A Biological Synopsis of the

European Green Crab, *Carcinus maenas*

Greg Klassen and Andrea Locke

Fisheries and Oceans Canada, Gulf Fisheries Centre,
P.O. Box 5030, Moncton, NB, E1C 9B6

2007

Canadian Manuscript Report of

Fisheries and Aquatic Sciences 2818

Fisheries and Oceans   Pêches et Océans

Canada

Canadian Manuscript Report of
Fisheries and Aquatic Sciences No. 2818

2007

A BIOLOGICAL SYNOPSIS OF THE

EUROPEAN GREEN CRAB, *CARCINUS MAENAS*

by

G. Klassen[1] and A. Locke[2]

[1]Tau Biodiversity
49 Parkindale Rd.
Pollett River, New Brunswick
E4Z 3A7

[2]Fisheries and Oceans Canada
Gulf Fisheries Centre
P.O. Box 5030
Moncton, New Brunswick
E1C 9B6

Cat. no. Fs -97-4/2818E ISSN 0706-6473

Correct citation for this publication:

Klassen, G. and A. Locke. 2007. A biological synopsis of the European green crab, *Carcinus maenas*. Can. Manuscr. Rep. Fish. Aquat. Sci. no. 2818: vii+75pp.

Klassen, G. and A. Locke. 2007. A biological synopsis of the European green crab, *Carcinus maenas*. Can. Manuscr. Rep. Fish. Aquat. Sci. no. 2818: vii+75pp.

Abstract

A native of Europe and Northern Africa, the green crab has invaded the Atlantic and Pacific coasts of North America, South Africa, Australia, South America, and Asia. In North America, the distribution of green crabs now extends from Newfoundland to Virginia and from British Columbia to California.

Green crabs live up to 4-7 years and can reach a maximum size of 9-10 cm (carapace width). The life cycle alternates between benthic adults and planktonic larvae. Green crabs are efficient larval dispersers, but most invasions have been attributed to anthropogenic transport.

The green crab has successfully colonized sheltered coastal and estuarine habitats and semi-exposed rocky coasts. It is commonly found from the high tide level to depths of 5-6m. It is eurythermic, being able to survive temperatures from 0 to over 35°C and reproduce at temperatures between 18 and 26°C. It is euryhaline, tolerating salinities from 4 to 52‰. It is reasonably tolerant of low oxygen conditions.

Green crabs prey on a wide variety of marine organisms including commercially important bivalves, gastropods, decapods and fishes. Impacts on prey populations are greater in soft-bottom habitat and in environments sheltered from strong wave action. The species potentially competes for food with many other predators and omnivores. The predominant predators of green crabs include fishes, birds, and larger decapods.

The effects of green crabs have been of particular concern to shellfish culture and fishing industries, as well as eel fisheries. Control efforts have included fencing, trapping and poisoning. Commercial fisheries for green crab have reduced its abundance in parts of its native range.

Klassen, G. and A. Locke. 2007. A biological synopsis of the European green crab, *Carcinus maenas*. Can. Manuscr. Rep. Fish. Aquat. Sci. no. 2818: vii+x75pp.

Résumé

Le crabe vert, espèce indigène de l'Europe et de l'Afrique du Nord, a envahi les côtes atlantique et pacifique de l'Amérique du Nord, ainsi que les côtes de l'Afrique du Sud, de l'Australie, de l'Amérique du Sud et de l'Asie. En Amérique du Nord, le crabe vert s'étend désormais de la Terre-Neuve jusqu'en Virginie, et de la Colombie-Britannique à la Californie.

Le crabe vert a un cycle biologique de quatre à sept ans et sa carapace atteint une largeur maximale de neuf ou dix centimètres. Son cycle biologique alterne entre le stade benthique et la larve planctonique. Les crabes verts sont efficaces à disperser leurs larves, mais la plupart des invasions ont été provoquées par le transport anthropique.

Le crabe vert a réussi à coloniser des habitats situés dans des zones côtières et estuariennes abritées et le long de côtes rocheuses partiellement à découvert. Il fréquente autant la laisse de haute mer que les eaux de cinq à six mètres de profondeur. Le crabe vert est une espèce eurytherme, capable de survivre à des températures allant de 0 à plus de 35 ^{o}C et de se reproduire à une température variant entre 18 et 26 ^{o}C. Il est également euryhaline, c'est-à-dire qu'il peut s'adapter à un taux de salinité de 4 à 52 %. Le crabe vert tolère relativement bien les eaux à faible teneur en oxygène.

Le crabe vert se nourrit d'une grande variété d'organismes marins, notamment des bivalves, des gastropodes, des décapodes et des poissons exploités commercialement. Son impact sur les espèces proies est plus grand en habitat sur fond meuble et dans les milieux protégés des vagues fortes. Le crabe vert fait également concurrence à de nombreux autres prédateurs et omnivores. Il est la proie surtout des poissons, des oiseaux et de plus grands décapodes.

L'invasion du crabe vert est particulièrement inquiétante pour les industries de la culture et de la récolte de mollusques de même que celle de la pêche à l'anguille. L'érection de clôtures, la pose de pièges ou l'empoisonnement comptent parmi les mesures prises en vue de contrôler cette espèce nuisible. La pêche commerciale du crabe vert dans certaines parties de son aire de distribution géographique a permis d'en réduire l'abondance.

Table of Contents

1. Introduction

The European green crab or shore crab *Carcinus maenas* (hereafter, "green crab") is ranked among the 100 'worst alien invasive species' in the world (Lowe et. al. 2000). In many ways it could be considered a model invader. A native of coastal and estuarine waters of Europe and Northern Africa, it has successfully invaded the Atlantic and Pacific coasts of North and South America, as well as South Africa, Australia, and Asia. It is a voracious omnivore and aggressive competitor with a wide tolerance for salinity, temperature, oxygen, and habitat type. A large number of planktonic larvae are produced, and dispersal occurs at all life history stages (Cohen et al. 1995).

