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PREDICTING THE IMPACT OF INTRODUCED MARINE SPECIES: LESSONS FROM THE MULTIPLE INVASIONS OF THE EUROPEAN GREEN CRAB *Carcinus maenas*

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Abstract

We compared ecological characteristics of three spatially independent invasions of the European green crab Carcinus maenas *to determine which characteristics were most consistent across invasions, and hence would be most predictable in future invasions. For invasions in western North America (WNA), eastern North America (ENA), and South Africa (SAF), we compared five characteristics: (1) habitat usage, (2) diet preferences, (3) size of individuals, (4) rate of range expansion, and (5) demonstrated and potential impacts. We found that two characteristics, diet preference and ecological impact were relatively similar across the three invasions. Diet preference was particularly consistent with the rank order of taxa being virtually identical at the three sites. In contrast, habitat usage, individual size, and rate of range expansion were more variable. Differences in habitat usage and size were particularly evident in the WNA invasion, where* C. maenas *have failed to colonize protected and exposed rocky shores used elsewhere and have grown much larger than at other sites. We suggest that the degree of similarity of these characteristics across invasions provides a valuable measure of how predictable they will be in future invasions. Copyright © 1996 Elsevier Science Limited*

Keywords: body size, *Carcinus maenas*, diet preference, ecological impact, green crabs, habitat usage, invasions, rate of spread.

INTRODUCTION

As species worldwide are being moved beyond their normal range due to human activities, biologists from a wide range of disciplines are attempting to assess the consequences of exotic species on native biotas. The few guidelines we have to predict the impact of introduced species come from studies of alien species in terrestrial and freshwater systems (Mooney & Drake, 1986; Mooney *et al.*, 1986; Groves & di Castri, 1992). The recent identification of large numbers of exotic marine species has brought about a new urgency to identify potential impacts in this habitat (Carlton, 1989; Carlton & Geller, 1993), although attempts to quantify the impact of introduced species in marine systems are extremely rare (Brenchley & Carlton, 1983; Allmon & Sebens, 1988; Lambert *et al.*, 1992; Grosholz & Ruiz, 1995). Instead, studies of marine invasions are usually inferential and rarely combine extensive descriptive data and quantitative or experimental results, providing a poor knowledge and low predictive power of the impact of introduced species. Nonetheless, the ability to predict which species will have severe impacts is not only essential for a fundamental understanding of the structure and function of communities and ecosystems, but should help focus already limited resources on management and control efforts of exotic species.

Perhaps one of the most instructive approaches to developing predictions about the impact of marine invasions is to compare multiple, spatially independent invasions of the same species in different communities. This approach allows us to test the repeatability, and hence predictability, of invasion characteristics for the same species across the different biotic and abiotic contexts in which it has been introduced. Ideally, we could make these comparisons for many of the species which have invaded multiple, disjunct communities around the world to determine whether characters such as diet breadth or habitat utilization are easily predicted for individual marine species or taxonomic groups.

Although multiple, spatially independent invasions have occurred for many marine species (Table 1), the quantitative data needed to make such comparisons of

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Table 1. Examples of marine species introduced from one source region to multiple recipient regions throughout the world

Taxon	Source region:	Recipient region (References)
Annelida		
Ficopomatus enigmaticus	SWP:	MED,HAW,NEA,NEP,NWA,SWA[1,2,3]
Coelenorata		
Anthozoa		
Haliplannella luciae	NWP:	MED,NEA,NEP,NWA[2,4,5]
Hydrozoa		
Cordylophora caspia	CAS:	AUST,BALT,MED,NEA,NEP,NWA[2,6,7]
Cordata		
Urochordata		
Molgula manhattensis	NWA:	AUST,NEP,NWP[2,8,9]
Styella clava	NWP:	AUST,NEA,NEP,NWA[2,4,8]
Vertebrata		
Acanthogobius flavimanus	NWP:	AUST,NEP[10]
Tridentiger trigonocephalus	NWP:	AUST,NEP[10]
Crustacea		
Cirripedia		
Balanus improvisus	NWA:	AUST,BALT,NEP,NWP[6,8,9]
Copepoda		
Mytilicola orientalis	NWP:	MED,NEA,NEP[5,11]
Oithona davisae	NWP:	NEP,SEP[12]
Pseudodiaptomus marinus	NWP:	HAW,NEP,IO[10,12]
Decapoda		
Carcinus maenas	NEA:	AUST,NEP,NWA,SAFR[13]
Eirorchier sinensis	NWP:	BALT,MED,NEP[5,6,14]
Palaemon macrodactylus	NWP:	AUST,NEP[2,8]
Rhithropanopeus harrisii	NWA:	BALT,CAS,MED,NEA,NEP[4,6,10,15]
Isopoda		
Sphaeroma walkeri	IO:	AUST,HAW,MED,NEP,NWP,SAFR[16]
Mollusca		
Bivalvia		
Musculista senhousia	SWP:	AUST,MED,NEP,NWA[1,5,8,17]
Mya arenaria	NWA:	BALT,NEP[4,6]
Gastropoda		
Crepidula fornicata	NWA:	MED,NEA,NEP[1,17]

