Prey Preferences and Relative Predation Rates of Adult European Green Crabs (*Carcinus maenas*) Feeding on Various Bivalve Species in British Columbia, Canada

D.L. Curtis, L. Sauchyn, L. Keddy, T.W. Therriault, and C.M. Pearce

Fisheries and Oceans Canada
Pacific Biological Station
3190 Hammond Bay Road
Nanaimo, BC
V9T 6N7

2012

Canadian Technical Report of
Fisheries and Aquatic Sciences 3014

Fisheries and Oceans / Pêches et Océans

Canada

Canadian Technical Report of Fisheries and Aquatic Sciences

Technical reports contain scientific and technical information that contributes to existing knowledge but which is not normally appropriate for primary literature. Technical reports are directed primarily toward a worldwide audience and have an international distribution. No restriction is placed on subject matter and the series reflects the broad interests and policies of Fisheries and Oceans Canada, namely, fisheries and aquatic sciences.

Technical reports may be cited as full publications. The correct citation appears above the abstract of each report. Each report is abstracted in the data base *Aquatic Sciences and Fisheries Abstracts*.

Technical reports are produced regionally but are numbered nationally. Requests for individual reports will be filled by the issuing establishment listed on the front cover and title page.

Numbers 1-456 in this series were issued as Technical Reports of the Fisheries Research Board of Canada. Numbers 457-714 were issued as Department of the Environment, Fisheries and Marine Service, Research and Development Directorate Technical Reports. Numbers 715-924 were issued as Department of Fisheries and Environment, Fisheries and Marine Service Technical Reports. The current series name was changed with report number 925.

Rapport technique canadien des sciences halieutiques et aquatiques

Les rapports techniques contiennent des renseignements scientifiques et techniques qui constituent une contribution aux connaissances actuelles, mais qui ne sont pas normalement appropriés pour la publication dans un journal scientifique. Les rapports techniques sont destinés essentiellement à un public international et ils sont distribués à cet échelon. Il n'y a aucune restriction quant au sujet; de fait, la série reflète la vaste gamme des intérêts et des politiques de Pêches et Océans Canada, c'est-à-dire les sciences halieutiques et aquatiques.

Les rapports techniques peuvent être cités comme des publications à part entière. Le titre exact figure au-dessus du résumé de chaque rapport. Les rapports techniques sont résumés dans la base de données *Résumés des sciences aquatiques et halieutiques.*

Les rapports techniques sont produits à l'échelon régional, mais numérotés à l'échelon national. Les demandes de rapports seront satisfaites par l'établissement auteur dont le nom figure sur la couverture et la page du titre.

Les numéros 1 à 456 de cette série ont été publiés à titre de Rapports techniques de l'Office des recherches sur les pêcheries du Canada. Les numéros 457 à 714 sont parus à titre de Rapports techniques de la Direction générale de la recherche et du développement, Service des pêches et de la mer, ministère de l'Environnement. Les numéros 715 à 924 ont été publiés à titre de Rapports techniques du Service des pêches et de la mer, ministère des Pêches et de l'Environnement. Le nom actuel de la série a été établi lors de la parution du numéro 925.

Canadian Technical Report of
Fisheries and Aquatic Sciences 3014

2012

PREY PREFERENCES AND RELATIVE PREDATION RATES OF ADULT EUROPEAN GREEN CRABS (*Carcinus maenas*) FEEDING ON VARIOUS BIVALVE SPECIES IN BRITISH COLUMBIA, CANADA

by

D.L. Curtis, L. Sauchyn, L. Keddy, T.W. Therriault, and C.M. Pearce

Fisheries and Oceans Canada
Pacific Biological Station
3190 Hammond Bay Road
Nanaimo, BC
V9T 6N7

Cat. No. Fs 97-6/3014E ISSN 0706-6457

Correct citation for this publication:

Curtis, D.L., Sauchyn, L., Keddy, L., Therriault, T.W., and Pearce, C.M. 2012. Prey preferences and relative predation rates of adult European green crabs (*Carcinus maenas*) on various bivalve species in British Columbia, Canada. Can. Tech. Rep. Fish. Aquat. Sci. 3014: iv + 14 p.

ABSTRACT

Curtis, D.L., Sauchyn, L., Keddy, L., Therriault, T.W., and Pearce, C.M. 2012. Prey preferences and relative predation rates of adult European green crabs (*Carcinus maenas*) on various bivalve species in British Columbia, Canada. Can. Tech. Rep. Fish. Aquat. Sci. 3014: iv + 14 p.

Laboratory experiments were carried out to establish prey preference and relative predation rates of recently established European green crabs (*Carcinus maenas*) on four commercially important bivalve species [Pacific littleneck clams (*Leukoma staminea*), Manila clams (*Venerupis philippinarum*), varnish clams (*Nuttallia obscurata*), and Gallo mussels (*Mytilus galloprovincialis*)] of varying sizes in British Columbia, Canada. In single-choice experiments, green crabs exhibited significantly higher predation rates on small prey and those with thinner shells (i.e. varnish clams and Gallo mussels) than larger prey or those with thicker shells (i.e. littleneck and Manila clams). Similar preference was also observed when multiple prey types and sizes were present, with a size threshold between 20 and 30 mm shell length for Manila clams and 30 and 40 mm shell length for varnish clams. The results of this study suggest that populations of green crabs in British Columbia have the potential to negatively impact commercially important bivalve species.