Green crab was first detected in Canadian waters in 1951 when the introduced New England population spread into Passamaquoddy Bay in the Bay of Fundy (Leim 1951). In reference to its arrival, Hart (1955) wrote:

> The green crab (*Carcinides maenas*), which has entered and spread throughout the Bay of Fundy since 1950, has become our most serious clam predator. It destroys adult clams as well as those of seed size. Feeding experiments conducted this year have demonstrated that it will also destroy young oysters and quahaugs. Studies of its spread show that there is serious risk of its extending its range to the Gulf of St. Lawrence where it might do enormous damage.

Subsequently, the green crab did arrive in the Gulf of St. Lawrence as well as western Canadian waters (Jamieson 2000).

In all areas where the green crab has invaded, its potential for significant impacts on fisheries, aquaculture, and the ecosystem has caused concern. Numerous studies have shown the potential for green crab to adversely affect many ecosystem components, directly and indirectly, by predation, competition and habitat modification (Grozholz and Ruiz 1996). Because green crab has the ability to modify entire ecosystems, it is considered an "ecosystem engineer" (Crooks 2002).

Published estimates of the cost of green crabs in Canadian waters are incomplete and of questionable validity. Colautti et al. (2006) used economic losses attributed to 21 other non-indigenous species to propose median (52% loss) and half-quartile (20%) cases as projections of maximum and minimum cost range for any invasive species. Using these projections, the potential economic impact of green crabs on bivalve and crustacean fisheries and aquaculture in the Gulf of St. Lawrence was estimated as \$42-\$109 million (Colautti et al. 2006). The only other published estimate of costs of green crab on the Atlantic coast of North America, a value of \$44 million, has been shown by Carlton (2001) and Hoagland and Jin (2006) to be based on an incorrect citation in a summary paper by Pimentel (2000). Unfortunately, repeating Pimentel's error, this estimate has been widely cited in the scientific literature as the actual cost of the green crab invasion of New England and Atlantic Canada. In fact, the \$44 million represented an estimate by

Lafferty and Kuris (1996) of the potential, not actual, cost of green crab for a hypothetical (at that time) invasion of the west coast up to Puget Sound.

Apart from fisheries, ecosystem services, biodiversity, and other values could potentially be affected by green crabs. Just one example is the removal of nutrients from eutrophic coastal systems by bivalves, a major prey of green crabs. Rice (2001) estimated that for every kg of shellfish tissue harvested, 16.8 g of nitrogen is removed from the water body. In eutrophic coastal waters, this is a valuable ecosystem service that in some watersheds may be responsible for preventing anoxia.

Fisheries and Oceans Canada will be undertaking an ecological risk assessment of green crab in Canada in 2008. The purpose of the present document is to review the literature relevant to the history, ecology and potential consequences of green crabs in Canadian waters, as a precursor to the risk assessment.

1.1. Name and classification

Phylum Arthropoda
  Class Malacostraca
    Order Decapoda
      Family Portunidae
        Genus and species: *Carcinus maenas* (Linnaeus, 1758)
        (In older literature, the genus was *Carcinoides*, sometimes written as *Carcinides*.)

Common Names: European green crab, green crab, shore crab, European shore crab; le crabe vert, le crabe vert europeén, le crabe enragé.

In this document, we refer to the species as “green crab”.

1.2. Description

The following description of the adult green crab is based on Say (1817) and Squires (1990). Larval stages typically include four zoeal stages and a megalopa stage (described in detail by Rice and Ingle 1975).

Portunidae are characterized by wide carapaces, a dentate anterior margin, and a leaf-shaped, dorso-ventrally flattened fifth leg that is usually adapted for swimming.

The genus *Carcinus* has 5 teeth on the antero-lateral margin of the carapace, orbit with a dorsal fissure, the front of carapace slightly projected with rounded rostral area. The fifth leg is only slightly dilated and not paddle-like.

Carcinus maenas is a medium sized crab, broader than long (width to length ratio approximately 1.5:1). Adult size: length up to about 6 cm; width up to about 9 cm.

Thorax granulate, with five lateral spines/teeth of about equal size on either side of the rostrum. Sides of the thorax beneath, furnished with silky hair. Orbit subovate, a fissure above, an obtuse tooth beneath the anterior canthus, and a fissure beneath the hind one. Rostrum (Say's clypeus) only slightly protruding with three very obtuse subequal teeth, middle one smaller. Body and feet spotted with brown and covered with minute, crowded granules, those of the thorax more conspicuous, distant and tuberculiform; spots of the feet and abdomen impressed and placed in more or less obvious lines. Chelae large and slightly unequal with the second and third joint ciliate before, the latter concave above, not longer than the edge of the thorax, with a very obtuse tooth at tip and impressed transverse line; Carpus acutely spined within, no spine on the opposite edge; Hand convex on the back, an elevated line above on the inner side, fingers striate with impressed lines, about four on the thumb, not falcate at tip. Second to fourth walking legs about equal. Fifth leg more compressed with dactyl wider but not spatulate as in other Portunidae. Abdomen of male triangular, somites 3-5 fused.

1.3. Potential for misidentification

In Europe, the green crab can be mistaken for its congener *Carcinus aestuarii* (Nardo, 1847), which replaces *C. maenas* as the common representative of this genus in the Mediterranean Sea and is therefore sometimes called *C. mediterranae* or *C. mediterraneus* Czerniavsky, 1884. *C. aestuarii* is an invasive species in Japan and South Africa but has not been reported from North America. Following much discussion in the scientific literature as to whether the two taxa are distinct species or subspecies (see Clark et al. 2001), Roman and Palumbi (2004) have identified a clear genetic break between Mediterranean and Atlantic forms, supporting their species-level status.