AUST, Australia; BALT, Baltic Sea; CAS, Caspian Sea; HAW, Hawaii; IO, Indian Ocean; MED, Mediterranean; NEA, Northeast Atlantic; NEP, Northeast Pacific; NWA, Northwest Atlantic; NWP, Northwest Pacific; SAFR, South Africa; SWP, Southwest Pacific. References: [1]Zibrowius (1994), [2]Carlton (1979), [3]Hoagland & Turner (1980), [4]Carlton (1989), [5]Boudouresque (1994), [6]Leppakoski (1994), [7]Roch (1924), [8]Pollard & Hutchings (1990), [9]Asakura (1992), [10]Carlton (1985), [11]Lauckner (1983), [12]Carlton & Geller (1993), [13]Cohen *et al.* (1995), [14]Carlton & Cohen (1995), [15]Por (1978), [16]Carlton & Iverson (1981), [17]Carlton (1992).

invasion characteristics across communities are simply not available. However, for at least one species, the European green crab *Carcinus maenas* (Decapoda: Portunidae), there are sufficient qualitative data from three independent invasions to examine which characteristics of invading green crab populations were most repeatable, and, therefore, most predictable for future invasions. Thus, we used the green crab as a model system to explore the value of this approach.

The green crab is native to the Atlantic, Baltic, and North Sea coasts of Europe from Norway to Mauritania (Almaca, 1962; Christiansen, 1969; Manning & Holthuis, 1981; Williams, 1984; Cohen *et al.*, 1995; Carlton, this issue), but has growing populations in several sites around the world including eastern North America (Dow & Wallace, 1952; Scattergood, 1952; Glude, 1955; Ropes, 1968), western North America (Cohen *et al.*, 1995; Grosholz & Ruiz, 1995; Carlton, this issue), South Africa (Le Roux *et al.*, 1990, Griffiths *et al.*, 1992), and Australia (Zeidler, 1978). In particular, the studies from eastern and western North America as well as South Africa are detailed enough to allow comparisons of these independent invasions.

Our analysis of these invasions compared the following five characteristics for which data were sufficient for all three invasions as well as within their native European (EUR) distribution: (1) habitat usage, (2) diet preferences, (3) size of individuals, (4) rate of range expansion, and (5) likely ecological impact, to determine how predictable the characteristics might be across invasions in distinctly different habitats.

THREE INVASIONS OF THE EUROPEAN GREEN CRAB

Eastern North America (ENA)

Early in the 19th century, *C. maenas* was introduced to eastern North America, where it occurred between New

Jersey and Cape Cod, MA. In the early 1900s, the range expanded north of Cape Cod to include Maine and maritime Canada just east of Cape Sable, Nova Scotia by 1961 (Glude, 1955; Ropes, 1968; Welch, 1968).

Western North America (WNA)

Between 1989 and 1990, *Carcinus maenas* invaded San Francisco Bay, California, where it became widely distributed throughout the bay (Cohen *et al.*, 1995; Carlton, this issue). It remained limited to this embayment until 1993, when it spread 80 km northward to other bays as far as Bodega Harbor (Grosholz & Ruiz, 1995). The following year, green crabs also spread 125 km southward to the Elkhorn Slough area of Monterey Bay (Grosholz & Ruiz, unpubl. data).

South Africa (SAF)

The European green crab was first found at the Table Docks area near Cape Town in 1983 (Le Roux *et al.*, 1990). Based on limited collections of the species in the intervening 10 years, it has apparently spread northward to Saldanha Bay and southward to Camps Bay as recently as 1992 (Griffiths *et al.*, 1992).

HABITAT UTILIZATION

One of the most critical aspects of predicting the impact of introduced species is determining the range of habitats that are likely to be occupied. A species may occupy either a greater of lesser variety of habitats in its introduced range relative to its native range. This may be because of the presence or absence of a given habitat in the introduced range relative to the native range, or simply the result of expansion or contraction of its habitat use in the new range given the same diversity of available habitats.

In its native range, the European green crab is found in a variety of habitats including hard and soft substrates, from protected embayments to moderately exposed rocky shores (Table 2). Here, green crabs have been shown to be conspicuous members of the outer coast fauna except in the most wave-exposed areas (Kitching *et al.*, 1959; Ebling *et al.*, 1964; Muntz *et al.*, 1965; Crothers, 1967, 1968) and can exist in very low energy environments across a wide range of salinities (Reise, 1977, 1978; Scherer & Reise, 1982).

In WNA, *Carcinus maenas* has colonized protected embayments similar to those in EUR (Table 2), and is as common in estuarine environments as in fully marine habitats. However, in WNA, *C. maenas* is not found in rocky habitats, even in areas of transitional wave energy where it is typically found on the European coast (Grosholz & Ruiz, 1995; Grosholz, unpubl. data). What prevents green crabs from occupying these protected rocky shores remains unknown. It is difficult to pinpoint factors that are not also present in EUR, ENA, or SAF, where their distribution is not so limited (Table 2).