RESUME

Curtis, D.L., Sauchyn, L., Keddy, L., Therriault, T.W., and Pearce, C.M. 2012. Prey preferences and relative predation rates of adult European green crabs (*Carcinus maenas*) on various bivalve species in British Columbia, Canada. Can. Tech. Rep. Fish. Aquat. Sci. 3014: iv + 14 p.

Des expériences en laboratoire ont été réalisées afin d'établir les préférences en matière de proies et les taux de prédation relatifs du crabe européen (*Carcinus maenas*), récemment établi, par rapport à quatre espèces bivalves d'importance commerciale [palourde du Pacifique (*Leukoma staminea*), palourde japonaise (*Venerupis philippinarum*), *Nuttallia obscurata* et moule méditerranéenne (*Mytilus galloprovincialis*)] de tailles variables en Colombie-Britannique, au Canada. Dans les expériences où ils n'avaient qu'un seul choix, les crabes européens ont démontré des taux de prédation beaucoup plus élevés pour les proies petites aux coquilles minces (c.-à-d. les *Nuttallia obscurata* et les moules méditerranéennes) que pour les grosses proies aux coquilles épaisses (c.-à-d. les palourdes du Pacifique et japonaises). Une préférence similaire a été observée lorsque plusieurs types de proies de différentes tailles étaient présentes, le seuil de taille étant de 20 à 30 mm (longueur de la coquille) pour les palourdes japonaises et de 30 à 40 mm pour les *Nuttallia obscurata*. Les résultats de cette étude laissent entendre que les populations de crabes européens en Colombie-Britannique pourraient avoir des répercussions négatives sur des espèces bivalves d'importance commerciale.

INTRODUCTION

The European green crab (*Carcinus maenas* Linnaeus, 1758) is a pervasive invader. Since its first introduction from Europe to eastern North America in the 1800's, this species has established populations in a number of countries including Australia, Canada, Japan, South Africa, and the USA (Grosholz and Ruiz 1996). Within its native range, the green crab has been extensively studied and researchers have been quick to investigate its potential impacts when it appears as an invader (Walton et al. 2002; Audet et al. 2008). Within its invaded range, green crabs have had significant negative impacts on other benthic organisms, both as competitors and predators. In western North America, green crabs display aggressive behaviour towards similar-sized Dungeness crabs (*Cancer magister* Dana, 1852), out competing them for both food and shelter (McDonald et al. 2001). They are voracious predators, consuming up to 28% of their body weight per day (Pihl 1985), substantially more than many other crab species (Curtis et al. 2010). High densities of green crabs may substantially influence recruitment of a number of benthic invertebrate species including bivalves, gastropods, urchins, polychaetes, and barnacles (Kitching et al. 1959; Muntz et al. 1965; Reise 1977; Menge 1983; Jensen and Jensen 1985; Janke 1990; Tyrell et al. 2006). Studies have shown that green crabs can have significant effects on the structure of benthic communities (Reise 1977) and they have been implicated in the decline of the softshell clam (*Mya arenaria* Linnaeus, 1758) fishery in eastern North America (Glude 1955; Ropes 1968).

Throughout its native and invaded ranges, bivalve molluscs are the dominant prey item of green crabs (Ropes 1968; Grosholz and Ruiz 1996). Within their native range, predation by green crabs has been shown to have significant impacts on the density and distribution of mussels (*Mytilus edulis* Linnaeus, 1758) (Dare and Edwards 1976), cockles (*Cerastoderma edule* Linnaeus, 1758) (Jensen and Jensen 1985), and clams (*Spisula subtruncata* Gray, 1837; *Mactra stultorum* Linnaeus, 1758; *Venerupis senegalensis* Gmelin, 1791; *Abra alba* Lamarck, 1818) (Reise 1977). In its invaded range in eastern North America, common bivalve prey species include softshell clam (*M. arenaria* (Ropes, 1968), blue mussel (*M. edulis*) (Leonard et al. 1999), and the amethyst gem clam (*Gemma gemma* Totten, 1834) (Ropes 1968). In western North America, green crabs have been found to actively consume bent-nose macoma clam (*Macoma nasuta* Conrad, 1837) (Palacios and Ferraro 2003), California softshell clam (*Cryptomya californica* Conrad, 1837) (Palacios and Ferraro 2003), confusing dwarf venus (*Nutricola confusa* S. Gray, 1982) (Grosholz et al. 2000), Manila clam (*Venerupis philippinarum* Adams and Reeve, 1850) (Grosholz et al. 2001; Palacios and Ferraro 2003), mussel (*Mytilus trossulus* Gould, 1850) (Behrens Yamada et al. 2010), Olympia oyster (*Ostrea lurida* Carpenter, 1864) (Palacios and Ferraro 2003), and purple dwarf venus (*N. tantilla* Gould, 1853) (Grosholz et al. 2000).