Cohen et al. (1995) distinguished *C. maenas* from *C. aestuarii* based on the following characters: male pleopods curved outwards; carapace texture slightly granulated, not hairy; females with sparse or no hair on rostrum, males with no hair; rostrum not notably protuberant; no hair on antero-lateral border of carpus; fifth antero-lateral tooth of carapace directed forwards. For further comparison of the two species see Behrens Yamada and Hauck (2001).

In eastern Canada, the green crab has often been confused with native rock crabs (*Cancer irroratus, C. borealis*), lady crabs (*Ovalipes ocellatus*), and mud crabs (*Neopanope sayi, Rhithropanopeus harrisi*) (Locke, pers. obs., based on five years experience with an "invasive species reporting hotline"). Blue crabs (*Callinectes sapidus*) and gulf weed crabs (*Portunus sayi*), which are not native to eastern Canada but may be advected into Canadian waters by the Gulf Stream, have also been mistaken for green crabs. For more information on the taxonomic distinctions of these species the reader is referred to Squires (1990).

Crab diversity on the west coast is higher than on the east coast, and there is much potential for confusion about green crab identification. Most erroneous public reports of green crabs in British Columbia have been records of northern kelp crabs (*Pugettia* *productus*), helmet crabs (*Telmessus cheiragonus*), or, less frequently, spotted rock crabs (*Cancer antennarius*) or purple or yellow shore crabs (*Hemigrapsus nudus* and *H. oregonensis*, respectively) (G. Gillespie, pers. comm.). The widely used guide to British Columbia crabs by Hart (1982) does not address the differences between native species and the green crab because the latter was not present on the west coast at the time of publication.

2. Distribution

2.1. Native distribution

The green crab (*Carcinus maenas*) is native to European and North African coasts as far as the Baltic Sea in the east, Iceland and central Norway in the west and north, and Morocco and Mauritania in the south (Williams 1984). It is one of the most common crabs throughout much of its range.

In the Mediterranean Sea, it is replaced by the congeneric species *Carcinus aestuarii* (also known as *C. mediterranae* or *C. mediterranius*).

2.2. Non-native distribution

Green crabs were first observed on the east coast of North America in Massachusetts in 1817, and now occur from Newfoundland to Virginia (Grosholz and Ruiz 1996; C. McKenzie, Fisheries and Oceans Canada, pers. comm.). Densities of green crabs are reduced in the southern part of the range, with a marked transition zone of declining abundance in New Jersey (McDermott 1998). The range in eastern North America extends over about 1000 linear km of coast (Jamieson 2000).

In 1989, green crab was found in San Francisco Bay, California, on the Pacific coast of the United States (Grosholz and Ruiz 1996). It started extending its range in 1993 and reached Oregon in 1997, Washington state in 1998 and British Columbia in 1999 (Jamieson 2000). Genetic studies have shown that the west coast populations belong to the lineage that has been present on the east coast of North America since the 1800s (Bagley and Geller 1999).

Green crab was first reported in Australia in the late 19th century, in Port Phillip Bay, Victoria. It has since spread along the coast of Victoria, reaching New South Wales in 1971, South Australia in 1976 and Tasmania in 1993. One specimen was found in Western Australia in 1965, but no green crabs have been reported in the area since then (Thresher et al. 2003, Ahyong 2005).

Green crab first reached South Africa in 1983, near Cape Town (Le Roux et al. 1990). From genetic evidence, Geller et al. (1997) report multiple ‘cryptic’ invasions of both *Carcinus* species in South Africa.

In 2003, green crab was recorded from the Atlantic coast of South America in Patagonia, Argentina (Hidalgo et al. 2005). Size distribution of the crabs suggested that they had been present in the area for three to four years before their discovery, assuming they arrived as larvae. An analysis of seawater temperatures in the area indicated they should be able to colonize the east coast of South America from southern Brazil (29˚ S) to the mouth of the Magellan Strait (52˚ S) (Hidalgo et al. 2005). At least two introductions in Brazil north of this zone during the 1800s failed to establish (Carlton and Cohen 2003).

Green crab has been recorded, but apparently did not successfully establish populations, in waters of the Red Sea (before 1817), Brazil (Rio de Janeiro [23˚ S] in 1857 and Pernambuco [8˚ S] before 1899), Panama (Pacific coast, 1866), Sri Lanka (1866-1867), Hawaii (1873), Madagascar (1922), Myanmar (1933), Perth, Australia (1965) and Pakistan (1971) (Boschma 1972, Carlton and Cohen 2003).

A related crab, either *C. aestuarii* or a hybrid of *C. aestuarii* and *C. maenas,* has successfully invaded Japan (Rogers 2001, Carlton and Cohen 2003).