Table 2. Summary of the habitat usage for *Carcinus maenas* for eastern North America (ENA), western North America (WNA), South Africa (SAF), in comparison with its characteristics in its native European range (EUR)

Data are summaries of published reports for each area (see text). Symbols indicate relative abundance as common (++), lower abundance (+), or absent (0).

	EUR	ENA	WNA	SAF
Outer coast				
Hard substrate	+	+	0	+
Soft substrate	0	0	0	0
Protected embayments				
Hard substrate	++	++	0	++
Soft substrate	++	++	++	++

In ENA, green crabs are common in moderately exposed rocky shore areas on the outer coast, similar to habitats occupied in EUR (Table 2). Although typically associated with the undersides of boulders or macroalgae beds, nonetheless they are a common at low intertidal levels and are conspicuous members of protected outer coast areas north of Cape Cod (Welch, 1968; Menge, 1976). Consistent with the EUR distribution, green crabs are also common in soft-sediment areas especially south of Cape Cod (Malinowski & Whitlach, 1983; Ropes, 1988).

The distribution of green crabs in SAF is similar to that of the EUR distribution (Table 2). Green crabs are found on the outer coast but not in heavily wave-washed areas (Le Roux *et al.*, 1990; Griffiths *et al.*, 1992), and the crab also occurs in sheltered areas such as Saldanha Bay (Griffiths *et al.*, 1992).

Diet selection

Along with potential changes in habitat utilization, introduced marine species are often confronted with novel prey species composition and abundance patterns outside their native ranges. In the case of the European green crab, which encounters a different array of benthic invertebrate prey among the disjunct sites of introduction, only coarse-grained comparisons are possible. Based upon published literature, direct comparisons of diets across geographic regions with different species require pooling of the diet information into broad taxonomic groups (phyla) and across foraging habitats for each of the sites.

In WNA, our work has shown that green crabs in field enclosures will prey on a wide range of species found in taxonomic groups similar to those found in the native range (Grosholz & Ruiz, 1995). Gut contents of actively foraging green crabs collected at Bodega Harbor, CA, and fixed with formalin within one-half hour of collection, closely match the results of prey preferences in the field enclosure experiments (Grosholz & Ruiz, unpubl. data) (Table 3). There is a high percentage of molluscs, primarily bivalves, as well as crustaceans with smaller numbers of polychaetes and

Table 3. Summary of diet preferences for *Carcinus maenas* based on gut contents for eastern North America (ENA), western North America (WNA), South Africa (SAF), in comparison with its characteristics in its native European range (EUR)
Data are summaries of published reports for each area (see text). Numbers indicate the relative ranking of prey taxa within each site. Data for EUR do not indicate relative abundance and taxa are either present (+) or absent in the diet (–).

Prey taxon	EUR	ENA	WNA	SAF
Mollusca	+	1	1	1
Crustacea	+	2	2	2
Annelida	+	3	3	3
Chlorophyta	+	4	3	4
Echinodermata	–	–	–	–

green algae. Echinoderms are conspicuously absent from the diet here as they are elsewhere, which agrees with experiments conducted elsewhere where green crabs consistently rejected echinoderm prey although resident crabs readily consumed them (Muntz *et al.*, 1965; Le Roux *et al.*, 1990; Scheibling & Hamm, 1991).

In ENA, again, a similar pattern emerges with the same rank ordering for molluscs, crustaceans, polychaetes, and green algae (Ropes, 1968, 1988) (Table 3). Similar to the data for EUR and WNA, gut contents data also suggest that most of the molluscs consumed are bivalves, and that echinoderm prey are absent.

Finally, for SAF there is also a predominance of molluscs, crustaceans and polychaetes with a similar rank order (Le Roux *et al.*, 1990) (Table 3). Algae are also a part of the diet, although echinoderms are completely absent as they are elsewhere.

Size distribution

The size distribution of an invading population may be an important determinant of the potential for impact on native biota. Especially for a predator such as *Carcinus maenas*, the size of the crab may determine the outcome of interactions with other crab species as well as determining the depth to which the crab may forage in soft substrate environments (Jensen & Jensen, 1985; Hines, pers. comm.). In this comparison, crabs are grouped into 10 mm size classes either by the original author or by subsequent analysis to allow between-site comparisons, since available data are generally size class frequencies. Comparisons include the modal size class and range of size classes and are made separately for males (the larger sex) and females where possible. Using modal size class also avoids the influence that sampling bias such as excluding juvenile crabs has on mean values.