Prey preference experiments typically have shown that, given enough time or a shortage of food, all bivalve species are susceptible to predation by green crabs. When attempting to open bivalve prey, green crabs are typically faster, more coordinated, and display a wider variety of techniques than many other, larger species of decapods (Moody and Steneck 1993). However, green crabs tend to prefer bivalves with thin shells that have a shell length < 16% of their carapace width (Jensen and Jensen 1985). Although the specific impacts of green crabs will vary as a function of prey communities (Grosholz and Ruiz 1996), it is clear that the potential negative impacts of newly established green crab populations on commercially important species could be substantial.

Populations of green crabs first appeared in western North America in San Francisco Bay, USA in 1989 (Cohen et al. 1995) and expanded rapidly northward to Bodega Bay, Humboldt Bay, Coos Bay, Willapa Bay, and Grays Harbour (See and Feist 2010). These populations have had significant impacts on local bivalve communities (Grosholz et al. 2000). The species was first reported in British Columbia (BC), Canada in 1999 (Behrens Yamada and Hunt 2000; Jamieson 2000) and has generated a growing concern over its potential impact on commercial shellfish harvesting and aquaculture operations [predominantly Pacific oyster (*Crassostrea gigas* Thunberg, 1793), Manila clam (*V. philippinarum*), blue mussel (*M. edulis*), Gallo mussel (*M. galloprovincialis* Lamarck, 1819), and varnish clam (*Nuttallia obscurata* Reeve, 1857)]. No research, however, has examined bivalve prey preference or predation rates of green crabs in BC. The objective of the present study was to determine prey preference and relative predation rate of green crabs on various commercially-important bivalve species in BC.

METHODS

Adult male, intermoult European green crabs (carapace width: 80–90 mm) were collected with baited traps from Barkley Sound, BC (49.033° N; 125.333° W) and transferred to the Pacific Biological Station in Nanaimo, BC. Crabs were held in flowing aerated seawater at 15°C and maintained on a diet of frozen herring. Prior to experimentation, crabs were starved for 72 h to standardize hunger levels. During both holding and experiments, the photoperiod was 12 h L : 12 h D, with lighting provided solely by overhead fluorescent lights. Bivalves were sourced from local shellfish processors or aquaculture companies and held in flowing aerated seawater prior to use in experiments. All experiments were carried out between March and May 2010.

At the start of each experiment, bivalves were examined to ensure that they were in good health, as determined by active feeding and a strong closure response. Their shell length (SL, the length along the longest axis) was recorded, before transferring them to translucent plastic experimental chambers held in seawater tables. Each chamber was provided with flow-through sand-filtered seawater. We chose not to use sediment in any of the predation experiments since: (1) not all bivalve species tested were infaunal (e.g. *M. galloprovincialis*); (2) we wanted to test for prey selectivity independent of any other potential confounding factors such as burial depth; and (3) we wanted to assess maximal predation rates where bivalves were not allowed the chance to escape predation via burial. All replicates were carried out concurrently and the placement of replicate chambers within seawater tables was fully randomized. A single green crab was added to each chamber and allowed to feed, after which the crab was removed and the number of bivalves showing signs of predation was recorded. Each crab was used only once and crabs were never reused for any subsequent experiments. A bivalve was considered to have been preyed upon if its shell had been cracked by the crab, which would likely result in death in nature.

To determine the susceptibility of various local bivalve species to predation by green crabs and to establish relative predation rates, a single-choice predation experiment was initially carried out. Individual green crabs were introduced into a chamber (L x W x H: 210 x 140 x 160 mm) containing ten individuals of one of the following bivalve species: Manila clam (*V. philippinarum*), Pacific littleneck clam (*Leukoma staminea* Conrad, 1837), varnish clam (*N. obscurata*), or Gallo mussel (*M. galloprovincialis*) in either “small” (SL: ~40 mm) or “large” (SL: ~50 mm) size classes. The experimental design consisted of six randomly-distributed replicate containers for each of the eight treatments (four species in two size categories). Crabs were allowed to feed for 24h, after which the crab was removed and the number of bivalves showing signs of predation was recorded. Differences among the number of each size and species of bivalve preyed upon were compared using a two-way ANOVA with significant differences among species being determined with a Tukey’s post-hoc test ($P < 0.05$).

The preference of green crabs for a particular size and species of prey item was further tested using two separate multiple-choice predation experiments. The size classes for both multiple choice experiments were chosen based on the size distributions for each species that were available at the time (presumably an indication of natural cohorts or cultured size classes present) and because observations from the single-choice experiment suggested that crabs tended to favour varnish clams and Gallo mussels and rarely consumed large Manila or large littleneck clams. In the initial experiment, an individual crab was introduced into a chamber (L x W x H: 210 x 140 x 160 mm) containing three each of “small” (SL: 30–40 mm) and “large” (40–50 mm) varnish clams, “small” (35–50 mm) and “large” (50–60 mm) Gallo mussels, “small” (35–45 mm) Manila clams, and “small” (35–45 mm) littleneck clams. The experimental design consisted of 12 randomly-distributed replicate containers. This experiment was run over a 6 h period in daylight to provide a preliminary indication of prey preference and relative feeding rate when multiple sizes and species of prey are available. At the end of the experiment, the crab was removed and the number of bivalves preyed upon was recorded for each replicate container.

