hence detected in this study. Therefore, although we cannot conclude that *H. papillosus* is not present in the introduced New Zealand population, the evidence points strongly to its absence. There was also no evidence in the introduced population of greater individual size as a result of parasite release, since the maximum sizes of animals obtained in the Waitemata Harbour sample (males 110 mm CW, females 90 mm CW) were similar to those achieved by unparasitised animals in the Korean *C. japonica* population (males 109 mm CW, females 96 mm CW; Kim 2001).

External surfaces of *C. japonica* and *O. catharus* harboured relatively few taxa, with only two species

of fouling organism recorded from each crab. The prevalence and intensity of fouling by epibionts on crab exoskeletons is influenced by the moult cycle of the crab and its behaviour. In general, more epibionts could be expected in larger crabs where the intermoult period is longer (Gili et al. 1993). The tubes found on *C. japonica* resembled those of the serpulid *Pomatoceros caeruleus*, which is an abundant component of rocky and cobbled shorelines in Waitemata Harbour (Morton & Miller 1973; Francis et al. 2004). The greater prevalence and intensity of fouling by these tubeworms and barnacles on *C. japonica* in this study probably reflects differences in habitat occupation and behaviour of the two crab species. *Ovalipes catharus* spends much of its time buried in the sand, where little of the exoskeleton is exposed to the settling larvae of fouling organisms (McLay & Osborne 1985). Although only limited information is available on the behaviour of *C. japonica* in New Zealand (Gust & Inglis, 2006), it may be a less active burrower than *O. catharus*. In Japan, it is known as "rock crab" where it is commonly associated with muddy, sandy, and stony shorelines and tidepools on rocky shores (Sakai 1965).

Ovalipes catharus had few facultative epibionts on its external surfaces, but frequently hosted the obligate symbiotic bryozoan, *T. capsularis*. In their initial description of *T. capsularis*, Gordon & Wear (1999) reported it only from large (105–120 mm CW), terminal moult crabs. Our study suggests *T. capsularis* is present on most *O. catharus*, but that its abundance varies among locations in New Zealand and with the size of the crab, reaching greatest abundance on large crabs.

Our data on limb loss suggested that the introduced population of *C. japonica* was just as likely to suffer from aggressive intraspecific interaction and/or predator attacks as *O. catharus*. Although limb loss is a crude measure of predation pressure and is also influenced by intraspecific interactions, it does have fitness implications by imposing energetic costs on individuals, including reduced foraging efficiency (Smith 1990, 1995). Portunid species are known to be highly aggressive (Huntingford et al. 1995), and as such tend to have high rates of limb autotomy that may be the result of agonistic interactions among conspecifics or escape from predation (Smith & Hines 1991; Smith 1995). *O. catharus* is preyed upon by a wide range of fish, including snapper (*Pagrus auratus*), grouper (*Polyprion oxygenios*), blue cod (*Parapercis colias*), red cod (*Pseudophycis bacchus*), and rig (*Mustelus lenticulatus*) (McLay 1988). At present, there is no direct evidence of native predators consuming *C. japonica*, but our data show similar levels of autotomy in the wild sympatric populations.

Our study investigated the prevalence and intensity of parasite fauna in the introduced portunid, *C. japonica*, and in sympatric and allopatric populations of the New Zealand portunid, *O. catharus*. Although the identity of parasites and epibionts carried by each species differed, both *C. japonica* and *O. catharus* had relatively low parasite richness and similar rates of limb loss. By comparing sympatric populations of *C. japonica* and *O. catharus* with multiple, widely separated populations of the native portunid, we were able to obtain an overview of the local and total richness and prevalence of parasites within these species within New Zealand.

ACKNOWLEDGMENTS

This research was supported by a Tūāpapa Pūtaiao Māori Fellowship from the New Zealand Foundation for Research, Science and Technology (Contract number UOOX0233), Te Ohu Kai Moana grant, and the Brenda Shore Award for Women (Otago University). Field collections of the crabs were supported by Ministry of Fisheries contract ZBS2001/01. Ben Diggles (DigsFish Services Pty. Ltd) undertook the histological analysis and description of the melanised lesions found in *Charybdis japonica* and Robin Overstreet (Gulf Coast Research Laboratory, Ocean Springs, United States) examined the ascaridoid nematodes. Special thanks to Oli Floerl, Nick Gust, Graeme MacKay, Crispin Middleton, Matt Smith, and Rob Tasker for collecting the crabs. Nick Gust and Don Robertson provided useful comments on the manuscript.

REFERENCES

Aliabadi BW, Juliano SA 2002. Escape from gregarine parasites affects the competitive interactions of an invasive mosquito. Biological Invasions 4: 283–297.

Armstrong JH 1988. Reproduction in the paddle crab *Ovalipes catharus* (Decapoda: Portunidae) from Blueskin Bay, Otago, New Zealand. New Zealand Journal of Marine and Freshwater Research 22: 529–536.

Bell TA, Lightner DV 1988. A handbook of normal penaeid shrimp histology. Baton Rouge, Louisiana, World Aquaculture Society. 114 p.

