

The targeting of large-sized benthic macrofauna by an invasive portunid predator: evidence from a caging study

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Abstract The Portunid crab *Charybdis japonica* was first found in Waitemata Harbour, New Zealand, in 2000. It has established breeding populations and has been spreading, yet information on its dietary preferences in New Zealand are unknown. We conducted field caging experiments to elucidate prey choices and potential impacts of *Charybdis* on benthic communities. We tested the hypothesis that *Charybdis* would reduce the previously demonstrated positive influence of native pinnid bivalves, *Atrina zelandica*, on the abundance and richness of surrounding soft-sediment macrofauna. Adult male *Charybdis* were introduced to cages with and without *Atrina* that included soft-sediment macrofaunal communities of ambient composition and abundance. After leaving the crabs to feed overnight, changes in community structure (relative to sediments without crabs) were

determined by coring the sediment and analysing the resident macrofauna. Prey choices were verified by extracting taxa from the stomachs of crabs collected from the cages in which they had been feeding. The abundance of large taxa including burrowing urchins, bivalves and native crabs was lower in the presence of *Charybdis* compared to areas without this invader. The stomach contents of *Charybdis* were dominated by these same three taxa, constituting 85 % of the prey abundance when using stomach fullness as a weighting factor. Our hypothesis was supported with the greatest net losses occurring in cages with *Charybdis* and *Atrina*. Reduction in the abundance of *Echinocardium cordatum* by *Charybdis* could have cascading ecological effects, as these urchins play a critical role in benthic soft-sediment ecosystems in New Zealand via bioturbation and biogenic disturbance.

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Introduction

Coasts and estuaries are among the most invaded ecosystems worldwide and continue to accumulate non-native species at unprecedented rates (Carlton and Geller 1993; Ruiz et al. 1997). Biological invasions

result in new ecological relationships and modify established trophic pathways in the recipient communities (Callaway and Aschehoug 2000; King et al. 2006; Hollebone and Hay 2008), impacting biodiversity and community structure. Invasions can alter ecosystem functioning with the potential for cascading effects and economic impacts (Vitousek et al. 1996; Cohen and Carlton 1998; Sanders et al. 2003; Gurevitch and Padilla 2004). Marine systems, particularly harbours and estuaries, are subjected to high levels of stress from multiple anthropogenic sources and additional stresses from non-indigenous species can have severe consequences (Kennish 1997; Simberloff and Von Holle 1999; Lohrer and Whitlatch 2002).

Predation has long been recognized as an important driver of community structure (Brazao et al. 2009) and is an obvious mechanism through which native fauna are directly impacted by invasives. Portunid crabs, as a group, have been particularly successful, with invasions occurring all around the world including both coasts of the US, South America, the Mediterranean and Australasia (Cohen et al. 1995; Miron et al. 2005; Mantelatto and Garcia 2001; Galil 2000; Gust and Inglis 2006; Froglija 2012; Sant'Anna et al. 2012a, b). The swimming ability and generally large size of portunid crabs, coupled with their strong chelae, makes them adept predators (Choy 1986). Broad diets and environmental tolerances also likely contribute to the invasive success of these crabs (Ricciardi and Rasmussen 1998; Essink and Dekker 2002). Arguably the most widespread portunid invader is the European green crab, *Carcinus maenas* (Linnaeus, 1758), which has impacted bivalves and other invertebrate populations in a variety of nearshore habitats on both coasts of the US, Australia, Japan, South Africa and more recently South America (Le Roux et al. 1990; Cohen et al. 1995; Miron et al. 2005; Mantelatto and Garcia 2001; Galil 2000; Gust and Inglis 2006; Froglija 2012; Sant'Anna et al. 2012a, b; Hidalgo et al. 2005). Other notable portunid invaders are *Charybdis* spp. native to the north-western Pacific; *Charybdis hellerii* (Milne-Edwards, 1867) invaded the Indian River Lagoon in Florida, USA, and has extended northward into the Carolinas and southward into the Caribbean (Lemaitre 1995; Dineen et al. 2001; Tavares and Amouroux 2003; McMillen-Jackson 2008). *Charybdis japonica* (Milne-Edwards, 1861) has established breeding populations in New Zealand (Gust and Inglis 2006; Fowler et al. 2011) and has been recorded in Australia

(Ahyong and Wilkens 2011) and the Mediterranean (Froglija 2012).

The coastal waters of New Zealand have been successfully invaded numerous times during the last 30–40 years with the establishment of bivalves, gastropods, decapods, tunicates and polychaetes (Hayward 1997; Hayward et al. 1997; Cranfield et al. 1998; Townsend et al. 2010). Introduced species now have dominant roles and high numerical abundance in many locations (Lohrer et al. 2008a), particularly in areas surrounding the country's largest port in Waitemata Harbour (Auckland) (Inglis et al. 2005a, b). The Portunid crab *C. japonica* was first found in Waitemata Harbour in 2000 (Webber 2001; Smith et al. 2003). It originates from the Asian Western Pacific and has a native range across China, Japan, Korea, Taiwan and Malaysia (Smith et al. 2003). *C. japonica* is now found over 200 km away from Waitemata Harbour at various localities, extending northwards to Mahurangi Harbour and the Bay of Islands and eastwards to the Whitford Embayment and Whangapoua Harbour (Gust and Inglis 2006; Fowler et al. 2011; G. Inglis pers. comms, Fig. 1). This geographic range covers variation in substrate types and from the intertidal to shallow subtidal depths. In New Zealand *C. japonica* has been found on a range of strata from muds through to rocky reefs, but most commonly on firm estuarine muddy sands. In other locations, e.g., Sea of Japan, it has been observed in silty, sandy and rocky substrates (Kolpakov and Kolpakov 2011). Based on information from its native range, *C. japonica* is thought to be a generalist predator feeding predominantly on benthic bivalves, crustaceans, fishes and cephalopods (Jiang et al. 1998). *C. japonica* has also been observed to prey on juvenile, hatchery-reared flounder that are released to bolster fish stocks in its native Japan (Sudo et al. 2008). Within this native range it can attain a carapace width greater than 100 mm and exhibits strong sexual dimorphism (Jiang et al. 1998; Kim 2001 from Kolpakov and Kolpakov 2011). New Zealand has a relatively depauperate crab fauna in relation to similar habitats worldwide, with only one native portunid of similar large size. The largest native swimming crab that exists in New Zealand, *Ovalipes catharus* (White, 1843), is generally found in sands on the open coast (Wear and Haddon 1987), whereas *C. japonica* is more estuarine in nature (Smith et al. 2003). Despite the potential for *C. japonica* to have impacts on native communities in