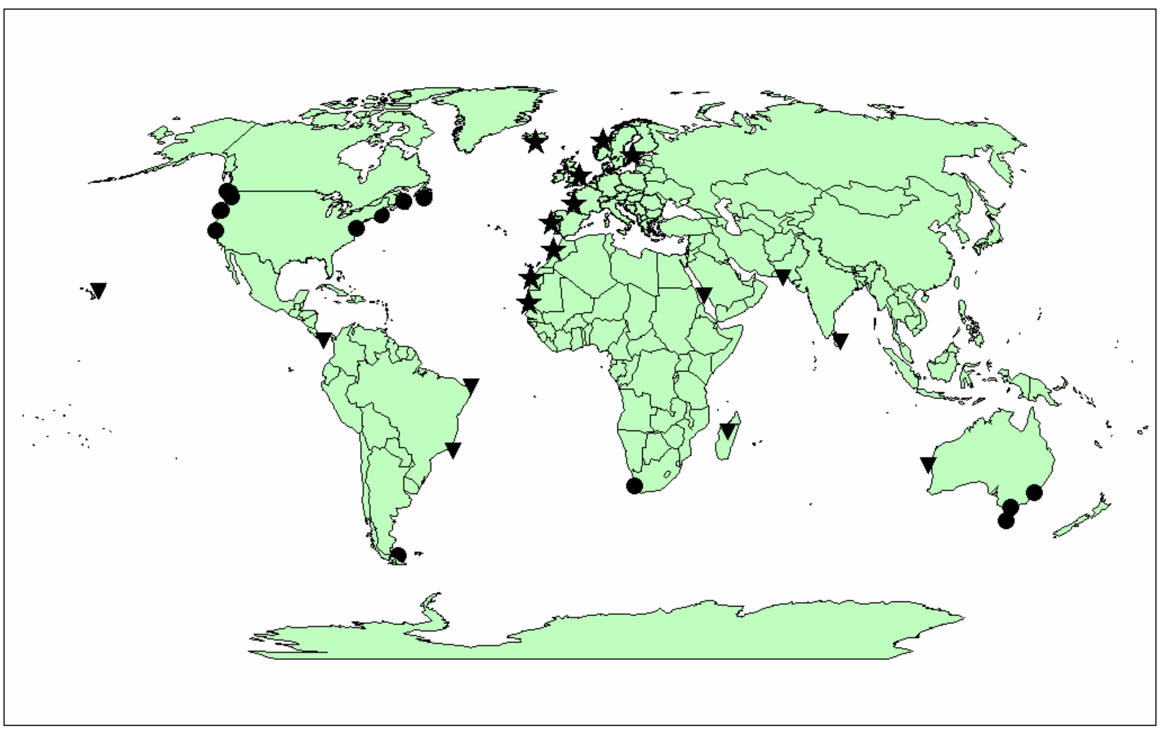

Fig. 1. Worldwide distribution of green crabs. Stars indicate native range. Circles indicate successful establishment of an introduced population. Triangles indicate failed introductions.

2.3. Distribution and history in Atlantic Canada

Distribution of green crab in Atlantic Canada in 2007 included the Bay of Fundy, Atlantic coast of Nova Scotia, Nova Scotian coast of Northumberland Strait and most of Cape Breton Island, Baie Verte and Cape Jourimain on the New Brunswick coast of Northumberland Strait, the eastern end of Prince Edward Island (Savage Harbour and Victoria are the western boundaries of distribution on the north and south coasts, respectively), the Magdalen Islands, and Placentia Bay, Newfoundland (Locke and Hanson unpub. ms., Paille et al. 2006, C. McKenzie pers. comm.).

The first report of green crab in Canadian waters was from the Digdeguash River, Passamaquoddy Bay, in July 1951 (Leim 1951, MacPhail 1953). The species was commonly observed at several points in the northeastern part of Passamaquoddy Bay in the summer of 1951, and on the American side of the Bay at Perry, Maine, in October 1951 (Leim 1951, Scattergood 1952). Green crab was seen again in Passamaquoddy Bay in 1952, but there was no evidence of it having extended further up the Bay of Fundy; extensive sampling on the Lepreau Ledges did not collect it (Day and Leim 1952). However, the species "appeared in great numbers" on all flats in Passamaquoddy Bay in the early summer of 1953, and by September was observed to be equally numerous in Pocologan Harbour and Lepreau Basin (MacPhail 1953). It was found at Sandy Cove on the northern shore of St. Mary Bay, NS, in August 1953 and at Pereau River in Minas Basin in November 1953 (MacPhail 1953). In 1954, MacPhail and Lord (1954) found a specimen at Wedgeport, NS, the first Canadian sighting outside the Bay of Fundy. The population in the Bay of Fundy continued to expand in 1954; during May and June, green crabs were again present in great numbers in the rocky areas of flats in Passamaquoddy Bay. It was not uncommon to find up to 50 crabs under a single rock, none of them > 5 cm in carapace width (CW) (MacPhail and Lord 1954). In July, MacPhail and Lord (1954) set two small traps at Holt's Point, Passamaquoddy Bay, one near low water in a rocky area where clam diggers were working, and the other on a sand beach without clams but with mussel beds. These baited traps were fished daily for 24 days, and caught an average 279-343 crabs/d. There was no evidence of a decrease in daily catch rate although a total of 14,915 crabs were taken. Only 23% of the crabs exceeded 5 cm CW. Trapping at Sissiboo River, NS, showed that green crabs were present but not yet abundant in that area. The mean catch/trap/day was < 2 crabs. Of the 207 crabs taken in 42 days by three traps, 57% of the crabs were > 5 cm CW. Shortly afterward, the numbers of green crabs in the Bay of Fundy started to decline: from 343 crabs/d in 1954, the site at the mouth of the Bocabec River yielded 53 crabs/d in 1958, 41 crabs/d in 1959 and 7.5 crabs/d in 1960 (Anon. 1961). A similar decline in northeastern Maine was attributed to a cooling trend and high overwintering mortality (Welch 1968).

During the early stages of invasion of the green crab, Hart (1955) wrote:

> The green crab (*Carcinides maenas*), which has entered and spread throughout the Bay of Fundy since 1950, has become our most serious clam predator. ... Progress Reports, Circulars and news reports have been issued to elicit information about the spread of the animal and to warn the

> public of the potential danger. It is hoped that in this way introductions of the animal to the Gulf of St. Lawrence through carelessness or ignorance may be avoided. So far there is no evidence that the crab has spread eastward beyond Wedgeport, N.S., the limit of its range last year. There is evidence from our trapping experiments of a decrease in abundance this year in parts of the Bay of Fundy. This may indicate that some natural control of abundance is taking effect.

Similarly from the circular written by Medcof and Dickie (1955), requesting information from the public:

> The green crab is a serious clam enemy…We know little about its food habits or what would happen if it pushed its way into other clam areas or into oyster areas like the Bras d'Or Lakes and the southern Gulf of St. Lawrence… While searching for some means of control the Fisheries Research Board is trying to keep up to date in knowing how far the animal has extended its range. We need all the information we can get about this new menace to our shellfish stocks.