Barton DP 1997. Introduced animals and their parasites: the cane toad, *Bufo marinus*, in Australia. Australian Journal of Ecology 22: 316–324.

Boone E, Boettcher AA, Sherman TD, O'Brien JJ 2004. What constrains the geographic and host range of the rhizocephalan *Loxothylacus texanus* in the wild? Journal of Experimental Marine Biology and Ecology 309: 129–139.

Brockerhoff A 1993. Parasitological investigations on *Portunus pelagicus* (Decapoda) in coastal waters of Australia and the Philippines. Unpublished MSc thesis, University of Kiel, Kiel, Germany. 112 p.

Cohen AN, Carlton JT 1998. Accelerating invasion rate in a highly invaded estuary. Science 279: 555–557.

Colautti RI, Ricciardi A, Grigorovich IA, MacIsaac HJ 2004. Is invasion success explained by the enemy release hypothesis? Ecology Letters 7: 1–13.

Francis MP, Smith P, Walsh C, Gomon MF 2004. First records of the Australian blenny, *Omobranchus andius*, from New Zealand. New Zealand Journal of Marine and Freshwater Research 38: 671–679.

Gaddes SW, Sumpton WD 2004. Distribution of barnacle epizoites of the crab *Portunus pelagicus* in the Moreton Bay region, Eastern Australia. Marine and Freshwater Research 55: 241–248.

Gili JM, Abelló P, Villanueva R 1993. Epibionts and intermoult duration in the crab *Bathynectes piperitis*. Marine Ecology Progress Series 98: 107–113.

Gordon DP, Wear RG 1999. A new ctenostome bryozoan ectosymbiotic with terminal-moult paddle crabs (Portunidae) in New Zealand. New Zealand Journal of Zoology 26: 373–380.

Gust N, Inglis GJ 2006. Adaptive multi-scale sampling to determine an invasive crab's habitat usage and range in New Zealand. Biological Invasions 8: 339–353.

Haddon M 1994. Size-fecundity relationships, mating behaviour and larval release in the New Zealand paddle crab, *Ovalipes catharus* (White 1843) (Brachyura: Portunidae). New Zealand Journal of Marine and Freshwater Research 28: 329–334.

Haddon M, Wear RG 1993. Seasonal incidence of egg-bearing in the New Zealand paddle crab *Ovalipes catharus* (Crustacea: Brachyura) and its production of multiple egg batches. New Zealand Journal of Marine and Freshwater Research 27: 287–293.

Hawkes CR, Meyers TR, Shirley TC 1987. Growth of Alaskan blue king crabs *Paralithodes platypus* (Brandt), parasitised by the rhizocephalan *Briarosaccus callosus* Boschma. Crustaceana 52: 78–84.

Høeg JT 1995. The biology and life cycle of the Rhizocephala (Cirripedia). Journal of the Marine Biological Association of the United Kingdom 75: 517–550.

Huntingford FA, Taylor AC, Smith IP, Thorpe KE 1995. Behavioural and physiological studies of aggression in swimming crabs. Journal of Experimental Marine Biology and Ecology 193: 21–39.

Innocenti G, Pinter N, Galil BS 2003. Observations on the agonistic behaviour of the swimming crab *Charybdis longicollis* Leene infected by the rhizocephalan barnacle *Heterosaccus dollfusi* Boschma. Canadian Journal of Zoology 81: 173–176.

Jiang W, Meng T, Chen R, Wei S 1998. Diet of *Charybdis japonica* (A. Milne-Edwards) and *Portunus trituberculatus* (Miers) in the Bohai Sea. Haiyan Shuichan Yanjiu 19: 53–59.

Johansson MW, Söderhäll K 1989. Cellular immunity in crustaceans and the proPO system. Trends in Ecology and Evolution 6: 171–176.

Kim KB 2001. Growth and reproduction of *Charybdis japonica* (A. Milne-Edwards) (Decapoda: Portunidae) in Korean waters. Unpublished PhD thesis, Pukyong National University, Busan, North Korea.

Kuris A, Gurney R 1997. Survey of Tasmanian crabs for parasites: a progress report. CRIMP Technical Report No. 11.

Lafferty KD, Kuris AM 1996. Biological control of marine pests. Ecology 77: 1989–2000.

Latham ADM, Poulin R 2001. Effect of acanthocephalan parasites on the behaviour and colouration of the mud crab *Macrophthalmus hirtipes* (Brachyura: Ocypodidae). Marine Biology 139: 1147–1154.

Latham ADM, Poulin R 2002a. Effect of acanthocephalan parasites on hiding behaviour in two species of shore crabs. Journal of Helminthology 76: 323–326.

Latham ADM, Poulin R 2002b. 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.

McArdle BH 1990. When are rare species not there? Oikos 57: 276–277.

McLay CL 1988. Brachyura and crab-like anomuran of New Zealand. Leigh Laboratory Bulletin No. 22. 462 p.

McLay CL, Osborne TA 1985. Burrowing behaviour of the paddle crab *Ovalipes catharus* (White, 1843) (Brachyura: Portunidae). New Zealand Journal of Marine and Freshwater Research 19: 125–130.