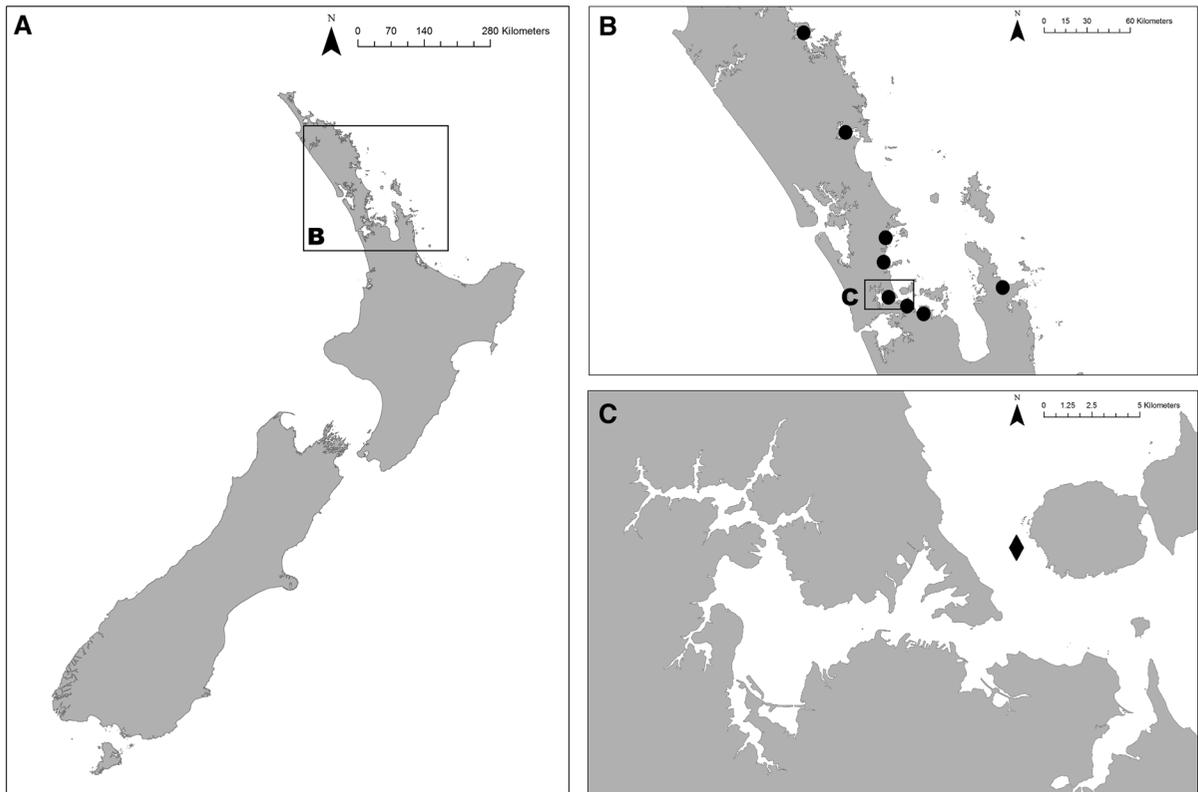


Fig. 1 Map showing New Zealand (A), sites on the East Coast of the North Island with confirmed occurrences of *C. japonica* (B, black circles) and the site of the subtidal caging experiment in the Tamaki Strait (C, black diamond)

New Zealand as a predator (Gust and Inglis 2006), the dietary preferences and ability of this species to impact prey populations have not to our knowledge been investigated.

The goal of this study was to assess the dietary preferences and predatory impacts of *C. japonica* (hereafter *Charybdis*) in the most realistic way possible using field experiments. To understand the diet of *Charybdis*, we aimed to collect a large number of individuals with full stomachs directly from the natural habitats in which they had been feeding. However, in Waitemata Harbour, collecting sufficient numbers of crabs with a dredge net or using SCUBA was not feasible for various reasons (busy port, turbid water, low density and cryptic nature of crabs spread out over a large area). Thus, as an alternative approach, we exposed defined areas of ambient sediments containing natural assemblages of macrofauna to predation by *Charybdis* during night (their prime feeding period). This enabled us to investigate

the types of items the crabs were eating (by gut content analysis) with knowledge of the types of prey available to them (by sampling the sediments and identifying the macrofauna). In addition to examining predation in “bare” sediments, predation was examined in the presence of large structure-forming pinnid bivalves, *Atrina zelandica* (Gray, 1835). *A. zelandica* (hereafter *Atrina*) are suspension-feeding bivalves that are anchored in benthic sediments, but which extend upward across the sediment–water interface (5–15 cm into the water column), adding vertical relief and organic rich biodeposits to the system. This element of the design was employed because we had previously observed *Charybdis* nestled next to *Atrina*, which are known to increase the abundance and diversity of macrofauna in sediments immediately adjacent to their shells (Norkko et al. 2001, 2006; Hewitt et al. 2002; Lohrer et al. 2013). We tested the hypothesis that the crabs would reduce the positive influence of *Atrina* on the abundance and richness of macrofauna.

Materials and methods

Field work was conducted in the middle of the austral summer in two consecutive years (Jan 2009 and Feb 2010) in Waitemata Harbour (Auckland, New Zealand). *Charybdis* were collected in Fukui box traps (60 × 45 × 20 cm) that were baited with pilchard and deployed throughout the harbour. Captured crabs were sorted according to condition, and the largest, healthiest (active, all limbs and chelae present), intermoult male crabs were retained for use. Crabs were held individually and retained in ambient seawater (at a dock) for a period of 6–8 h, ensuring standardised hunger levels and evacuated guts. Crabs were introduced to large benthic cages that had been deployed in 6–8 m water depth at a subtidal study site in Rangitoto Channel (W174 50.060, S36 48.030, Fig. 1) and allowed to feed for a period of 12–18 h (overnight). The steel framed cylindrical cages (40 cm height, 55 cm internal diameter) were covered with rigid plastic mesh (5 × 5 cm aperture) that was smaller than the *Charybdis* but much larger than any of the mobile macrofauna prey present at the site (i.e., prey could presumably enter and exit cages). The cages had open bottoms, allowing insertion into sediment without disturbing ambient fauna. The sides of the cages were pressed down into the sediment to a depth of >10 cm to prevent crabs from burrowing and escaping (there was only one escapee in 76 crab cage deployments). A hatch in the centre of each cage lid allowed us to add and retrieve crabs in a controlled way. At dawn after the overnight feeding period, all caged crabs were recovered and immediately frozen to halt digestion. Analysis of gut contents was performed at a later date back at the laboratory (see methods below).

Experimental approach to crab feeding trials

In year 1, we were interested in assessing the effects of *Charybdis* on benthic macrofauna in the presence and absence of biogenic structure (large live *Atrina*). With 22 cages total, 11 were deployed with one naturally settled, large live *Atrina* in the middle of the caged area (“*Atrina*”), and the remainder were deployed to areas of sediment without *Atrina* (“bare”). Cages were positioned along a 40 m transect in a subtidal soft-sediment habitat with sparse *Atrina*. *Charybdis* were introduced to all 22 cages, meaning that there were no

Table 1 Sizing criteria used in the classification of ‘large’ organisms for the various taxa and morphotypes collected in the core samples

Taxa/type	Size
Vermiform	
<i>Polychaeta</i>	Body width >5 mm
<i>Nemertea</i>	Body width >5 mm
Echinodermata	
<i>Ophiuroidea</i>	Disc width >5 mm
<i>Spatangoida</i>	Test length >5 mm
<i>Holothuroidea</i>	Body width >5 mm
Crustacea	
<i>Brachyura</i>	Carapace width >5 mm
<i>Caridea</i>	Body length >10 mm
<i>Cirripedia</i>	Shell height >5 mm
Mollusca	
<i>Bivalvia</i>	Shell length >10 mm
<i>Gastropoda</i>	Longest dimension >10 mm
<i>Polyplacophora</i>	Width >5 mm

Organisms falling below these thresholds were classed as ‘small’. *Amphipoda* and *Isopoda* were not included in the sizing criteria as common species for the locality are small