The spread of green crabs along the Atlantic coast of Nova Scotia was poorly documented. Audet et al. (2003) reconstructed part of this history from unpublished museum records and interviews with fishermen. From Lockeport in 1960, green crabs reached Peggy's Cove by 1964 and Prospect Bay by 1966. Studies of intertidal animals conducted along the coast between Halifax and St. Marys River between 1965 and 1973 did not detect any expansion of green crabs into this area. Roff et al. (1984) found larval green crabs in the Scotian Shelf plankton but only in the waters off southwestern Nova Scotia in 1977-1978. Interestingly, about this time a mussel grower at Whitehead, near Chedabucto Bay, collected green crabs 600 km north of this known distribution (Audet et al. 2003). By 1982-1983, green crabs were present along the eastern shore at Marie-Joseph and Tor Bay. Green crabs probably entered Chedabucto Bay around 1985 (Audet et al. 2003). Interviewees (mainly harvesters of lobsters, crabs, oysters, clams, or eels) had first seen green crabs in Cape Breton and the Bras d'Or Lakes in 1991-1995, and in Halifax, Guysborough, Victoria and Richmond counties in 1996-2000 (Tremblay et al. 2006). Green crabs were present throughout the Bras d'Or Lakes in 1997 and up the Atlantic coast of Nova Scotia at least to Ingonish (Audet et al. 2003). Annual sampling from 1997 to 2001 did not detect green crabs at South Harbour.

The earliest confirmed sighting of green crabs in the southern Gulf of St. Lawrence was recorded by M. Dadswell (Acadia University, pers. comm.), who collected settling green crabs in spat bags in Aulds Cove, St. Georges Bay, near the Canso Causeway ship locks in 1994. Green crabs were not present in similar samples collected by Dadswell in 1993. Dadswell's 1994 record predates published reports from St. Georges Bay, with adult crabs recorded in 1995 (Jamieson 2000) or 1997 (Audet et al. 2003). Previously, the earliest (but unverified) report of green crab in the southern Gulf had been at Margaree Harbour in 1994 or 1995, as recounted to Audet et al. (2003) by fishermen. In 1997, green crabs were present along the entire western shore of Cape

Breton Island as far north as Pleasant Bay, and west along the mainland to Malignant Cove.

The rate of dispersal throughout Northumberland Strait and Prince Edward Island has been rapid, with range expansions exceeding 100 km/yr in some cases (Locke and Hanson unpub. ms.). For the most part, the distribution is still restricted to the eastern part of the southern Gulf of St. Lawrence. From Malignant Cove in 1997, the western limit on the mainland moved to Merigomish in 1998, Caribou River in 1999, Tatamagouche Bay in 2000, Wallace Bay in 2001 and Baie Verte near the mouth of the Gaspereau River in 2002. Green crabs were detected at Cape Jourimain in 2006. The first report in PEI was from the Georgetown area in 1996. In 1998, green crabs were distributed from Naufrage to Vernon Bridge. In 1999, the distribution was from North Lake to Gascoigne Cove (Wood Island). In 2000, green crabs were found in the Charlottetown Harbour in Hillsborough River. In 2001, the distribution was from Savage Harbour to Victoria. An isolated green crab sighting in Malpeque Bay, PEI, in November 2000 (Locke et al. 2003), apparently did not result in establishment of a viable population, as no specimens have been found in the area since that time (N. MacNair, PEI Dept. of Agriculture, Fisheries and Aquaculture, pers. comm.).

There were unconfirmed reports of green crab in the Magdalen Islands before 2001, but those that have been followed up were other species such as mud crabs (L. Gendron, DFO, Mont-Joli, pers. comm.). Green crabs were, however, confirmed to be in the Magdalen Islands in 2004 (Paille et al. 2006). They were present in low numbers in 2005 and 2006, and as of December 2006 there had been no evidence of reproduction (Paille et al. 2006, N. Simard, DFO, Mont-Joli, QC, pers. comm.).

Green crab was reported for the first time in Newfoundland in August 2007 (C. McKenzie, DFO, St. John's, NL, pers. comm.). Specimens from juvenile to adult were discovered in North Harbour, Placentia Bay, on the southern coast of Newfoundland. While no ovigerous females were observed, the high abundance and presence of a range of what appeared to be three or four age groups as well as mated pairs in amplexus, suggested that this was an established population. Fishermen reported seeing similar crabs in the harbour for about four years. More extensive surveys conducted in September 2007 detected crabs at other sites in Placentia Bay: Davis Cove, Swift Current, Goose Cove, Come-By-Chance, Arnold's Cove, Southern Harbour, and Black River. Green crab populations at these sites appeared to be in early stages of establishment, dominated by juvenile crabs, with only a few adults at each site (C. McKenzie, pers. comm.).

An interesting element of the dispersal history of green crabs in Atlantic Canada is the way that the invasion apparently "stalled" on the Atlantic coast of Nova Scotia south of Halifax with a time lag of over a decade before green crab appeared at Chedabucto. Genetic analysis by Roman (2006) indicated a shift in green crab genotypes in this zone, consistent with a *de novo* introduction to northern Nova Scotia. Populations found all along the eastern seaboard of the USA were of a single type. At least five genotypes found in northern Nova Scotia and the southern Gulf of St. Lawrence occurred nowhere else in eastern North America; several of these lineages originated from North Sea populations (Roman 2006). South of Halifax, and into the Bay of Fundy, there was a mixture of genotypes with both the US form and northern Nova Scotian forms represented. Roman (2006) suggested that the *de novo* introduction occurred either in Halifax or Chedabucto Bay, both of which are major ports receiving commercial traffic from northern Europe. Predominantly southerly coastal currents would have more readily spread the new genotypes from Chedabucto Bay to Halifax than the reverse, although current reversals can occur (D. Brickman, DFO, Dartmouth, pers. comm.). It is tempting to speculate that the observation of green crabs in the late 1980's at Whitehead, just south of Chedabucto Bay (Audet et al. 2003), was the *de novo* introduction suggested by Roman's data.