A second multiple-choice experiment was carried out to determine if a more precise preferred size range for varnish and Manila clams could be identified. The procedure for this experiment was similar to the first multiple-choice experiment, except that each individual crab was placed in a larger chamber (L x W x H: 500 x 300 x 300 mm) containing four individuals of each of five size classes (SL: ~20, 30, 40, 45, and 50 mm) of Manila clams and four individuals of each of four size classes (SL: ~30, 40, 45, and 50 mm) of varnish clams (the 20 mm size class of varnish clams was not available for testing).The experimental design consisted of 10 randomly-distributed replicate containers. After 24 h, the crab was removed and the number of bivalves preyed upon was recorded for each replicate container.

For both multiple-choice experiments, Manly's α for variable prey populations (Manly et al., 1972) was used as an index to determine prey preference, using the following equation (Wellborn 1994; Mattson 1999):

$$\alpha_{\mathrm{i}} = \frac{\ln(p_i)}{\sum_{j=1}^{m} \ln(p_j)}$$

where p_i and p_j are the proportion of prey type *i* or *j* remaining at the end of each trial relative to the initial number of each prey type and *m* is the number of prey types offered. Each size and species was considered to be a separate prey type. Preference was determined for each experiment based on the following equations:

$\alpha_i = 1/m$ = no preference for prey type *i*
$\alpha_i < 1/m$ = avoidance of prey type *i*
$\alpha_i > 1/m$ = preference for prey type *i*

Preference or avoidance was considered to be significant if the 95% confidence interval did not overlap 1/*m*, as suggested by Dudas et al. (2005).

RESULTS

When provided with a single prey type, mussels, littleneck clams, Manila clams, and varnish clams were all susceptible to predation by green crabs. However, the crabs preyed upon significantly more mussels and varnish clams than littleneck or Manila clams (two-way ANOVA, $F = 36.667$, df = 3, 40, $P < 0.001$, followed by Tukey's test; Fig. 1). They also preyed upon significantly more small than large individuals (two-way ANOVA, $F = 75.721$, df = 1, 40, $P < 0.001$; Fig. 1), regardless of species. There was no significant interaction between species and size (two-way ANOVA, $F = 1.817$, df = 3, 40, $P > 0.05$).

When presented with multiple prey types and sizes, green crabs showed a significant preference for small varnish clams ($\alpha_i = 0.180$, $P < 0.05$). There was no preference for small or large Gallo mussels or large varnish clams (Fig. 2A), although mean α_i values were not significantly different from that of small varnish clams. Green crabs avoided small littleneck and Manila clams when other prey items were present. When provided with a broader size range of Manila and varnish clams concurrently, green crabs did not prey on Manila clams greater than 20 mm SL (Fig. 2B). There was a significant preference for 30 mm varnish clams (α_i = 0.358, P < 0.05), but crabs readily consumed all varnish clam sizes smaller than 50 mm.

DISCUSSION

In BC, green crabs have the potential to be an important predator on commercially-harvested bivalve species. However, the magnitude of this impact is likely dependant on prey size and species. Although there have been many studies examining predation by green crabs on bivalves, in both its native and invaded ranges (*e.g.* Elner and Hughes 1978; Grosholz and Ruiz 1995; Palacios and Ferraro 2003; Breen and Metaxas 2008), to our knowledge, only one other study (Behrens Yamada et al. 2010) has examined crabs > 75 mm carapace width. While differences in experimental conditions make comparisons between studies difficult, we found that green crabs of 80–90 mm carapace width consumed about 4 Manila clams (SL: 40 mm) per day, whereas a recent study by Palacios and Ferraro (2003) found that green crabs of 75 mm carapace width consumed 2.7 Manila clams (SL: 27 mm) per day. In the northeastern Pacific, green crabs attain a much larger size than in their native range and populations in BC are comprised of a greater percentage of large individuals (McGaw et al. 2011), potentially leading to a greater impact than would otherwise be assumed based on the current literature (Grosholz et al. 2011).

When presented with a single, commercially-important bivalve species commonly found in BC, green crabs preyed upon many more varnish clams and Gallo mussels than they did littleneck or Manila clams. Varnish clams and mussels have thinner shells than either littleneck or Manila clams and require 7–8 times less pressure to crack for a given tissue mass (Byers 2002), making them a potentially more profitable prey item. The upper size threshold for energy maximization by a predator on a given bivalve species is a function of breaking time, which increases exponentially with thickness and asymptotically with SL (Elner and Hughes 1978; Boulding 1984; Juanes 1992).

When small prey items were available, a size threshold between 20 and 30 mm SL for Manila clams and 30 and 40 mm SL for varnish clams was observed. The mechanism used for prey selection, rather than an inability to consume larger prey, is likely responsible for these thresholds. When presented with only a single prey type, green crabs readily consumed littleneck and Manila clams up to 40 mm in SL and mussels and varnish clams up to 50 mm in SL. When a green crab encounters a bivalve it will spend a finite amount of time attempting to open it, after which it will give up and move on to the next nearest prey item (Elner and Hughes 1978). If the next bivalve is small, the crab will break it open and eat it, but if the next bivalve is large, the crab likely will move on to the next prey item. However, there appears to be a point after encountering a number of large (and less profitable) bivalves sequentially at which the crab will spend more time attempting to break and consume larger bivalves (Elner and Hughes 1978). Therefore, in situations where more profitable prey items are scarce, larger individuals and less profitable species will be preyed upon at higher rates.