“cage controls” assessing the effects of the caging itself on macrofauna. This was done to maximise the replication of crab treatments (Hall et al. 1990), given the low likelihood of cage effects on macrofauna (short experimental duration, small size of macrofauna relative to cage mesh aperture). Nevertheless, despite the lack of true “cage controls”, samples were collected from 11 ambient (un-caged) plots in both “bare” and “*Atrina*” sediments to assess the abundance, richness and community structure of macrofauna in the absence of *Charybdis* predation pressure (there were no *Charybdis* present at the experimental site in the Rangitoto Channel). Two sediment cores (10 cm internal diameter, 15 cm deep) were collected from each replicate of the four types of treatments (bare, *Atrina*, bare + *Charybdis*, *Atrina* + *Charybdis*) to quantify the macrofauna. The paired cores were collected 15–20 cm apart, in the centre of cages and next to *Atrina* when applicable. All cores of sediment were sieved through a 500 µm mesh screen, with the retained macrofauna preserved in 70 % isopropyl alcohol and stained with Rose Bengal. Macrofauna were identified to the lowest taxonomic level practicable (usually species level) under compound microscope and categorized as “small” or “large” from

Table 2 Summary of taxa found and the identifying features in food types consumed

Taxa	Types of fragments found in the gastric mills
<i>Polychaeta</i>	Phylum identified from Jaws and chaetae. Likelihood of 3 different species based on chaetae but without certainty Body wall material in poor condition and of low volume contribution
<i>Crustacea</i>	
<i>Brachyura</i>	(Crab) recognised from fragments of carapace, chelipeds and leg joints, species unidentified Largely crushed into fragments, low frequency of occurrence and contribution to gut fullness variable
<i>Anomura</i>	(Hermit crab) <i>Paguristes</i> sp identified from the cephalothorax, telson and uropods Largely crushed into fragments and of low frequency in occurrence. Minor contribution to gut fullness variable
<i>Cirripedia</i>	(Barnacle) infraclass recognised from fragments of the carina, probably <i>Austrominius modestus</i> but without certainty Rare and low contribution to gut fullness variable
<i>Mollusca</i>	
<i>Limidae</i>	<i>Limaria orientalis</i> identified from the pale thin shell, distinctive shell striations, umbo and teeth fragments Relatively common, but low contribution to gut fullness
<i>Mytiloidea</i>	<i>Arcuatula (Musculista) senhousia</i> identified from shell fragments, colouration and thickness Rare and low contribution to gut fullness variable
<i>Bivalvia</i> unident	Separated from the <i>Limaria</i> and <i>Musculista</i> from shell thickness and depth/shape of concentric ridges Rare and low contribution to gut fullness variable
<i>Gastropoda</i>	Gastropod sp. identified from fragments of shell, specifically the shell whorls and opercula Rare and variable contribution to gut fullness
Echinodermata	
<i>Spatangoida</i>	<i>Echinocardium cordatum</i> identified from fragments of mesodermal skeleton and spines in both the cardiac and pyloric stomachs. Tissue and sediment associated with the <i>E. cordatum</i> digestive system also found, but variable between specimens depending on digestion stage Gut contents ranging from 100 % full with 100 % comprised of <i>Echinocardium</i> to <5. In the emptiest <i>Charybdis</i> , only a few remnants of test of spines found in the pyloric stomach. Extremely common and a dominant contributor to gut fullness

knowledge of local species and their typical size ranges (Table 1) with the aid of image capture and analysis software (modified Epson Perfection V100 Photo scanner; Image J analysis software). Biomass could not be used as a measure of size, as organisms did not always remain intact during preservation processes. Data from the two paired cores collected per treatment were combined (summed) prior to statistical analysis to avoid pseudoreplication.

In year 2, cages were deployed to “bare” and “*Atrina*” sediments on three consecutive days. The principal focus was to increase the replication of the gut content data by maximising the total number of crabs used. High replication offset data gaps from crabs that were recovered with empty guts (defecated prior to recollection or did not feed). Available *Charybdis* were used each day based on the morning’s

trapping success and distributed evenly between bare and *Atrina* treatments. Twenty crabs were used on each of the first 2 days, and 14 on the third day. Individual crabs were not used more than once (frozen after collection) and cages were moved to new patches of sediment after every feeding episode. After the third day, sediment cores were collected inside and outside of eight empty “bare” cages (see previous methodology for macrofauna), utilising the unavailability of crabs as an opportunity to perform a “cage control” experiment.

Stomach content analysis technique

Crabs were defrosted, wet-weighed (g) and measured to the nearest mm (carapace width and length; chelae width, height and gape). The gastric mill of each crab

was dissected out under a compound microscope, the percent fullness of the stomach was estimated, whereupon the stomach contents were emptied into a petri dish for examination. Food items were identified based on key features (shell fragments, setae, jaws, appendages, skin, soft tissue; Table 2), and the amount of each food type was estimated as a percent relative to the total contents present in the dish. The proportional contribution of each food item to the diet of *Charybdis* was calculated using stomach fullness as a weighting factor, following the methods of Hines (1982).

Data analysis

Macrofaunal data

Two way analyses of variance (ANOVA, Type III Sums of Squares, fixed) were conducted using SAS 9.3 software to assess the influence of *Atrina*, *Charybdis* addition and *Atrina***Charybdis* interactions on the number of species (S), number of individuals (N), Margalef Species Richness (d), Pielou's evenness (j') and large individuals in the macrofauna community (calculated using PRIMER 6 software). Large individuals (Table 1) were observed from 15 different species across treatments and required log transformation prior to analysis to maintain normality of variance (Shapiro–Wilk, $W = 0.96$, $p = 0.15$). Generalised Linear Models with appropriate error structures (Poisson distribution, log link function) were used to compare individual species/taxa groups between habitats in the presence and absence of *Charybdis* using SAS 9.3 software.

Multivariate statistics (PRIMER 6) were used to compare the community composition of 'caged' and 'uncaged' controls from year 2. Macrofauna data (square root transformed, Bray-Curtis similarity) were analysed using One Way Analysis of Similarity (ANOSIM) with presence/absence of cages as a factor. Multi-Dimensional Scaling (MDS) plots of the data were created and SIMPER analysis used to identify species accounting for differences or similarities in community composition between treatments.

Crab stomach contents

Gut fullness percentage, wet-weight and carapace width for crabs in "bare" and "*Atrina*" treatments

were compared using median two sampled t test. The mean proportion of each of food category in the diet, p_i , was assessed using gut fullness as a weighting factor following Hines (1982),

$$p_i = \frac{\sum_{j=1}^n x_{ij}y_j}{\sum_{i=1}^k \sum_{j=1}^n x_{ij}y_j}$$

where x_{ij} was the proportion of the contents of the i th food category of the j th crab, and y_j was the fullness of the stomach of the j th crab.

Results

Assessment of potential caging artefacts

ANOSIM indicated no significant difference in community composition between caged and uncaged controls (Global R 0.076, Significance level 15.4 %). Multi-dimensional scaling plots (not shown) indicated a scattering of samples across ordination space with no sign of clumping according to treatment type. None of the species present in the sediments appeared to drive a high level of dissimilarity between the caged and uncaged controls (judging from the SIMPER analysis, highest species dissimilarity ~9 %). Unpaired t tests found similar numbers of the non-indigenous semelid bivalve *Theora lubrica* (Gould, 1861) ($p = 0.80$) and non-indigenous capitellid polychaete *Barantolla lepte* (Hutchings, 1974) ($p = 0.77$), the top two most abundant species at the site, in both caged and uncaged controls.

Crab behaviour

Charybdis explored the sediment surface around the internal perimeter of the cages for a short period of time after introduction. Once accustomed to the cages, crabs were observed feeding, processing material with their chelipeds and sometimes burrowing into the sediment. A few crabs were observed climbing the walls of the cages, but this was relatively rare and short-lived. Prior to removal from the cages, the majority of *Charybdis* specimens were found to be burrowed into the sediment with evidence of feeding events (broken shells, excavations) within the caged areas. Crabs extracted from the *Atrina* treatments were typically nestled close to the bivalve, rather than at the base of the cage walls.