In EUR, green crabs live for up to five years, during which time males may reach a maximum size of 86 mm (Carlisle, 1957; Crothers, 1967, 1968), although an extremely large adult male (*c.* 90 mm) has been noted from northern Europe (G. Vermeij, pers. comm.). The data for EUR are shown in Table 4. For WNA, our most recent data for two-year old male crabs shows carapace widths in excess of 92 mm (Table 4). Although the growth of these second-year crabs has slowed considerably, they should continue to molt at least once per year (Carlisle, 1957; Crothers, 1967) and, with a minimum 10% growth increment, the largest males may exceed 110 mm by their fifth year. Comparing the size range of crabs from WNA, which are at most two years old, with those from ENA and SAF, it is clear that the green crabs are already larger in WNA.

For ENA (Table 4), data are only available for males and females combined. Nonetheless, even with the pooled data, the size range of crabs is clearly smaller than for WNA (Ropes, 1968) (Table 4). For SAF, the size distribution is similar to EUR and ENA and also smaller than WNA (Table 4) (Le Roux *et al.*, 1990).

RATE OF RANGE EXPANSION

The impact of an introduced species also depends in part upon the extent of the invasion (i.e. density) and the area that the species will eventually occupy. Knowing how far and how fast the alien species will increase its range is an integral part of predicting the eventual range of the exotic species (Roughgarden, 1986). Further, the rate of spread is related to the growth rate of the invading population, and, thus, may provide information about changes in the growth of the invading population (Skellam, 1951; Okubo, 1980). To this end, we have calculated the linear rate of range increase or spread of green crabs along the shorelines of WNA, ENA, and SAF. These rates can be calculated from range maps and collection records indicating the change in the range of green crabs per unit time typically expressed in km/year.

The rate of range expansion for WNA is based on the fewest time points and should be interpreted as such. Over the last five years since the introduction, the northward expansion of the range of green crabs has been 80 km or 20 km/year, and the southward expansion has been 125 km or approximately 31 km/year. This is close to the mean rate of range expansion for marine species generally (Grosholz, 1996).

Table 4. Summary of size distribution for *Carcinus maenas* for eastern North America (ENA), western North America (WNA), South Africa (SAF), in comparison with its characteristics in its native European range (EUR)
All sizes represent width of the carapace in mm and size classes are in increments of 10 mm for comparison between sites. Data are summaries of published reports for each area (see text). Data for ENA (*) represent combined totals for males and females.

	EUR	ENA	WNA	SAF
Males				
Modal size class	45–55	50–60*	65–75	55–65
Size class range	15–75	5–80*	45–95	15–75
Females				
Modal size class	45–55	—	50–60	45–55
Size class range	15–75	—	40–75	15–75

For ENA, data are not available for the initial expansion in the early 1800s after the presumed initial introduction. However, the more recent range expansion north of Cape Cod in the early 1900s has been well documented by fisheries biologists concerned with the impact of *Carcinus maenas* on commercially important bivalve populations (Glude, 1955; Welch, 1968). The data for the northward expansion to the Nova Scotia coast indicate a considerably faster mean rate of range expansion of 63 km/year. The expansion of green crabs in this invasion has been very episodic, so there is much year-to-year variation in this long-term average.

For SAF, the rate of range expansion has been slower and over a more restricted area (Le Roux *et al.*, 1990; Griffiths *et al.*, 1992). The range expansion is based on a longer time period than the WNA invasion, but the range data are not collected systematically and are based on several independent reports. The mean rate of range expansion for this invasion is considerably slower than for the other two invasions with a rate of spread of 16 km/year from the first record in 1983 to 1992.

Potential ecological impact

Whether or not the impact of an introduced species will be felt beyond a single trophic level is at the heart of current debates about the structure of foodwebs (Carpenter & Kitchell, 1988; Power, 1990, 1992; Strong, 1992; Hunter & Price, 1992; Menge, 1992). Ultimately, we would like to know if the impacts of green crabs are limited only to the trophic level occupied by their infaunal prey, or if there will be significant changes at other trophic levels such as other crabs, fishes, and even shorebirds that share the same food resources. Diet selection discussed in the previous section only considers the similarity of prey choice. The simple occurrence of a species in the green crab diet does not indicate whether its predatory activities will significantly influence the abundance and distribution of that prey species, or other species that utilize the same prey. In this section, we discuss the demonstrated impact of the green crab in EUR and its potential impacts in its introduced ranges in ENA, WNA, and SAF.

In its native range in EUR, the green crab has been shown to have a significant impact on at least two dominant molluscs in Lough Ine on the British coast, *Mytilus edulis* and *Nucella lapillus* (Kitching *et al.*, 1959; Ebling *et al.*, 1964; Muntz *et al.*, 1965). This work suggests that *C. maenas* increasingly influences the distribution of both the mussel, *Mytilus edulis*, and the snail, *Nucella lapillus*, with decreasing wave exposure, having little effect on highly exposed shores (Table 5). However, this work also indicates that there is no impact of green crab predation on a local echinoderm, the urchin *Paracentrotus lividus*. This result is consistent with the lack of predation by *C. maenas* on *P. lividus* in experimental feeding trials, which contrasts extensive predation by other local crabs including *Necora puber* and *Cancer pagurus* (Muntz *et al.*, 1965). The impact of *Carcinus maenas* on other bivalve species has been demonstrated elsewhere in EUR (Reise, 1977, 1978; Scherer & Reise, 1982). Populations of *Cerastoderma edule* have been shown to be strongly influenced and even limited in their distribution by *C. maenas* (Jensen & Jensen, 1985; Sanchez-Salazar *et al.*, 1987).