Maeda M, Itami T, Furumoto A, Hennig O, Imamura T, Kondo M, Hirono I, Aoki T, Takahashi Y 1998. Detection of penaeid rod-shaped DNA virus (PRDV) in wild-caught shrimp and other crustaceans. Fish Pathology 33: 381–387.

Messick GA 1998. Diseases, parasites, and symbionts of blue crabs (*Callinectes sapidus*) dredged from Chesapeake Bay. Journal of Crustacean Biology 18: 533–548.

Moravec F, Fredensborg BL, Latham ADM, Poulin R 2003. Larval spirurida (Nematoda) from the crab *Macropthalmus hirtipes* in New Zealand. Folia Parasitologia 50: 109–114.

Morton JE, Miller MC 1968. The New Zealand sea shore. London, Collins. 653 p.

Osborne TA 1987. Life history and population biology of the paddle crab *Ovalipes catharus*. Unpublished PhD thesis, University of Canterbury, Christchurch, New Zealand. 156 p.

Overstreet RM 1978. Marine Maladies? Worms, germs and other symbionts from the Northern Gulf of Mexico. Mississippi-Alabama Sea Grant Consortium. Ocean Springs, Mississippi, Blossman Printing Inc. 140 p.

Poinar G, Brockerhoff AM 2001. *Nectonema zealandica* n. sp. (Nematomorpha: Nectonematoidea) parasitising the purple rock crab *Hemigrapsus edwardsi* (Brachyura: Decapoda) in New Zealand, with notes on the prevalence of infection and host defence reactions. Systematic Parasitology 50: 149–157.

Poulin R 2004. Parasite species richness in New Zealand fishes: a grossly underestimated component of biodiversity? Diversity and Distributions 10: 31–37.

Poulin R, Mouillot D 2003. Host introductions and the geography of parasite taxonomic diversity. Journal of Biogeography 30: 837–845.

Poulin R, Nichol K, Latham ADM 2003. Host sharing and host manipulation by larval helminths in shore crabs: cooperation or conflict? International Journal for Parasitology 33: 425–433.

Sakai T 1965. The crabs of Sagami Bay. Collected by His Majesty the Emperor of Japan. East West Centre Press, Honolulu. 206 p.

Shea K, Chesson P 2002. Community ecology theory as a framework for biological invasions. Trends in Ecology & Evolution 17: 170–176.

Shields JD 1992. Parasites and symbionts of the crab *Portunus pelagicus* from Moreton Bay, Eastern Australia. Journal of Crustacean Biology 12: 94–100.

Shields JD, Wood FEI 1993. Impact of parasites on the reproduction and fecundity of the blue sand crab *Portunus pelagicus* from Moreton Bay, Australia. Marine Ecology Progress Series 92: 159–170.

Smith LD 1990. Patterns of limb loss in the blue crab, *Callinectes sapidus* Rathbun, and the effects of autotomy on growth. Bulletin of Marine Science 46: 23–36.

Smith LD 1995. Effects of limb autotomy and tethering on juvenile blue crab survival from cannibalism. Marine Ecology Progress Series 116: 65–74.

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

Smith PJ, Webber WR, McVeagh SM, Inglis GJ, Gust N 2003. DNA and morphological identification of an invasive swimming crab, *Charybdis japonica*, in New Zealand waters. New Zealand Journal of Marine and Freshwater Research 37: 753–762.

Sparks AK 1980. Multiple granulomas in the midgut of the Dungeness crab, *Cancer magister*. Journal of Invertebrate Pathology 35: 323–324.

Sumpton WD, Potter MA, Smith GS 1994. Parasitism of the commercial sand crab *Portunus pelagicus* (L.) by the Rhizocehpalan *Sacculina granifera* Boschma, 1973 in Moreton Bay, Queensland, Australia. Australian Journal of Marine and Freshwater Research 45: 169–175.

SYSTAT 2000. SYSTAT 10: Statistics I. SPSS Inc., Chicago. 663 p.

Torchin ME, Lafferty KD, Kuris AM 2001. Release from parasites as natural enemies: increased performance of a globally introduced marine crab. Biological Invasions 3: 333–345.

Torchin ME, Lafferty KD, Kuris AM 2002. Parasites and marine invasions. Parasitology 124: 137–151.

Torchin ME, Lafferty KD, Dobson AP, McKenzie VJ, Kuris AM 2003. Introduced species and their missing parasites. Nature 421: 628–629.

Walker G, Lester RJG 2000. The cypris larvae of the parasitic barnacle *Heterosaccus lunatus* (Crustacea, Cirripedia, Rhizocephala): some laboratory observations. Journal of Experimental Marine Biology and Ecology 254: 249–257.

Wear RG 1984. Paddle crabs are probable predators. Catch 22: 11–13.

Wear RG, Haddon M 1987. Natural diet of the crab *Ovalipes catharus* (Crustacea, Portunidae) around central and northern New Zealand. Marine Ecology Progress Series 35: 39–49.

Webber R 2001. Space invaders: crabs that turn up in New Zealand unannounced. Seafood New Zealand, November: 80–84.