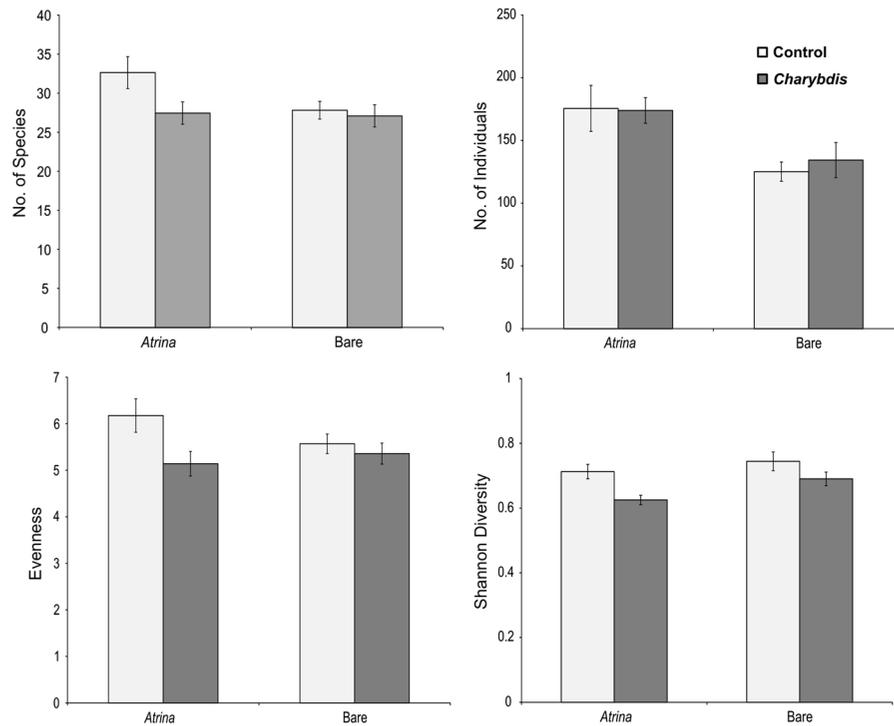


Fig. 2 The mean differences in univariate community measures, ($n = 11$) \pm standard error, between the different habitat types (bare sediment/presence of *Atrina*) and the addition of *Charybdis*

Community composition and diversity

In the 44 plots sampled with macrofaunal cores, 132 different taxa were identified. Sixty of the taxa were represented by fewer than 5 individuals summed across all cores, and 85 taxa were found in 8 or fewer plots (<20 %). Two non-indigenous species, *T. lubrica* and *B. lepte*, constituted 55 % of the total macrofaunal abundance. Both species are very small (typically <5 mm) and neither was found to be consumed by *C. japonica* (pers. obs. cf gut content results). Thus, while the number of individuals showed no response to *Charybdis* ($p = 0.774$), the number of individuals differed significantly in “bare” and “*Atrina*” sediments ($p = 0.002$), with higher numbers in the presence of *Atrina* (Fig. 2). There was a trend of higher taxonomic richness next to *Atrina*, and fewer taxa in the presence of *Charybdis* (Fig. 2), although both factors were only marginally significant at $p \leq 0.10$ (overall ANOVA $p = 0.049$; Table 3). Shannon diversity was unaffected by *Atrina* ($p = 0.475$), but reduced in the presence of *Charybdis* ($p = 0.027$), with an overall ANOVA model p value

of 0.059 (Fig. 2, Table 3). There was greater evenness in the distribution of macrofaunal individuals across taxa in the presence of *Atrina* and in the absence of *Charybdis*, with both factors and the overall ANOVA model significant at $\alpha = 0.05$ (Fig. 2, Table 3).

Specific species impacts

The burrowing spatangoid urchin, *Echinocardium cordatum* (Pennant, 1777) was three times more common in the bare sediment than in the presence of *Atrina*, and was reduced in the presence of *Charybdis* both with and without *Atrina* present (Table 4; Fig. 3). The non-indigenous file shell *Limaria orientalis* (Adam and Reeve, 1850) was rare in bare sediment but occurred commonly near to *Atrina*. In the presence of *Atrina*, *Charybdis* reduced *Limaria* from an average of >2.5 individuals/0.016 m⁻² to <0.25 individuals/0.016 m⁻² (a tenfold decrease; Fig. 3, Table 4). For the complex of native crabs (*Halicarcinus cookii*, *Halicarcinus whitei*, *Hemiplax hirtipes*, *Notomithrax minor*, *Paguristes* sp. and *Pagurus* sp.), abundances were twice as high in the presence of *Atrina* as

Table 3 Two-way ANOVA model output of univariate indices

Source	DF	Sum of squares	Mean square	F value	p value
No. of species					
Overall model	3	224.43	74.81	2.86	0.049
<i>Atrina</i>	1	73.84	73.84	2.82	0.101
<i>Charybdis</i>	<i>1</i>	<i>96.02</i>	<i>96.02</i>	<i>3.67</i>	<i>0.063</i>
<i>Atrina</i> × <i>Charybdis</i>	1	54.57	54.57	2.08	0.157
No. of individuals					
Overall model	3	22,762.64	7,587.55	3.97	0.014
<i>Atrina</i>	1	22,275.00	22,275.00	11.65	0.002
<i>Charybdis</i>	1	160.36	160.36	0.08	0.774
<i>Atrina</i> × <i>Charybdis</i>	1	327.27	327.27	0.17	0.681
Shannon diversity					
Overall model	3	6.54	2.18	2.70	0.059
<i>Atrina</i>	1	0.42	0.42	0.52	0.475
<i>Charybdis</i>	1	4.26	4.26	5.27	0.027
<i>Atrina</i> × <i>Charybdis</i>	1	1.86	1.86	2.30	0.137
Evenness					
Overall model	3	0.08	0.03	5.13	0.004
<i>Atrina</i>	1	0.03	0.03	4.69	0.036
<i>Charybdis</i>	1	0.06	0.06	10.13	0.003
<i>Atrina</i> × <i>Charybdis</i>	1	0.01	0.01	0.55	0.461

Factors are *Atrina* (present or absent i.e. “bare”) and *Charybdis* (addition or not). $p < 0.05$ indicated in bold. $p > 0.05$ but < 0.1 indicated in italics. *DF* = degrees of freedom

compared to bare sediment. Moreover, in the cages that contained both *Atrina* and *Charybdis*, there was a trend of fewer native crabs (a 45 % decline on average; $p = 0.08$; Table 4). There was no apparent effect of *Charybdis* on native crabs in the bare sediments (Fig. 4). Overall the clearest impact of *Charybdis* was collectively on large macrofauna (Table 5), calculated as the sum of individuals from taxa including gastropods (e.g. *Bulla quoyii*, *Amalda novaezelandiae*), polychaetes (e.g. *Terebellidae*, *Aglaophamus macro-ura*) and Shrimp (*Alpheus novaezealandiae*) in addition to the aforementioned crabs, bivalves and echinoderms. The bare sediment had approximately half the number of large individuals relative to the *Atrina* sediments. The addition of *Charybdis* had a relatively comparable effect in the bare sediments and next to *Atrina*; reducing the number of large individuals present by ~50 % (Fig. 4; Table 5).