In WNA, our long-term sampling (begun 10 years in advance of the introduction), suggests that a significant reduction in the abundance of bivalve populations occurred in Bodega Harbor, since the arrival of green crabs. Core samples taken approximately quarterly in Bodega Harbor indicate a significant decline in the abundance of bivalves (*Transennella* spp.) at lower tide levels (Grosholz & Ruiz, unpubl. data), which is most likely due to green crab predation, although confirmation awaits the evaluation of concurrent experimental studies. Our long-term data also show a decline in the abundance of a small grapsid crab, *Hemigrapsus oregonensis*, whose distribution overlaps almost completely with the exotic green crab (Grosholz & Ruiz, unpubl. data). These results are consistent with gut contents and feeding trials showing that green crabs readily prey on *H. oregonensis* and *Transennella* spp.

Past data suggest that if the impact of green crabs on benthic invertebrates is large enough at the WNA site, this will result in changes at higher trophic levels such as shorebird populations (Table 5). Sampling data from Bodega Harbor documented a significant decline of many invertebrate populations in the mid-1980s as the result of an unusually large, infrequent settlement event involving enormous numbers of juvenile Dungeness crabs *Cancer magister*, a native west coast crab (Ruiz, 1987). The dramatic decline of benthic invertebrates populations that resulted from the predatory activities of this numerous year class of *C. magister* was followed by significant declines in the harbor-wide abundances of several shorebird species that also feed on benthic invertebrates (Ruiz, unpubl. data).

Table 5. Summary of the potential ecological impact of *Carcinus maenas* for eastern North America (ENA), western North America (WNA), South Africa (SAF)

The strength of the demonstrated or potential impact is indicated as either high (++), moderate (+), or low/none (0). Categories for which no impact can be estimated are indicated as (?).

	EUR	ENA	WNA	SAF
Impacts on other crabs	+	+	++	0
Impacts on bivalve molluscs	++	++	++	+
Impacts on echinoderms	0	0	0	0
Impacts on fishes and birds	?	?	+	?

In ENA, the work examining the broader impact of green crabs has been less comprehensive. Declines in the abundances of the commercial bivalve *Mya arenaria* were documented during the first half of the 20th century and were correlated with the northeastward expansion of green crabs through Maine and maritime Canada, suggesting that changes were predator-related (Glude, 1955; Ropes, 1968). Clam abundance at one site decreased by 50% in 4 years in the face of minimal fishing intensity (Glude, 1955). Studies of the exposed coast rocky shores of northern New England are also consistent with the results from EUR, suggesting that *C. maenas* has little if any impact on prey in this community (Menge, 1976). Finally, regarding the impact of green crabs on echinoderms, predation studies in both lab and field experiments confirm that *C. maenas* does not prey on the urchin *Strongylocentrotus droebachiensis*, although native crabs such *Cancer irroratus* significantly do so, a finding also consistent with data from EUR.

In SAF, the potential for ecological impact of the green crabs is rather more speculative than in ENA, since studies have not comprehensively addressed this issue (Griffiths *et al.*, 1992). Although the exotic mussel *Mytilus galloprovincialis* is apparently displacing the native mussel *Aulacomya ater*, there appears to be little consequence of the invasion of green crabs on the native mussel in protected outer coast areas (Griffiths *et al.*, 1992). There seems to be little overlap in diet and habitat with native crabs, and thus little potential for predation or competition between these species (Griffiths *et al.*, 1992). However, the authors suggest that there is the potential for significant impact in more protected embayments, but no significant impacts of *Carcinus maenas* have been identified at present. Finally, consistent with results in other habitats, *C. maenas* refused to eat the native urchin *Paraechinus angulosus* in laboratory trials even when it was the only prey offered (Le Roux *et al.*, 1990).

DISCUSSION: PREDICTING FUTURE IMPACTS

Clearly what is needed are studies that rigorously quantify the impacts of introductions in marine systems. At present, there are few if any that have successfully combined the descriptive and experimental data required to assess impact. Obviously, our present abilities to predict the consequences of these introductions on native taxa are as limited as the lack of study. Increasing our understanding of the mechanisms influencing the invasion process will require the same quantitative and experimental approach that has been a cornerstone of modern ecology, but will also need to incorporate processes operating on scales much larger than are experimentally tractable (Vermeij, this issue).

Our goal here is to compare what is known about the multiple invasions of the European green crab *Carcinus maenas*, as a model system to examine the potential value of this approach in providing predictions of invasion characteristics. By comparing three spatially independent invasions of this species on different continents and ocean basins, we have shown that diet and ecological impact are qualitatively similar across sites (Table 6). In particular, the diet preferences of this predator are extremely consistent across invasions and with the data for this species in EUR. Bivalve molluscs are clearly the most preferred prey taxa, while echinoderms are uniformly ignored at all sites in contrast to most resident crabs.