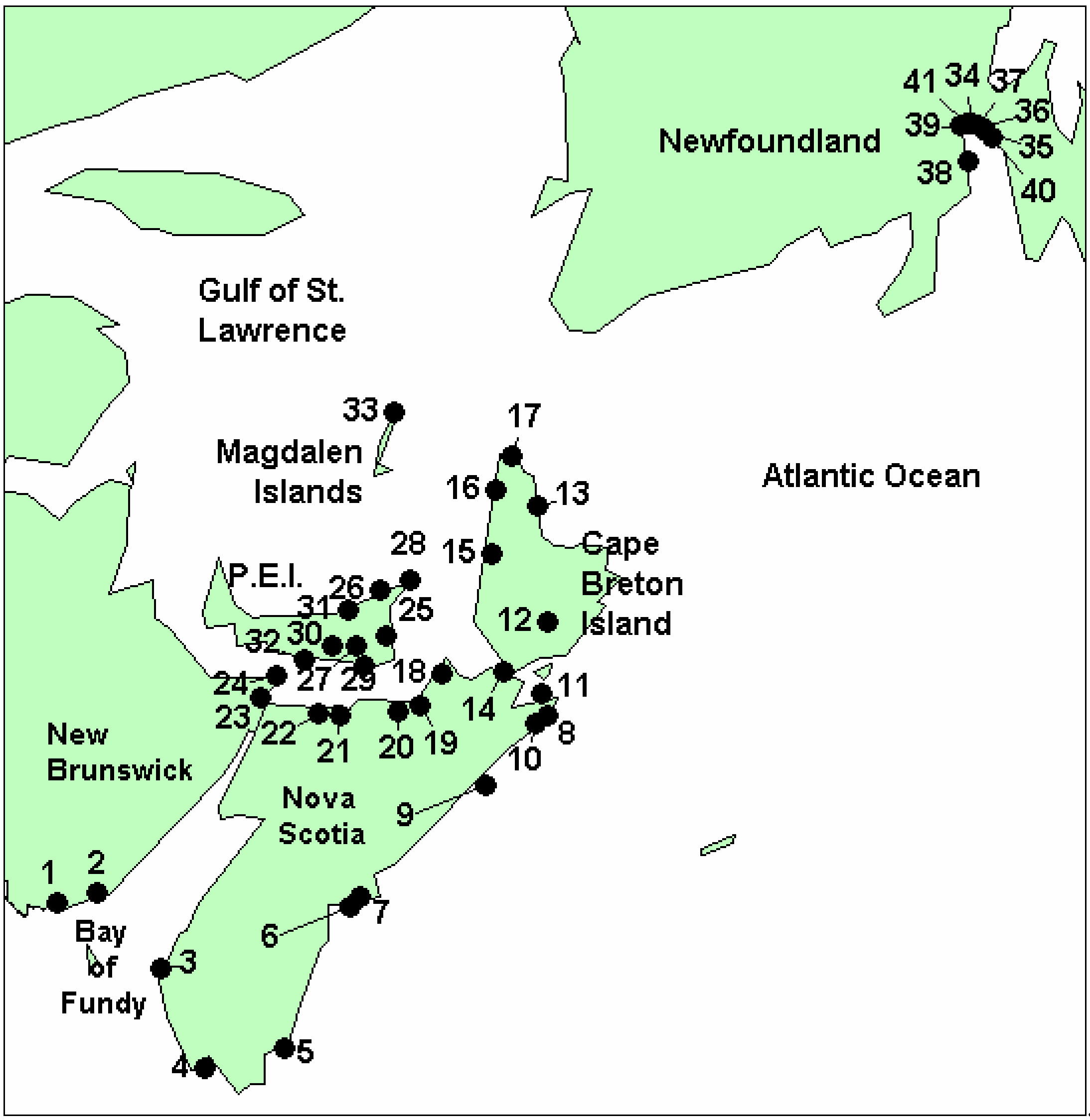

Fig. 2. Distribution of green crabs in Atlantic Canada. Locations are identified by number, see Table 1.

Table 1. Distribution and timing of spread of green crabs in Atlantic Canada. This is not a comprehensive list of green crab locations, but tracks the expansion of green crabs from Passamaquoddy Bay, across the Bay of Fundy, up the Atlantic coast of Nova Scotia, and into the Gulf of St. Lawrence, from 1951 to the present.

Region	Site (and number for Fig. 2)	Latitude	Longitude	Year reported	Notes	Reference
Bay of Fundy	Digdeguash R.; Passamaquoddy Bay (1)	45.150	-66.967	1951	First observation in Canada.	Leim 1951
Bay of Fundy	Lepreau Basin, NB (2)	45.133	-66.500	1953		MacPhail 1953
Bay of Fundy	Sandy Cove (St. Mary Bay), NS (3)	44.491	-66.089	1953		MacPhail 1953
Atlantic shore NS	Wedgeport, NS (4)	43.740	-65.980	1954		MacPhail and Lord 1954
Atlantic shore NS	Lockeport, NS (5)	43.700	-65.099	1960		Audet et al. 2003
Atlantic shore NS	Peggy’s Cove, NS (6)	44.483	-63.916	1964		Audet et al. 2003
Atlantic shore NS	Prospect Bay, NS (7)	44.517	-63.782	1966		Audet et al. 2003
Atlantic shore NS				1965-1973	Not present between Halifax and St. Marys River	Audet et al. 2003
Atlantic shore NS	Whitehead, NS (8)	45.250	-61.166	~1978	~600 km N of known distribution; possible *de novo* introduction?	Audet et al. 2003