Charybdis stomach contents

In year 1, 22 *Charybdis* were recovered for prey identification but 10 had empty guts and only 4 had

guts with >30 % fullness. In year 2, 53 *Charybdis* were recovered with 16 having empty guts and 17 with guts >30 % fullness. Across the 2 years, there were 21 crabs from which to assess diet, 10 from the bare sediment and 11 from cages with *Atrina*. Due to the low occurrence of full stomachs, data from crabs in bare and *Atrina* sediments were pooled to provide a generalised assessment of diet and trophic impacts of *Charybdis*. There was no difference in average gut fullness for crabs feeding in bare sediments versus *Atrina* cages, indicating that feeding rates were likely comparable. Across all *Charybdis* specimens including those with empty guts, there was no difference in the mean wet-weight (t value -1.18 , $p = 0.24$) or the mean carapace width (t value -1.15 , $p = 0.25$) of crabs introduced to bare and *Atrina* sediments. Across both years and treatments the mean wet-weight of *Charybdis* specimens was 71.9 g and the carapace width 70.5 mm (ranging from 56 to 82 mm).

In *Charybdis* stomachs that were >30 % full, 8 different taxa were recorded as prey items. The dominant prey in terms of both frequency and proportion was *E. cordatum* (Fig. 5). Despite *Echinocardium*

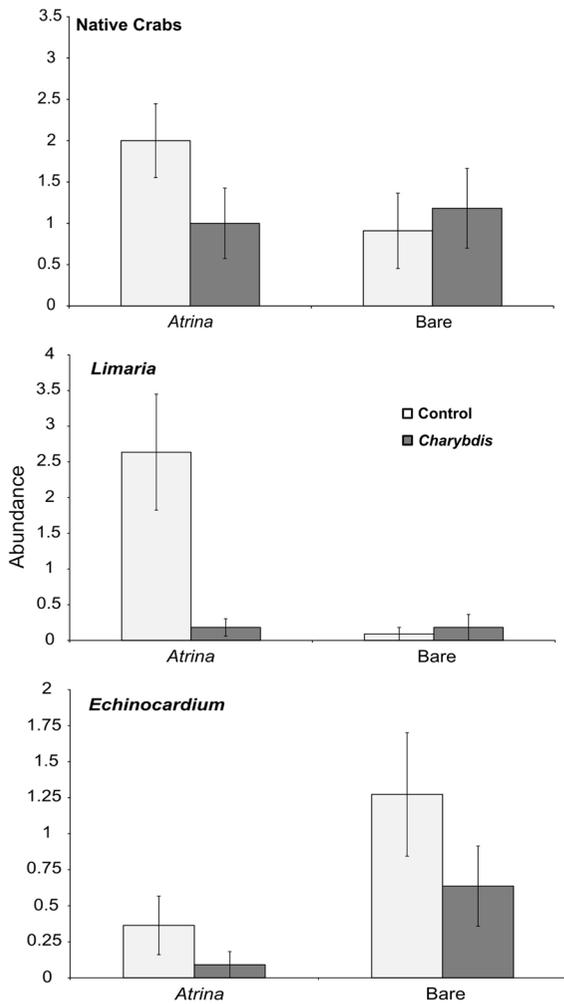


Fig. 3 The mean differences, ($n = 11$) \pm standard error, between habitat types (bare sediment/presence of *Atrina*) and the addition of *Charybdis* for specific taxa. Abundance of each taxa is the sum of individuals counted from the two sediment cores collected from each replicate

being more abundant in bare sediments, it was still found in 6 of the 11 *Charybdis* from cages with *Atrina*. Across both types of cages, *Echinocardium*, *Limaria* and native crab species constituted 85 % of the prey when using stomach fullness as a weighting factor (Fig. 6). The proportion fullness and frequency of occurrence showed similar patterns.

Discussion

More than a decade after the establishment of the *C. japonica* in New Zealand, there is very little

information on the crab's feeding habits and its patterns of resource use. This limits our understanding of the risk posed by the invader and the consequences for ecological and economic impacts. Although the present study was simple and limited to cages (see Virnstein 1978; Hall et al. 1990; Fernandes et al. 1999 for reviews of the positive and negative aspects of caging studies), it provided the first fundamental information on the types of prey being targeted by *Charybdis* in New Zealand and how its feeding varied in the presence and absence of a key native species, the structure-forming bivalve *A. zelandica*. We observed *Charybdis* feeding in the sediment and found broken shells atop the surface where the crabs had been caged. Reductions in the abundance of several macrofauna species from sediments exposed to *Charybdis* (Figs. 3, 4), coupled with occurrences of the same macrofaunal species in *Charybdis* stomachs, was unequivocal evidence of feeding. Based on the types of prey disappearing from cages and appearing in crab guts, some guarded inferences can be made about the prey being targeted and potentially at risk from increases in abundance or range expansion of *Charybdis*. We are not over interpreting the cage data by attempting to quantify per capita feeding rates or magnitudes of impact on populations of prey. We readily acknowledge that the inclusion of predators with large daily foraging ranges relative to cage size can amplify feeding impacts. Alternatively, the normal feeding patterns of the crabs may have been interrupted inside the cages, with crabs spending less time feeding and more time trying to escape. Given the large number of crabs with empty guts, we think that the probability of the latter was greater than the former. Nevertheless, the experiment provided a wealth of useful information and accomplished the goal of observing the dietary choices of crabs feeding on an undisturbed natural assemblage of benthic macrofaunal prey in situ.

Portunid crabs have been reported to select prey based on criteria such as the size and strength of the prey's calcified shell relative to their own size and shell crushing capabilities (Elner and Hughes 1978; Seed and Hughes 1995). It is advantageous for the predators to maximise energy intake whilst minimising prey handling time and the risk of damage to their chelae (MacArthur and Pianka 1966). Thus, the apparent targeting of large macrofaunal species by *Charybdis* (*Echinocardium*, *Limaria* & native brachyuran and

Table 4 (a) Overall significance of GLM models (Poisson distribution, log link function) for *Echinocardium*, *Limaria* and native crabs. (b) Significance of factors from the GLM models

for specific species for the presence or absence of *Charybdis* in sediments with or without *Atrina* (Wald Chi square statistics and *p* values)

		Analysis of deviance				
		Source	DF	Deviance	Deviance/DF	<i>p</i> value
<i>(a)</i>						
<i>Echinocardium</i>	Model		3	14.9	5	0.002
<i>Limaria</i>	Model		3	55.3	18.4	<0.001
Native crabs	Model		3	9.6	3.2	0.022
		Source		Chi square		<i>p</i> value
<i>(b)</i>						
<i>Echinocardium</i>	<i>Atrina</i>			10.6		0.001
	<i>Charybdis</i>			3.9		0.047
	<i>Atrina</i> × <i>Charybdis</i>			0.4		0.550
<i>Limaria</i>	<i>Atrina</i>			26.8		<0.001
	<i>Charybdis</i>			22.5		<0.001
	<i>Atrina</i> × <i>Charybdis</i>			6.0		0.015
Native crabs	<i>Atrina</i>			4.0		0.046
	<i>Charybdis</i>			3.0		0.084
	<i>Atrina</i> × <i>Charybdis</i>			2.6		0.104