This similarity in diet may allow predictions regarding the evolutionary impact of green crabs as well. Studies by Vermeij (1982*a*,*b*) have demonstrated significant evolutionary changes in the shell morphology of snail populations in ENA presumably in response to selection resulting from green crab predation. The consistent preference of green crabs for molluscan prey across the three invasions suggests the potential for a similar response to selection at other sites (WNA, SAF).

Unlike the similarity of green crab diet and impact among sites, the habitat usage, size of individual crabs, and rate of spread are more variable among the three invasions (Table 6). This dissimilarity in habitat usage may seem at odds with the previous statement describing similar ecological impacts. This is interpretable by considering that the ecological impacts of green crabs are strongest and most predictable in protected embayments, which are uniformly occupied by green crabs in all invasions. Green crabs have been less predictable in colonizing outer coast areas, but nowhere in their native or introduced ranges do they have a significant ecological impact in these more exposed habitats.

The lack of consistency for some characteristics across invasions underscores the potential interactions between invader and recipient community that may yield unpredictable results. For example, the large size of green crabs in WNA may alter the predicted impact of this species relative to predictions based upon attributes in its native range. Since larger green crabs can forage to deeper depths in the sediment, and are capable of taking larger prey (Jensen & Jensen, 1985),

Table 6. Summary characteristics of three invasions of the European green crab *Carcinus maenas* in eastern North America (ENA), western North America (WNA), South Africa (SAF), in comparison with its characteristics in its native European range (EUR)

Data are summaries of published reports for each area (see text). Characteristics in the introduced range that are qualitatively similar to that in their native range (EUR) are indicated by a '+' symbol, whereas characteristics that are qualitatively different are indicated by a '–' symbol.

Characteristic	ENA	WNA	SAF
Habitat usage	+	–	+/–
Diet preferences	+	+	+
Size distribution	+/–	–	+
Ecological impacts	+	+	+/–

the impact on the prey community may be much greater in WNA than would be initially predicted based on population characteristics in the native range. Secondly, interactions among crustaceans such as other crab species are very size-dependent; therefore, the size increase may also alter the predator–prey relationships among crabs in this introduced range.

To conclude, the characteristics examined in this study do differ in their similarity across invasions, thus allowing a distinction to be made between them in the likelihood of their being predictable in future invasions. The more important question remains unanswered, however, whether the degree of similarity (predictability) or even the rank order of the characters investigated in this study apply to other invading marine species, or even to other invading marine predators. The generality of these results for other species demands further investigation.

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REFERENCES

Allmon, R. A. & Sebens, K. P. (1988). Feeding biology and ecological impact of an introduced nudibranch, *Tritonia plebeia*, New England, USA. *Mar. Biol.*, **99**, 375–85.

Almaca, C. (1962). Sur la distribution géographique du genre *Carcinus* Leach (Crust. Dec. Brach.). *Rev. Fac. Cienc., Univ. Lisboa*, Ser. 2, **10**, 109–13.

Asakura, A. (1992). Recent introductions of marine benthos into Tokyo Bay (Review): process of invasion into an urban ecosystem with discussion on the factors inducing their successful introduction. *Chiba Central Natural History Journal Research Report*, **1**, 1–14.

Boudouresque, C. F. (1994). Les espèces introduites dans les eaux côtières d'Europe et de Mediterranée: Etat de la question et consequences. In *Introduced species in European coastal waters*, ed. C. Boudouresque, F. Briand & C. Nolan. *Ecosystems Research Reports*, No. 8, European Commission, Luxembourg, pp. 8–24.

Brenchley, G. A. & Carlton, J. T. (1983). Competitive displacement of native mud snails by introduced periwinkles in the New England intertidal zone. *Biol. Bull.*, **165**, 543–58.

Carlisle, D. B. (1957). On the hormonal inhibition of moulting in decapod Crustacea, II. The terminal anecdysis in crabs. *J. Mar. Biol. Ass., U.K.*, **36**, 291–307.

Carlton, J. T. (1979). History, biogeography, and ecology of the introduced marine and estuarine invertebrates of the Pacific coast of North America. PhD dissertation, Univ. of California, Davis, CA.

Carlton, J. T. (1985). Transoceanic and interoceanic dispersal of coastal marine organisms: The biology of ballast water. *Oceanogr. Mar. Biol. Ann. Rev.*, **23**, 313–74.

Carlton, J. T. (1989). Man's role in changing the face of the ocean: biological invasions and implications for conservation of near-shore environments. *Conserv. Biol.*, **3**, 265–73.

Carlton, J. T. (1992). Introduced marine and estuarine mollusks of North America: an end-of-the-century perspective. *J. Shellfish Res.*, **11**, 489–505.

Carlton, J. T. (1996). Pattern, process, and prediction in marine invasion ecology. *Biol. Conserv.*, **78**, 97–106.