Region	Site (and number for Fig. 2)	Latitude	Longitude	Year reported	Notes	Reference
Atlantic shore NS	Marie-Joseph, NS (9)	44.950	-62.066	1982-1983		Audet et al. 2003
Atlantic shore NS	Tor Bay, NS (10)	45.233	-61.316	1982-1983		Audet et al. 2003
Atlantic shore NS	Chedabucto Bay, NS (11)	45.400	-61.132	~1985		Audet et al. 2003
Atlantic shore NS	Bras d'Or Lake, NS (12)	45.860	-60.779	1997		Audet et al. 2003
Atlantic shore NS	Ingonish, NS (13)	46.633	-60.416	1997		Audet et al. 2003
Atlantic shore NS				1997-2001	Not present at South Harbour (Aspy Bay, NS)	Audet et al. 2003
Gulf of St. Lawrence	Aulds Cove, NS (14)	45.648	-61.437	1994	First observation in Gulf of St. Lawrence; near the ship lock at Canso Causeway	M. Dadswell, pers. □omm..
Gulf of St. Lawrence	Margaree Harbour, NS (15)	46.433	-61.099	1994 or 1995		Audet et al. 2003
Gulf of St. Lawrence	Pleasant Bay (Cape Breton I.), NS (16)	46.830	-60.799	1997		Audet et al. 2003
Gulf of St. Lawrence	St. Lawrence Bay (Cape Breton I.), NS (17)	47.017	-60.482	1998		Jamieson 2000

Region	Site (and number for Fig. 2)	Latitude	Longitude	Year reported	Notes	Reference
Gulf of St. Lawrence	Malignant Cove (St. Georges Bay), NS (18)	45.783	-62.082	1997		Audet et al. 2003
Gulf of St. Lawrence	Merigomish, NS (19)	45.633	-62.449	1998		Locke et al. unpub. data
Gulf of St. Lawrence	Caribou River, NS (20)	45.633	-62.699	1999		Locke et al. unpub. data
Gulf of St. Lawrence	Tatamagouche Bay, NS (21)	45.750	-63.316	2000		Locke et al. unpub. data
Gulf of St. Lawrence	Wallace Bay, NS (22)	45.817	-63.532	2001		Locke et al. unpub. data
Gulf of St. Lawrence	Gaspereau River (Baie Verte), NB (23)	46.050	-64.083	2002		Locke et al. unpub. data
Gulf of St. Lawrence	Cape Jourimain (Northumberland Strait), NB (24)	46.150	-63.833	2006		R. Hart, pers. comm.
Gulf of St. Lawrence (PEI)	Georgetown, PEI (25)	46.167	-62.533	1996		N. MacNair, pers. comm.
Gulf of St. Lawrence (PEI)	Naufrage, PEI (26)	46.467	-62.417	1998		N. MacNair, pers. comm.
Gulf of St. Lawrence (PEI)	Vernon Bridge, PEI (27)	46.167	-62.883	1998		N. MacNair, pers. comm.

Region	Site (and number for Fig. 2)	Latitude	Longitude	Year reported	Notes	Reference
Gulf of St. Lawrence (PEI)	North Lake, PEI (28)	46.467	-62.067	1999		N. MacNair, pers. comm.
Gulf of St. Lawrence (PEI)	Gascoigne Cove (Wood Island), PEI (29)	46.017	-62.883	1999		N. MacNair, pers. comm.
Gulf of St. Lawrence (PEI)	Charlottetown Harbour, PEI (30)	46.217	-63.133	2000		Locke et al. unpub. data; N. MacNair pers. comm.
Gulf of St. Lawrence (PEI)	Savage Harbour, PEI (31)	46.417	-62.833	2001		N. MacNair, pers. comm.
Gulf of St. Lawrence (PEI)	Victoria, PEI (32)	46.200	-63.483	2001		N. MacNair, pers. comm.
Gulf of St. Lawrence (PEI)				2002-2006	No spread in PEI.	N. MacNair, pers. comm.
Gulf of St. Lawrence	Grande Entrée Lagoon (Magdalen Islands), QC (33)	47.585	-61.551	2004		N. Simard, pers. comm.
Atlantic shore Newfoundland	North Harbour, Placentia Bay, NL (34)	47.860	-54.103	2007	First observation in Newfoundland.	C. McKenzie, pers. comm.

Region	Site (and number for Fig. 2)	Latitude	Longitude	Year reported	Notes	Reference
Atlantic shore Newfoundland	Arnold’s Cove, Placentia Bay, NL (35)	47.765	-53.989	2007		C. McKenzie, pers. comm.
Atlantic shore Newfoundland	Come-by-Chance, Placentia Bay, NL (36)	47.808	-54.022	2007		C. McKenzie, pers. comm.
Atlantic shore Newfoundland	Goose Cove, Placentia Bay, NL (37)	47.905	-53.807	2007		C. McKenzie, pers. comm.
Atlantic shore Newfoundland	Davis Cove, Placentia Bay, NL (38)	47.635	-54.340	2007		C. McKenzie, pers. comm.
Atlantic shore Newfoundland	Swift Current, Placentia Bay, NL (39)	47.891	-54.235	2007		C. McKenzie, pers. comm.
Atlantic shore Newfoundland	Southern Harbour, Placentia Bay, NL (40)	47.714	-53.969	2007		C. McKenzie, pers. comm.
Atlantic shore Newfoundland	Black River, Placentia Bay, NL (41)	47.880	-54.169	2007		C. McKenzie, pers. comm.

2.4. Distribution in Pacific Canada

Green crab was first reported in British Columbia in 1999 (Jamieson 2000). It was thought to have reached British Columbia in 1998 by larval transport from the northwestern USA either in strong northbound currents associated with El Niño (Jamieson et al. 2002, Behrens Yamada et al. 2005) or via shipping (Jamieson 2000). Jamieson (2000) originally suggested an anthropogenic vector was likely as green crab was initially found only at the heads of two bays in areas frequented by vessels, but the crabs found in Canada were all of a size consistent with the 1997/1998 year class and this combined with ocean current analyses conducted by Jamieson et al. (2002) suggested that oceanographic transport between November 26 1997 and February 25 1998 was the most likely vector. This dispersal event displaced green crabs approximately 650 km from Coos Bay, Oregon, their most northerly recorded location before the 1997/98 El Niño (Jamieson et al. 2002).