DF = degrees of freedom

p < 0.05 indicated in bold. *p* > 0.05 but <0.1 indicated in italics

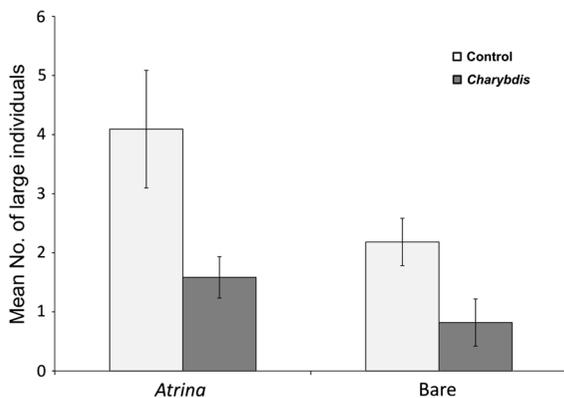


Fig. 4 Differences between habitat types and the addition of *Charybdis* on large species (see Table 1 for the size ranges or large species)

anomuran crabs) makes intuitive sense given its large and powerful chelae (Jiang et al. 1998). *Echinocardium* may not have a high caloric value (Thorson 1957 from Godfriaux 1969), but it is large, relatively abundant, has a very fragile test and does not burrow deeply into the sediment (Buchanan 1966; Nakamura 2001). *Limaria* is

a large fleshy bivalve that sits exposed on the sediment surface, with its body tissues permanently protruding from the valves of its shell (Morton 1979). The native crab species being targeted only grow to about the size of a large male *Charybdis* claw and feed on material at the sediment surface. Thus, populations of these types of prey would appear to be the most vulnerable to increases in the abundance and range of *Charybdis*. Although there were other types of macrofauna in the sediments that were far more abundant than the aforementioned species (e.g., *B. lepte*, *T. lubrica*), it is likely that they were ignored by *Charybdis* because the energetic costs of extracting and handling the small infauna outweighed the energetic gains of consuming them. This would explain the lack of impact of *Charybdis* on the total number of individuals, but the significant impact on the larger individuals.

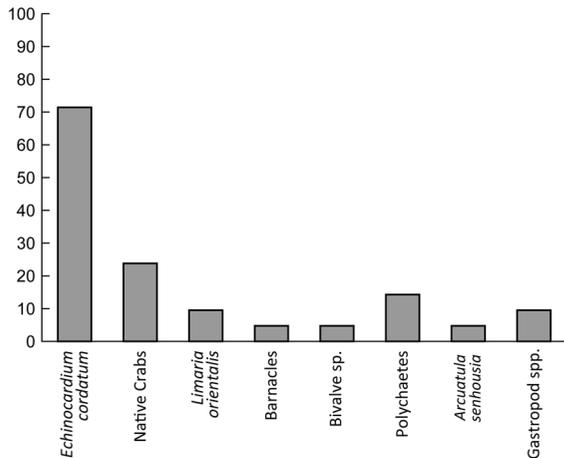
We hypothesised that the presence of *Charybdis* would reduce the known positive influences of *Atrina* on the abundance and richness of macrofauna (Norkko et al. 2001, 2006; Hewitt et al. 2002; Lohrer et al. 2013) which our findings supported: Firstly, in the absence of *Charybdis* the results confirmed *Atrina* to

Table 5 Two-way ANOVA model output of log abundances of large species

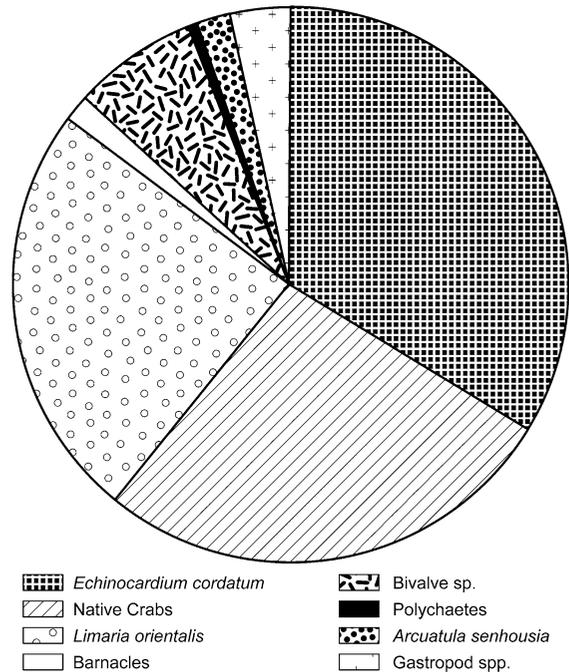
Source	DF	Sum of squares	Mean square	F value	<i>p</i> value
Two way					
Large species					
Overall model	3	1.29	0.43	8.38	0.0002
<i>Atrina</i>	1	0.33	0.33	6.41	0.0154
<i>Charybdis</i>	1	0.96	0.96	18.69	<.0001
<i>Atrina</i> × <i>Charybdis</i>	1	0.002	0.002	0.04	0.8521

DF degrees of freedom

Factors are *Atrina* (present or absent i.e. “bare”) and *Charybdis* (addition or not). *p* < 0.05 indicated in bold

**Fig. 5** Percentage frequency of occurrence of prey items in the diet

have a positive impact on the benthos, with a higher total number of species and individuals next to *Atrina* relative to bare sediment (Figs. 2, 3; Table 3). For the large species, *Atrina* had a positive influence with twice the number compared to bare sediment ($p = 0.015$). The addition of *Charybdis* caused a proportional reduction in both treatment types for large species; however the greatest net loss occurred when *Charybdis* were introduced into cages containing *Atrina* (dropping from average of 4.09–1.58 large organisms, Fig. 4). For some community metrics (e.g., evenness), individual species (e.g., *Limaria*) and groups of species (e.g., native crabs), losses associated with the presence of *Charybdis* were more pronounced next to *Atrina*. In short, *Charybdis* is capable of altering ecological interactions and interfering with processes such as the facilitation of macroinfauna by key native species.

**Fig. 6** Mean proportion of a prey items in the diet, with gut fullness as a weighting factor

Contemporary research appears to indicate the existence of a positive relationship between biodiversity (e.g., taxonomic richness) and ecosystem functioning (Loreau et al. 2002). However, not all species in an assemblage make equal contributions to functioning, just as not all species are equally susceptible to impacts from invasive predators. Potentially large impacts on ecosystem functioning could occur if the species that are most susceptible to invasive predators also happen to make the greatest contributions to ecosystem functioning. Based on our results and our

understanding of the *C. japonica* invasion in New Zealand, this set of circumstances could be applicable. Our research indicates that *Charybdis* feeds on at least one functionally important marine benthic species in New Zealand, *E. cordatum* (Lohrer et al. 2004, 2008a, b, 2013), and perhaps others (e.g., native crabs; Needham et al. 2011). *Echinocardium* plays a critical role in benthic communities by burrowing through and mixing sediment, which enhances pore water and solute (e.g., inorganic nutrient) exchange with overlying waters. The level of bioturbation can be such that in shallow euphotic areas, greater rates of benthic photosynthesis and more microalgae are found in patches with high densities of urchins, despite their grazing (Lohrer et al. 2004). Bioturbation by *Echinocardium* also plays a role in deterring invasive colonists by destabilising surface sediments (Rhoads and Young 1970). For example, increased rates of biogenic disturbance by *Echinocardium* have been shown to be negatively correlated with the invasion success of two invaders, *T. lubrica* and the gobiid fish *Acentrogobius pflaumi* (Bleeker, 1853) (Lohrer et al. 2008a, 2008b, 2013). Thus, reductions in the abundance of *Echinocardium* through *Charybdis* predation may influence soft-sediment community dynamics in New Zealand harbours and estuaries and their susceptibility to further non-indigenous species impacts. Community dynamics appear to be complex, as *Charybdis* also consumes invasive species such as *Limaria* and *Arcuatula (Musculista) senhousia*. However, given the negative influence of *Echinocardium* on *Theora*, the negative effect of *Charybdis* on *Echinocardium*, and no apparent impact of *Charybdis* on *Theora*, it is likely that *Charybdis* will have an indirect positive effect on *Theora*. Community composition in our system is heavily influenced by non-indigenous species. However, with the exception of *Limaria*, the results suggest a larger impact on native species. This highlights concerns about interactions among alien species and emergence of cascading impacts and invasional meltdown (Simberloff and Von Holle 1999; Simberloff 2006; Simberloff et al. 2013).