In previous studies, green crabs have been found to consume substantially larger numbers of prey items than other species of crabs sharing the same habitat (Mascaro and Seed 2001; Lohrer and Whitlatch 2002; Breen and Metaxas 2008). The green crabs observed in the present study were also voracious predators, often consuming more than seven individual mussels or varnish clams over 40 mm SL per day. However, potential predation impacts in the wild will not only be a function of consumption rate, but also of the distribution of green crabs and prey. Although the overall density of green crabs in BC is low, recent surveys have shown disparate, but highly dense populations (Klassen and Locke 2007). Thus, the high consumption rate combined with high population densities suggests that the potential population level effects may be greater than would be predicted based on laboratory feeding experiments or population density studies alone (Lohrer and Whitlatch 2002). Caution should be exercised, however, when extending laboratory results to the field, as previous work has reported that laboratory estimates of feeding rate may be higher than those in nature (Breen and Metaxas 2008). This is most likely the case in the present research where infaunal bivalves were not allowed to escape predation by burial in sediment.

Although the current laboratory based study has shown a clear preference for varnish clams and Gallo mussels, the dynamics of predation in the field are likely much more complex and affected by a plethora of biotic and abiotic factors. In BC, green crabs generally are restricted to the upper and mid-intertidal zone of enclosed bays and estuaries and rarely are found on exposed shores (Hunt and Behrens Yamada 2003). Manila and littleneck clams co-occur in highest densities in the lower intertidal zone on sheltered beaches with sand and gravel substrates (Harbo 1997) whereas varnish clams typically are found in lower salinity waters in the upper intertidal zone (Gillespie et al. 2001), providing them some degree of refuge from more stenohaline native crab species such as *C. magister*, *C. gracilis* Dana, 1852, and *C. productus* Dana, 1852 (Hunt and Behrens Yamada 2003; Curtis et al. 2007; Curtis and McGaw 2008, 2011). This environmental refuge is not available from green crabs, however, as they are able to thrive in warm, low-salinity conditions and adult green crabs often are forced into these habitats because they are unable to compete with larger, adult native crab species (Hunt and Behrens Yamada 2003; Jensen et al. 2007). While weaker osmoregulating crabs, such as *C. magister*, show a reduction in feeding rates when exposed to low salinity waters (Breen and Metaxas 2008; Curtis et al. 2010), more efficient osmoregulators like the green crab display little change (Ropes 1968) or even increase feeding rates to help cope with increased metabolic demands. In the present study, green crabs strongly preferred recently established, non-indigenous varnish clams over any other prey offered. Since varnish clams are often present in high densities on the same beaches as littleneck and Manila clams, this preference may help to alleviate some of the negative impacts of green crab predation on the littleneck and Manila clam fisheries. However, this preference may create challenges over the longer term on the developing market for varnish clams (often marketed as 'savoury clams').

The physical attributes of the substrate in which a bivalve species is found may also affect predation rate (Byers 2002). In the current study, the experimental chambers intentionally did not contain substrate in order to standardize prey preference and predation rates among species (one of which was not an infaunal) without the confounding factor of burial depth. Although this likely increased predation rates (Byers 2002), differences in the depth and coarseness of substrate provided, or allowing species such as mussels to attach, also introduces bias (Palacios and Ferrarro 2003; Miron et al. 2005; Breen and Metaxas 2008; Behrens Yamada et al. 2010) and makes comparisons among species or with previous studies difficult.

In the field, varnish clams are usually segregated from Manila and littleneck clams by intertidal height, though they often co-occur at densities greater than those used in the current study (Fisheries and Oceans Canada, unpublished data). In general, varnish clams bury deeper (>20 cm) than littleneck or Manila clams (<20 cm), although varnish clam burial depth may be restricted in coarser substrates (Byers 2002; Dudas et al. 2005). The shallower burial depth of littleneck and Manila clams may increase encounter frequency and subsequently predation rate as green crabs dig for prey (Elner and Hughes 1978).

The results of this study suggest that the interactions between green crabs and commercially important bivalves are complex. Smaller and thinner-shelled bivalves are particularly susceptible to predation, but larger individuals may also fall prey to green crabs, particularly if high densities of crabs reduce the density of smaller bivalves. On beaches where varnish clams are present, they may alleviate some predation pressure on currently more marketable species such as Manila clams. We have shown that the potential impact of green crabs on commercially important bivalve species in BC could be great and further study is necessary to determine the specific impacts that dense populations of larger green crabs may be having in natural environments.

ACKNOWLEDGEMENTS

We thank Mac's Oysters Ltd. and Island Sea Farms Inc. for providing shellfish.

REFERENCES

Audet, D., Miron, G., and Moriyasu, M. 2008. Biological characteristics of a newly established green crab (*Carcinus maenas*) population in the southern gulf of St. Lawrence, Canada. J. Shellfish Res. 27: 427-441.

Behrens Yamada, S., and Hunt, C. 2000. The arrival and spread of the European green crab, *Carcinus maenas*, in the Pacific Northwest. Dreissena! 11: 1-7.