Carlton, J. T. & Cohen, A. (1995). Nonindigenous species in a United States estuary: a case history of the ecological and economic effects of biological invasions in the San Francisco and Delta region. Report to U.S. Fish & Wildlife Service.

Carlton, J. T. & Geller, J. B. (1993). Ecological roulette: the global transport of non-indigenous marine organisms. *Science, N.Y.*, **261**, 78–82.

Carlton, J. T. & Iverson, E. W. (1981). Biogeography and natural history of *Sphaeroma walkeri* Stebbing (Crustacea: Isopoda) and its introduction to San Diego Bay, California. *J. Nat. Hist.*, **15**, 31–48.

Carpenter, S. & Kitchell, J. (1988). Consumer control of lake productivity. *BioScience*, **38**, 764–9.

Christiansen, M. E. (1969). *Crustacea Decapoda Brachyura. Marine invertebrates of Scandinavia.* Universitetsforlage, Oslo.

Cohen, A. N., Carlton, J. T. & Fountain, M. (1995). Introduction, dispersal, and potential impacts of the green crab *Carcinus maenas* in San Francisco Bay, CA. *Mar. Biol.* **122**, 225–37.

Crothers, J. H. (1967). The biology of the shore crab *Carcinus maenas* (L.), 1. The background—anatomy, growth, and life history. *Field Stud.*, **2**, 407–34.

Crothers, J. H. (1968). The biology of the shore crab *Carcinus maenas* (L.), 2. The life of the adult crab. *Field Stud.*, **2**, 597–614.

Dow, R. L. & Wallace, D. E. (1952). II. Observations on green crabs (*C. maenas*) in Maine. *Maine Dep. Sea Shore Fish., Fish. Circ.*, **8**, 11–15.

Ebling, F. J., Kitching, J. A., Muntz, L. & Taylor, M. C. (1964). The ecology of Lough Ine, XIII. Experimental destruction of *Mytilus edulis* and *Nucella lapillus* by crabs. *J. Anim. Ecol.*, **33**, 73–82.

Glude, J. B. (1955). The effects of temperature and predators on the abundance of the soft-shell clam, *Mya arenaria*, in New England. *Trans. Amer. Fish. Soc.*, **84**, 13–26.

Griffiths, C. L., Hockey, P. A. R., van Erkom Schurink, C. & Le Roux, P. J. (1992). Marine invasive aliens on South African shores: implications for community structure and trophic functioning. *S. Afr. J. Mar. Sci.*, **12**, 713–22.

Grosholz, E. D. (1996). Contrasting the rates of spread for introduced species in terrestrial and marine systems. *Ecology* (in press).

Grosholz, E. D. & Ruiz, G. M. (1995). The spread and potential impact of the recently introduced European green crab, *Carcinus maenas*, in central California. *Mar. Biol.*, **122**, 239–47.

Groves R. H. & di Castri, F. (1992). *Biogeography of Mediterranean invasions.* Cambridge University Press, Cambridge.

Hoagland, K. E. & Turner, R. D. (1980). Range extensions of teredinids (shipworms) and polychaetes in the vicinity of a temperate-zone nuclear generating station. *Mar. Biol.*, **58**, 55–64.

Hunter, M. D. & Price, P. W. (1992). Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology*, **73**, 724–32.

Jensen, K. T. & Jensen, J. N. (1985). The importance of some epibenthic predators on the density of juvenile benthic macrofauna in the Danish Wadden Sea. *J. Exp. Mar. Biol. Ecol.*, **89**, 157–74.

Kitching, J. A., Sloane, J. F. & Ebling, F. J. (1959). The ecology of Lough Ine, VIII. Mussels and their predators. *J. Anim. Ecol.*, **28**, 331–41.

Lambert, W. J., Levin, P. S. & Berman, J. (1992). Changes in the structure of a New England (USA) kelp bed: the effects of an introduce species? *Mar. Ecol. Prog. Ser.*, **88**, 303–7.

Lauckner, G. (1983). Diseases of Mollusca: Bivalvia. In *Diseases of marine animals, Volume II. Introduction, Bivalvia to Scaphopoda*, ed. O. Kinne. Biologische Anstalt Helgoland, Hamburg, pp. 477–962.

Leppakoski, E. (1994). Non-indigenous species in the Baltic Sea. In *Introduced species in European coastal waters*, ed. C. Boudouresque, F. Briand & C. Nolan. *Ecosystems Research Reports*, No. 8, European Commission, Luxembourg, pp. 60–6.

Le Roux, P. J., Branch, G. M. & Joska, M. A. P. (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**, 85- 93.

Malinowski, S. M. & Whitlach, R. B. (1983). Natural survivorship of young hard clams, *Mercenaria mercenaria* (Linne) in eastern Long Island Sound. *Nat Shell Ass. (Abst)*, p. 94.

Manning, R. B. & Holthius, L. B. (1981). West African brachyuran crabs (Crustacea: Decapoda). *Smithsonian Contrib. Zool.*, 89.