In assessing the impacts of *Charybdis*, consideration must be given not only to the prey species but to potential native competitors and functionally analogous species. The native species most similar to *Charybdis* is the large portunid crab *O. catharus*. Although *O. catharus* are found predominantly in different habitats (off wave exposed sandy beaches),

there may be some overlap and interaction within estuaries. *Ovalipes* is versatile opportunistic feeder, consuming a wide variety of items including plant material, benthic invertebrates, fish and bivalves. Selection of prey for *Ovalipes* is related to the size of crab specimens (Davidson 1986). As *Ovalipes* can grow to a large size (up to 140 mm carapace width), it may target larger prey items much like *Charybdis*. Further information is needed to evaluate the effects of *Charybdis* and other invasive species on the valuable goods and services provided by New Zealand's marine ecosystems, as the effects of invasions like *Charybdis* have the potential to cascade through the ecosystem and interact with the effects of other stressors, including other non-indigenous species.

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References

- Ahyong ST, Wilkens SL (2011) Aliens in the antipodes: non-indigenous marine crustaceans of New Zealand and Australia. In: Galil BS, Clark PF, Carlton JT (eds) In the wrong place—alien marine crustaceans: distribution, biology and impacts. Invading nature—Springer series in invasion ecology 6:451–485
- Brazao SAE, Silva ACF, Boaventura DM (2009) Predation: a regulating force of intertidal assemblages on the central Portuguese coast? J Mar Biol Assoc UK 89:1541–1548
- Buchanan JB (1966) The biology of *Echinocardium cordatum* [Echinodermata: Spatangoidae] from different habitats. J Mar Biol Assoc UK 46:97–114
- Callaway RM, Aschehoug ET (2000) Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. Science 290:2075
- Carlton JT, Geller JB (1993) Ecological roulette: the global transport of nonindigenous marine organisms. Science 261:78–82
- Choy SC (1986) Natural diet and feeding habits of the crabs *Liocarcinus puber* and *L. holsatus* (Decapoda, Brachyura, Portunidae). Mar Ecol Prog Ser 31:87–99
- Cohen AN, Carlton JT (1998) Accelerating invasion rate in a highly invaded estuary. Science 279:555–558

- Cohen AN, Carlton JT, Fountain MC (1995) Introduction, dispersal and potential impacts of the green crab *Carcinus maenas* in San-Francisco Bay, California. *Mar Biol* 122:225–237
- Cranfield HJ, Gordon DP, Willan RC et al (1998) Adventive marine species in New Zealand. NIWA Technical Report 34, p 48. <http://docs.niwa.co.nz/library/public/NIWAtr34.pdf>
- Davidson, RJ (1986) Natural food and predatory activity of the paddle crab *Ovalipes*. MSc Thesis, University of Canterbury Christchurch. http://ir.canterbury.ac.nz/bitstream/10092/6681/1/davidson_thesis.pdf
- Dineen JF, Clark PF, Hines AH et al (2001) Life history, larval description, and natural history of *Charybdis hellerii* (Decapoda, Brachyura, Portunidae), an invasive crab in the western Atlantic. *J Crustacean Biol* 21:774–805
- Elner RW, Hughes RN (1978) Energy maximization in the diet of the shore crab, *Carcinus maenas*. *J Anim Ecol* 47:103–116
- Essink K, Dekker R (2002) General patterns in invasion ecology tested in the Dutch Wadden Sea: the case of a brackish-marine polychaetous worm. *Biol Invasions* 4:359–368
- Fernandes TF, Huxham M, Piper SR (1999) Predator caging experiments: a test of the importance of scale. *J Exp Mar Biol Ecol* 241:137–154
- Fowler AE, Gerner NV, Sewell MA (2011) Temperature and salinity tolerances of Stage 1 zoeae predict possible range expansion of an introduced portunid crab, *Charybdis japonica*, in New Zealand. *Biol Invasions* 13:691–699
- Froggia D (2012) First record of *Charybdis japonica* (Crustacea: Decapoda: Portunidae) in the Mediterranean Sea. *Mar Biodivers Rec* 5:0-3
- Galil BS (2000) A sea under siege—alien species in the Mediterranean. *Biol Invasions* 2:177–186
- Godfriaux BL (1969) Food of predatory demersal fish in Hauraki Gulf. *N Z J Mar Freshw Res* 3:518–544
- Gurevitch J, Padilla DK (2004) Are invasive species a major cause of extinctions? *Trends Ecol Evol* 19:470–474
- Gust N, Inglis GJ (2006) Adaptive multi-scale sampling to determine an invasive crab's habitat usage and range in New Zealand. *Biol Invasions* 8:339–353
- Hall SJ, Raffaelli D, Robertson MR et al (1990) The role of the predatory crab, *Liocarcinus depurator*, in a marine food web. *J Anim Ecol* 59:421–438
- Hayward BW (1997) Introduced marine organisms in New Zealand and their impact in the Waitemata Harbour, Auckland. *Tane* 36:197–223
- Hayward BW, Stephenson AB, Morley M et al (1997) Faunal changes in Waitemata Harbour sediments, 1930s–1990s. *J R Soc N Z* 27:1–20
- Hewitt JE, Thrush SF, Legendre P et al (2002) Integrating heterogeneity across spatial scales: interactions between *Atrina zelandica* and benthic macrofauna. *Mar Ecol Prog Ser* 239:115–128
- Hidalgo FJ, Baron PJ, Orensanz JM (2005) A prediction come true: the green crab invades the Patagonian coast. *Biol Invasions* 7:547–552
- Hines AH (1982) Coexistence in a kelp forest: size population dynamics and resource partitioning in a guild of spider crabs (Brachyura, Majidae). *Ecol Monogr* 52:17–198
- Hollebone AL, Hay ME (2008) An invasive crab alters interaction webs in a marine community. *Biol Invasions* 10:347–358
- Inglis G, Gust N, Fitridge I, Floerl O, Hayden BJ, Fenwick G (2005a) Port of Auckland: baseline survey for non-indigenous marine species. Biosecurity New Zealand Technical Paper No: 2005/08: 58. <http://www.biosecurity.govt.nz/files/pests/salt-freshwater/2005-08-port-of-auckland.pdf>
- Inglis GJ, Gust N, Fitridge I et al (2005b) Gulf Harbour Marina: baseline survey for non-indigenous marine species. Biosecurity New Zealand Technical Paper 2005/12. <http://maxa.maf.govt.nz/mafnet/publications/biosecurity-technical-papers/2005-12-gulf-harbour-marina.pdf>
- Jiang W, Meng T, Chen R et al (1998) Diet of *Charybdis japonica* (A. Milne-Edwards) and *Portunus trituberculatus* (Miers) in the Bohai Sea. *Mar Fish Res* 19:53–59
- Kennish MJ (1997) Pollution impacts on marine biotic communities. CRC Press, Boca Raton
- Kim KB (2001) Growth and Reproduction of *Charybdis japonica* (A. Milne-Edwards) (Decapoda: Portunidae) in Korean Waters, Ph.D. Thesis, Department of Marine Biology, Graduate School, Pukyong National University, Pusan (in Korean)
- King RB, Ray JM, Stanford KM (2006) Gorging on gobies: beneficial effects of alien prey on a threatened vertebrate. *Can J Zool* 84:108–115
- Kolpakov NV, Kolpakov EV (2011) On the biology of the Japanese Swimming Crab *Charybdis japonica* (Portunidae) in waters of primorye at the northern boundary of their range. *Russ J Mar Biol* 37(7):570–578
- le Roux PJ, Branch GM, Joska MAP (1990) On the distribution, diet and possible impact of the invasive European shore crab *Carcinus maenas* (L.) along the South African coast. *S Afr J Mar Sci* 9(1):85–93
- Lemaitre R (1995) *Charybdis hellerii* (Milne Edwards, 1867), a nonindigenous portunid crab (Crustacea: Decapoda: Brachyura) discovered in the Indian River lagoon system of Florida. *Proc Biol Soc Wash* 108:643–648
- Lohrer AM, Whitlatch RB (2002) Interactions among aliens: apparent replacement of one exotic species by another. *Ecology* 83:719–732
- Lohrer AM, Thrush SF, Gibbs MM (2004) Bioturbators enhance ecosystem function through complex biogeochemical interactions. *Nature* 431:1092–1095
- Lohrer AM, Chiaroni LD, Hewitt JE et al (2008a) Biogenic disturbance determines invasion success in a subtidal soft-sediment system. *Ecology* 89:1299–1307
- Lohrer AM, Chiaroni LD, Hewitt JE et al (2008b) Isolated and interactive effects of two key species on ecosystem function and trophic linkages in New Zealand soft-sediment habitats. NZ Aquatic Environment and Biodiversity Report for the Ministry of Fisheries (Project ZBD200419). NIWA Report number HAM2008-106. <http://docs.niwa.co.nz/library/public/NZAEBR44.pdf>
- Lohrer AM, Rodil IF, Townsend M et al (2013) Biogenic habitat facilitation influence facilitation in a marine soft-sediment ecosystem. *Ecology* 94:136–145
- Loreau M, Naeem S, Inchausti P (2002) Biodiversity and ecosystem functioning: synthesis and perspectives. Oxford University Press, Oxford
- MacArthur RH, Pianka ER (1966) On optimal use of a patchy environment. *Am Nat* 100:603–609