Behrens Yamada, S., Mathias Davidson, T., and Fisher, S. 2010. Claw morphology and feeding rates of introduced European green crabs (*Carcinus maenas* L, 1758) and native Dungeness crabs (*Cancer magister* Dana, 1852) J. Shellfish Res. 29: 471-477.

Boulding, E.G. 1984. Crab resistant features of shells of burrowing bivalves: decreasing vulnerability by increasing handling time. J. Exp. Mar. Biol. Ecol. 76: 201-223.

Breen, A., and Metaxas, A. 2008. A comparison of predation rates by non-indigenous and indigenous crabs (juvenile *Carcinus maenas*, juvenile *Cancer irroratus*, and adult *Dyspanopeus sayi*) in laboratory and field experiments. Estuaries Coasts 31: 728-737.

Byers, J.E. 2002. Physical habitat attribute mediates biotic resistance to non-indigenous species invasion. Oecologia 130: 146-156.

Cohen, A.N., Carlton, J.T., and Fountain, M.C. 1995. Introduction, dispersal and potential impacts of green crab *Carcinus maenas* in San Francisco Bay, California. Mar. Biol. 122: 225-237.

Curtis, D.L., Jensen, E.K., and McGaw, I.J. 2007. Behavioural influences on the physiological responses of *Cancer gracilis*, the graceful crab, during hypersaline exposure. Biol. Bull. 212: 222-231.

Curtis, D.L., and McGaw, I.J. 2008. A year in the life of a Dungeness crab: methodology for determining the microhabitat conditions experienced by large decapod crustaceans in estuaries. J. Zool. 274: 375-385.

Curtis, D.L., and McGaw, I.J. 2011. Salinity and thermal preference of Dungeness crabs in the lab and in the field: Effects of food availability and starvation. J. Exp. Mar. Biol. Ecol. 413: 113-120.

Curtis, D.L., Vanier, C.H., and McGaw, I.J. 2010. The effects of starvation and acute low salinity exposure on food intake in the Dungeness crab, *Cancer magister*. Mar. Biol. 157: 603-612.

Dare, P.J., and Edwards, D.B. 1976. Experiments on the survival, growth and yield of relaid seed mussels (*Mytilus edulis* L.) in the Menai Straits, North Wales. ICES J. Mar. Sci. 37: 16-28.

Dudas, S.E., McGaw, I.J., and Dower, J.F. 2005. Selective crab predation on native and introduced bivalves in British Columbia. J. Exp. Mar. Biol. and Ecol. 325: 8-17.

Elner, R.W., and Hughes, R.N. 1978. Energy maximization in the diet of the shore crab, *Carcinus maenas*. J. Anim. Ecol. 47: 103-116.

Gillespie, G.E., Rusch, B., Gormican, S.J., Marshall, R., and Monroe, D. 2001. Further investigations of the fisheries potential of the exotic varnish clam (*Nuttallia obscurata*) in British Columbia. Fisheries and Oceans Canada. Canadian Science Advisory Secretariat Research Document 2001/143.

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

Grosholz, E.D., and Ruiz, G.M. 1995. Spread and potential impact of the recently introduced European green crab, *Carcinus maenas*, in central California. Mar. Biol. 122: 239-247.

Grosholz, E.D., and Ruiz, G.M. 1996. Predicting the impact of introduced marine species: lessons from the multiple invasions of the European green crab *Carcinus maenas*. Biological Conservation 78: 59-66.

Grosholz, E.D., Ruiz, G.M., Dean, C.A., Shirley, K.A., Maron, J.L., and Connors, P.G. 2000. The impact of a nonindigenous marine predator in a California bay. Ecology 81: 1206-1224.

Grosholz, E.D., Olin, P., Williams, B., and Tinsman, R. 2001. Reducing predation on Manila clams by nonindigenous European green crabs. J. Shellfish Res. 20: 913-919.

Grosholz, E., Lovell, S., Besedin, E., and Katz, M. 2011. Modeling the impacts of the European green crab on commercial fisheries. Ecological Applications 21: 915-924.

Harbo, R.M. 1997. Shells and Shellfish of the Pacific Northwest. Harbour Publishing, Madeira Park.

Hunt, C.E., and Behrens Yamada, S. 2003. Biotic resistance experienced by an invasive crustacean in a temperate estuary. Biological Invasions 5: 33-43.

Jamieson, G.S. 2000. European green crab, *Carcinus maenas*, introductions to North America: Differences between the Atlantic and Pacific experiences. Proceedings of the 10th International Aquatic Nuisance Species and Zebra Mussel Conference, Toronto, ON, Feb 13-17, 2000 pp. 307-312.

Janke, K. 1990. Biological interactions and their role in community structure in the rocky intertidal of Helgoland (German Bight, North Sea). Helgoland Marine Research 44: 219-263.

Jensen, G.C., McDonald, P.S., and Armstrong, D.A. 2007. Biotic resistance to green crab, *Carcinus maenas*, in California bays. Mar. Biol. 151: 2231-2243.

Jensen, K.T., and 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: 157-174.

Juanes, F. 1992. Why do decapod crustaceans prefer small-sized molluscan prey? Mar. Ecol. Prog. Ser. 87: 239-249.