Menge, B. A. (1976). Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. *Ecol. Monogr.*, **42**, 67–94.

Menge, B. A. (1992). Community regulation: under what conditions are bottom-up factors important on rocky shores? *Ecology*, **73**, 755–65.

Mooney, H. A. & Drake, J. A. (1986). *Ecology of biological invasion of North America and Hawaii.* Springer, New York.

Mooney, H. A., Hamburg, S. P. & Drake, J. A. (1986). The invasions of plants and animals into California. In *Ecology of biological invasions of North America and Hawaii*, ed. H. A. Mooney & J. A. Drake. Springer, New York, pp. 250–72.

Muntz, L., Ebling, F. J. & Kitching, J. A. (1965). The ecology of Lough Ine, XIV. Predatory activity of large crabs. *J. Anim. Ecol.*, **34**, 315-29.

Okubo, A. (1980). Diffusion and ecological problems: mathematical models. *Biomathematics*, **10**, Springer, Berlin.

Pollard, D. A. & Hutchings, P. A. (1990). A review of exotic marine organisms introduced to the Australian Region. II. Invertebrates and algae. *Asian Fish. Sci.*, **3**, 223-50.

Por, F. D. (1978). *Lessepsian migration: the influx of Red Sea biota into the Mediterranean by way of the Suez Canal.* Springer, Heidelberg.

Power, M. E. (1990). Effects of fish in river food webs. *Science, N.Y.*, **250**, 811-14.

Power, M. E. (1992). Top-down and bottom-up forces in food webs: do plants have primacy? *Ecology*, **73**, 733–46.

Reise, K. (1977). Predator exclusion experiments in an intertidal mud flat. *Helgol. Meeres.*, **30**, 263–71.

Reise, K. (1978). Experiments on epibenthic predation in the Wadden Sea. *Helgol. Meeres.*, **31**, 55–101.

Roch, F. (1924). Experimentelle Untersuchungen an *Cordylophora caspia* (Pallas) [=*Lacustrus* Allman] uber die Abhangingkeit ihrer geographischen Verbreiting und ihrer Wuchsformen von den Physikalischchemischen Bedingungen des umgebenden Mediums. *Z. Morph. Okol. Tiere*, **2**, 250–426.

Ropes, J. W. (1968). The feeding habits of the green crab *Carcinus maenas* (L.). *Fish. Bull.*, **67**, 183–203.

Ropes, J. W. (1988). The food habits of five crab species at Pettaquamscutt River, Rhode Island. *Fish. Bull.*, **87**, 197–204.

Roughgarden, J. (1986). Predicting invasion and rates of spread. In *Ecology of biological invasions of North America and Hawaii*, ed. H. A. Mooney & J. A. Drake. Springer, New York, pp. 179–88.

Ruiz, G. M. (1987). Interactions among shorebird, crab, and their invertebrate prey populations. PhD dissertation, Univ. of California, Berkeley.

Sanchez-Salazar, M. E., Griffiths, C. L. & Seed, R. (1987). The interactive roles of predation and tidal elevation in structuring populations of the edible cockle, *Cerastoderma edule*. *Estuar. Coast. Shlf. Sci.*, **25**, 245–60.

Scattergood, L. W. (1952). I. The distribution of the green crab, *Carcinides maenas* (L.) in the northwestern Atlantic. *Maine Dep. Sea Shore Fish., Fish. Circ.*, **8**, 2–10.

Scheibling, R. E. & Hamm, J. (1991). Interactions between sea urchins (*S. droebachiensis*) and their predators in field and laboratory experiments. *Mar. Biol.*, **110**, 105–16.

Scherer, B. & Reise, K. (1982). Significant predation on micro- and macrobenthos by the crab *Carcinus maenas* L. in the Wadden Sea. *Kiel. Meeresfor.*, **5**, 490–500.

Skellam, J. G. (1951). Random dispersal in theoretical populations. *Biometrika*, **38**, 196–218.

Strong, D. R. (1992). Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology*, **73**, 747–54.

Vermeij, G. (1996). An agenda for invasion biology. *Biol. Conserv.*, **78**, 3–9.

Welch, W. R. (1968). Changes in abundance of the green crab, *Carcinus maenas* (L.), in relation to recent temperature changes. *Fish. Bull.*, **67**, 337- 45.

Williams, A. B. (1984). *Shrimps, lobsters, and crabs of the Atlantic Coast of the Eastern United States, Maine to Florida.* Smithsonian Institution Press, Washington, D.C.

Zeidler, W. (1978). Note on the occurrence of the European shore crab *Carcinus maenas* (Linn., 1758) in Australia. *S. Aust. Nat.*, **53**, 11–12.

Zibrowius, H. (1994). Introduced invertebrates: examples of success and nuisance in the European Atlantic and in the Mediterranean. In *Introduced species in European coastal waters*, ed. C. Boudouresque, F. Briand & C. Nolan. *Ecosystems Research Reports*, No. 8, European Commission, Luxembourg, pp. 44–9.