- Mantelatto FLM, Garcia RB (2001) Biological aspects of the nonindigenous portunid crab *Charybdis hellerii* in the western tropical south Atlantic. *Bull Mar Sci* 68:469–477
- McMillen-Jackson AL (2008) First record of the Indo-Pacific swimming crab, *Charybdis hellerii* (A. Milne-Edwards, 1867) in the Gulf of Mexico. *Crustac Int J Crustac Res* 81:889–894
- Miron G, Audet D, Landry T et al (2005) Predation potential of the invasive green crab (*Carcinus maenas*) and other common predators on commercial bivalve species found on Prince Edward Island. *J Shellfish Res* 24:579–586
- Morton B (1979) A comparison of lip structure and function correlated with other aspects of the functional morphology of Lima lima, *Limaria* (Platilimaria) *fragilis*, and *Limaria* (Platilimaria) *hongkongensis* sp.nov. (Bivalvia: Limacea). *Can J Zool* 57:728–742
- Nakamura Y (2001) Autoecology of the heart urchin, *Echinocardium cordatum*, in the muddy sediment of the Seto Inland Sea, Japan. *J Mar Biol Assoc UK* 81:289–297
- Needham HR, Pilditch CA, Lohrer AM et al (2011) Context-specific bioturbation mediates changes to ecosystem functioning. *Ecosystems* 14:1096–1109
- Norkko A, Hewitt JE, Thrush SF et al (2001) Benthic-pelagic coupling and suspension-feeding bivalves: linking site-specific sediment flux and biodeposition to benthic community structure. *Limnol Oceanogr* 46:2067–2072
- Norkko A, Hewitt JE, Thrush SF et al (2006) Conditional outcomes of facilitation by a habitat-modifying subtidal bivalve. *Ecology* 87:226–234
- Rhoads DC, Young DK (1970) The influence of deposit-feeding organisms on sediment stability and community trophic structure. *J Mar Res* 28:150–178
- Ricciardi A, Rasmussen JB (1998) Predicting the identity and impact of future biological invaders: a priority for aquatic resource management. *Can J Fish Aquat Sci* 55:1759–1765
- Ruiz GM, Carlton JT, Grosholz ED et al (1997) Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extent, and consequences. *Am Zool* 37:621–632
- Sanders NJ, Gotelli NJ, Heller NE et al (2003) Community disassembly by an invasive species. *Proc Nat Acad Sci USA* 100:2474–2477
- Sant’Anna BS, Watanabe TT, Turra A et al (2012a) Relative abundance and population biology of the non-indigenous crab *Charybdis hellerii* (Crustacea: Brachyura: Portunidae) in a southwestern Atlantic estuary-bay complex. *Aquat Invasions* 7:347–356
- Sant’Anna BS, Watanabe TT, Turra A et al (2012b) First record of the non-indigenous portunid crab *Charybdis variegata* from the western Atlantic coast. *BioInvasions Rec* 1:11–16
- Seed R, Hughes RN (1995) Criteria for prey size-selection in molluscivorous crabs with contrasting claw morphologies. *J Exp Mar Biol Ecol* 193:177–195
- Simberloff D (2006) Invasional meltdown 6 years later: important phenomenon, unfortunate metaphor, or both? *Ecol Lett* 9(8):912–919
- Simberloff D, Von Holle B (1999) Positive interactions of nonindigenous species: invasional meltdown? *Biol Invasions* 1(1):21–32
- Simberloff D, Martin JL, Genovesi P et al (2013) Impacts of biological invasions: what’s what and the way forward. *Trends Ecol Evol* 28(1):58–66
- Smith PJ, Webber WR, McVeagh SM et al (2003) DNA and morphological identification of an invasive swimming crab, *Charybdis japonica*, in New Zealand waters. *N Z J Mar Freshw Res* 37:753–762
- Sudo H, Kajihara N, Fujii T (2008) Predation by the swimming crab *Charybdis japonica* and piscivorous fishes: a major mortality factor in hatchery-reared juvenile Japanese flounder *Paralichthys olivaceus* released in Mano Bay, Sado Island, Japan. *Fish Res* 89:49–56
- Tavares M, Amouroux JM (2003) First record of the non-indigenous crab, *Charybdis hellerii* (A. Milne-Edwards, 1867) from French Guyana (Decapoda, Brachyura, Portunidae). *Crustac Int J Crustac Res* 76:625–630
- Thorson G (1957) Bottom communities. In: Hedgpeth JW (ed) *Treatise on marine ecology and paleoecology*, Ch. 17 (vol 1). *Ecology. Mem Geol Soc Am* 67:461–534
- Townsend M, Marshall BA, Greenfield BL (2010) First records of the Australian dog whelk, *Nassarius* (Plicarcularia) *burchardi* (Dunker in Philippi, 1849) (Mollusca: Gastropoda) from New Zealand. *N Z J Mar Freshw Res* 44:343–348
- Virnstein RW (1978) Predator caging experiments in soft sediment: caution advised. In: Wiley ML (ed) *Estuarine interactions*. Academic Press, New York, pp 261–273
- Vitousek PM, Dantonio CM, Loope LL et al (1996) Biological invasions as global environmental change. *Am Sci* 84:468–478
- Wear RG, Haddon M (1987) Natural diet of the crab *Ovalipes catharus* (Crustacea, Portunidae) around central and northern New Zealand. *Mar Ecol Prog Ser* 35:39–49
- Webber R (2001) Space invaders, crabs that turn up in New Zealand unannounced. *Seaf N Z* 9:80–84