Kitching, J.A., Sloane, J.F., and Ebling, F.J. 1959. The ecology of Lough Ine: VII. Mussels and their predators. J. Anim. Ecol. 28: 331-341.

Klassen, G., and Locke, A. 2007. A biological synopsis of the European green crab, *Carcinus maenas*. Can. Manuscr. Rep.Fish. Aquat. Sci. 2818: vii+75 pp.

Leonard, G.H., Bertness, M.D., and Yund, P.O. 1999. Crab predation, waterborne cues, and inducible defenses in the blue mussel, *Mytilus edulis*. Ecology 80: 1-14.

Lohrer, A.M., and Whitlatch, R.B. 2002. Relative impacts of two exotic brachyuran species on blue mussel populations in Long Island Sound. Mar. Ecol. Prog. Ser. 227: 135-144.

Manly, B.F.J., Miller, P., and Cook, L.M. 1972. Analysis of a selective predation experiment. Am. Nat. 106: 719-736.

Mascaro, M., and Seed, R. 2001. Choice of prey size and species in *Carcinus maenas* (L.) feeding on four bivalves of contrasting shell morphology. Hydrobiologia 449: 159-170.

Mattson, N.S. 1999. Trophic interactions between two tropical omnivorous fishes, *Oreochromis shiranus* and *Barbus paludinosus*: feeding selectivities and food web responses. Hydrobiologia 380: 195-207.

McDonald, P.S., Jensen, G.C., and Armstrong, D.A. 2001. The competitive and predatory impacts of the nonindigenous crab *Carcinus maenas* (L.) on early benthic phase Dungeness crab *Cancer magister* Dana. J. Exp. Mar. Biol.Ecol. 258: 39-54.

McGaw, I.J., Edgell, T.C., and Kaiser, M.J. 2011. Population demographics of native and newly invasive populations of the green crab *Carcinus maenas*. Mar. Ecol. Prog. Ser. 430: 235-240.

Menge, B.A. 1983. Components of predation intensity in the low intertidal zone of the New England rocky intertidal region. Oecologia 58: 141-155.

Miron, G., Audet, D., Landry, T., and Moriyasu, M. 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.

Moody, K.E., and Steneck, R.S. 1993. Mechanisms of predation among large decapod crustaceans of the Gulf of Maine coast: functional vs. phylogenetic patterns. J. Exp. Mar. Biol.Ecol. 168: 111-124.

Muntz, L., Ebling, F.J., and Kitching, J.A. 1965. The ecology of Lough Ine: XIV. Predatory activity of large crabs. J. Anim. Ecol. 34: 315-329.

Palacios, K.C., and Ferraro, S.P. 2003. Green crab (*Carcinus maenas* Linnaeus) consumption rates on and prey preferences among four bivalve species. J. Shellfish Res. 22: 865-871.

Pihl, L. 1985. Food selection and consumption of mobile epibenthic fauna in shallow marine areas. Mar. Ecol. Prog. Ser. 22: 169-179.

Reise, K. 1977. Predator exclusion experiments in an intertidal mud flat. Helgolander wiss. Meeresunters 30: 263-271

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

See, K.E., and Feist, B.E. 2010. Reconstructing range expansion and subsequent invasion of introduced European green crab along the west coast of the United States. Biological Invasions 12: 1305-1318.

Tyrell, M.C., Guarino, P.A., and Harris, L.G. 2006. Predatory impacts of two introduced crab species: Inferences from microcosms. Northeastern Naturalist 13: 375-390.

Walton, W.C., MacKinnon, C., Rodriguez, L.F., Proctor, C., and Ruiz, G.M. 2002. Effect of an invasive crab upon a marine fishery: green crab, *Carcinus maenas*, predation upon a venerid clam, *Katelysia scalarina*, in Tasmania (Australia). J. Exp. Mar. Biol. Ecol. 272: 171-189.

Wellborn, G.A. 1994. Size-biased predation and prey life histories: a comparative study of freshwater amphipod populations. Ecology 75: 2104-2117.

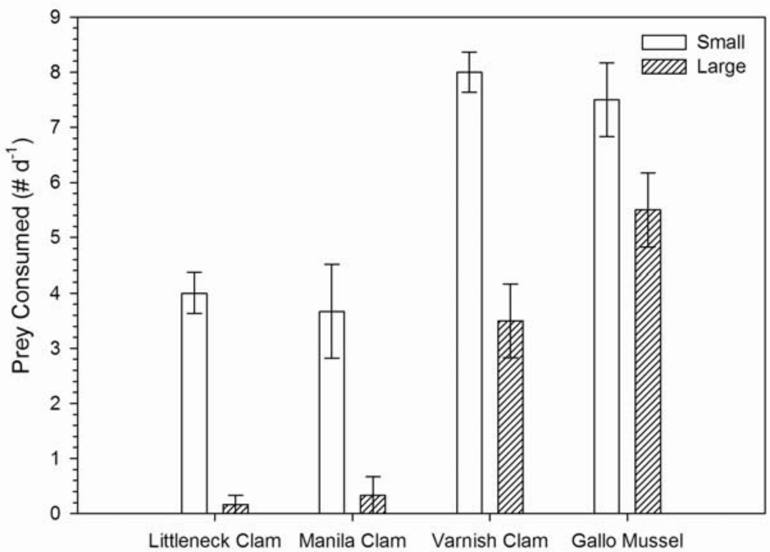

Figure 1. Mean (± SE) number of small and large littleneck clams (*Leukoma staminea* Conrad 1837), Manila clams (*Venerupis philippinarum* Adams and Reeve, 1850), varnish clams (*Nuttallia obscurata* Reeve 1857), and Gallo mussels (*Mytilus galloprovincialis* Lamarck 1819) preyed upon per day (n = 6 for each size and species combination) by individual adult green crabs (*Carcinus maenas*).

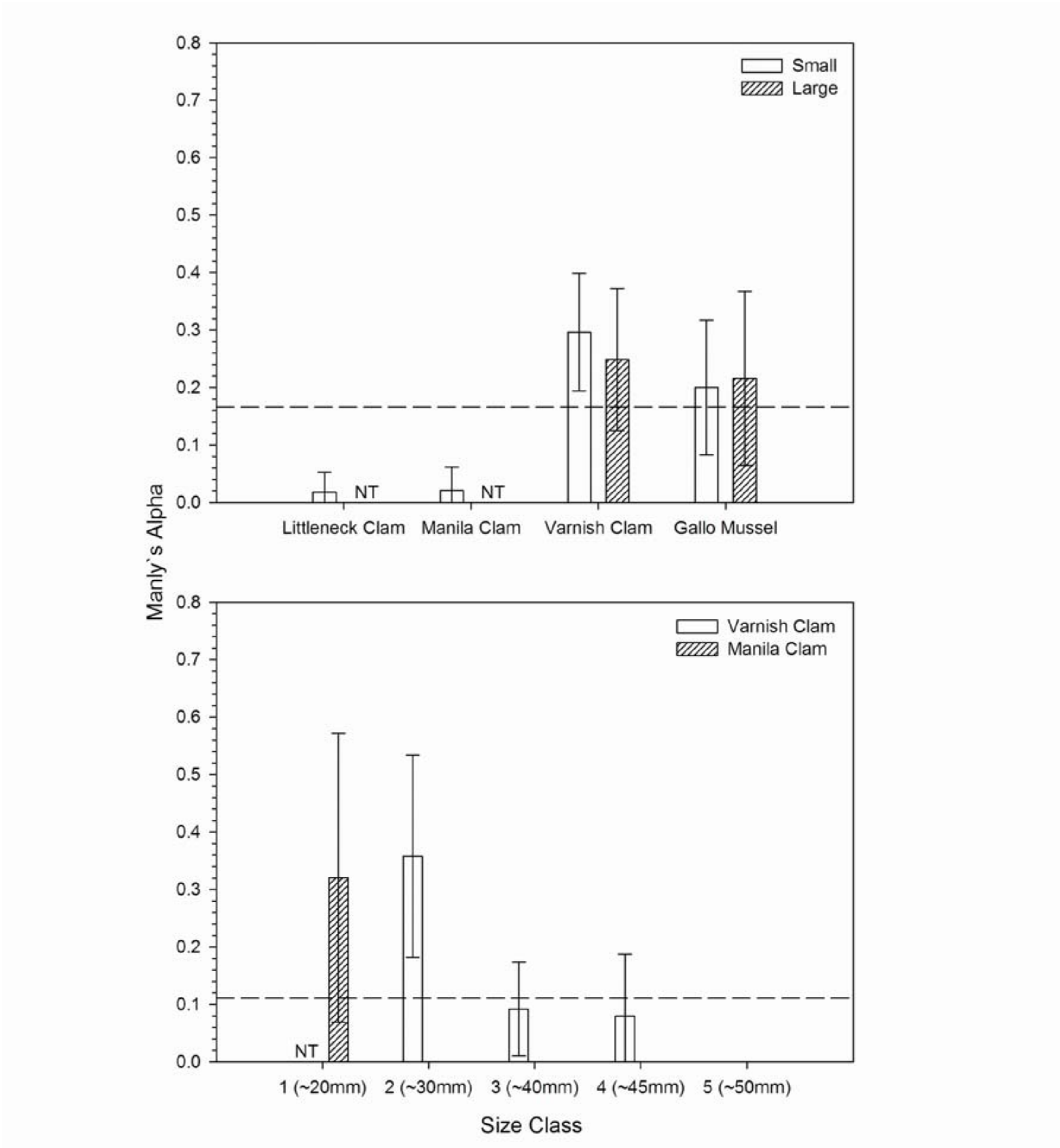

Figure 2. Mean (± 95% CI) adult green crab (*Carcinus maenas* Linnaeus, 1758) prey preference values (Manly's α) for (A) small littleneck clams (*Leukoma staminea* Conrad 1837), small Manila clams (*Venerupis philippinarum* Adams and Reeve, 1850), small and large varnish clams (*Nuttallia obscurata* Reeve, 1857), and small and large Gallo mussels (*Mytilus galloprovincialis* Lamarck, 1819) (n = 12) and (B) five size classes of Manila clams and four size classes of varnish clams (n = 10). NT = not tested. Dashed lines denote value of zero preference (0.167 and 0.111 for A and B, respectively). Values above dashed lines indicate prey preference, values below indicate avoidance. Values where CI does not overlap the dashed line are significant (P < 0.05).