The initial reports of green crab in 1999 came from Barkley Sound on the southwestern coast of Vancouver Island, and Esquimalt Harbour on the southeastern tip of Vancouver Island near Victoria (Gillespie et al. 2007). By 2000, green crab was reported further north along the southwestern coast of Vancouver Island, in the Clayoquot Sound and Nootka/Esperanza areas. In 2005, it was found as far north as Kyoquot on the northwestern coast of Vancouver Island. No comprehensive surveys were undertaken until 2006, when green crabs were confirmed from sites throughout the previously reported range on the west coast of Vancouver Island, bounded by Brooks Peninsula to the north and Barkley Sound to the south. No green crabs were found in sites sampled on the eastern side of Vancouver Island (Johnstone Strait, Desolation Sound, Discovery Passage, Saanich Inlet) or in Juan de Fuca Strait (Sooke). Preliminary results of the 2007 survey continued to indicate no green crabs on the east side of Vancouver Island (Knight Inlet, Booker Lagoon, Drury Inlet and Blunden Harbour) or the British Columbia mainland north of Vancouver Island (Smith Sound and Rivers Inlet) (G. Gillespie, pers. comm.). On the west coast of Vancouver Island, green crabs were captured at three sites (Winter Harbour, Quatsino Sound and Klaskino Inlet) north of the previously known limit at Brooks Peninsula, as well as sites south of Brooks Peninsula (G. Gillespie, pers. comm.). To date, the only sighting in British Columbia other than on the west coast of Vancouver Island is the single specimen reported at Esquimalt Harbour in 1999.

Abundance of green crabs on Vancouver Island in 2006 and 2007 remained low in comparison to Atlantic Canada. In 2006, green crabs were captured at 60% of sites in Barkley Sound, 44% of sites in Clayoquot Sound and 58% of sites in Nootka/Esperanza. Catch rates based only on the sites where green crabs were found were: 1.93 crabs/trap-day for Barkley Sound, 0.47 crabs/trap-day for Nootka/Esperanza and 0.37 crabs/trap-day for Clayoquot Sound. The site with the highest abundance, Pipestem Inlet, yielded 2.28 crabs/trap-day (Gillespie et al. 2007). In 2007, green crabs were captured in 11% of sites in Quatsino Sound, 100% of sites in Winter Harbour, 80% of sites in Klaskino Inlet, 80% in Kyoquot Sound, 67% in Mary Basin, 25% in Tlupana Inlet, and 75% in Sydney Inlet. Most catch rates were low, with fewer than 1 crab/trap-day captured in Klaskino and

Sydney Inlets. Preliminary data indicated >10 crabs/trap-day captured in Winter Harbour and >20 crabs/trap-day in Pipestem Inlet (G. Gillespie, pers. comm.).

In 2002, Jamieson et al. (2002) found no evidence of successful reproduction of green crabs on Vancouver Island. By 2006, local breeding populations had apparently been established, with multiple year-classes present at several sites and one ovigerous female captured during surveys (Gillespie et al. 2007). Five ovigerous and 13 spent females were captured in Pipestem Inlet in April 2007, and three mating pairs were collected there in July 2007 (G. Gillespie, pers. comm.).

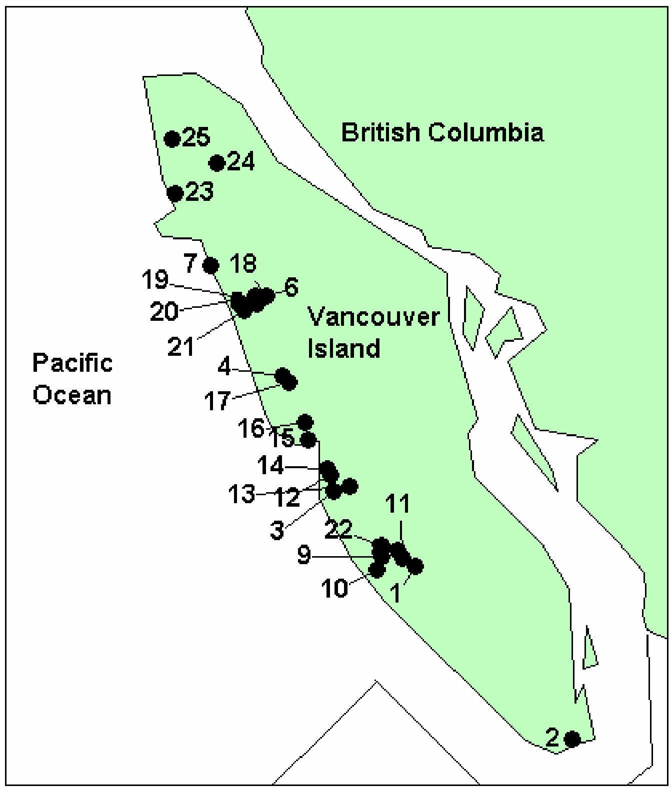

Fig. 3. Distribution of green crabs in Pacific Canada. Locations are identified by number, see Table 2.

Table 2. Distribution of green crabs in Pacific Canada, with year of first report at location.

Region	Site (and number for Fig. 3)	Latitude	Longitude	Year reported	Notes	Reference
Barkley Sound	Useless Inlet (1)	48.992	-125.030	1999		Jamieson 2000; Gillespie et al. 2007
Southeastern Vancouver I.	Esquimalt Harbour (2)	48.433	-123.433	1999		Gillespie et al. 2007
Clayoquot Sound	Lemmens Inlet (3)	49.213	-125.838	2000		Gillespie et al. 2007
Nootka/Esperanza	Bligh Island (4)	49.650	-126.517	2000		Gillespie et al. 2007
Nootka/Esperanza	Little Espinosa Inlet (5)	49.930	-126.907	2001		Gillespie et al. 2007
Nootka/Esperanza	Port Eliza (6)	49.915	-127.045	2002		Gillespie et al. 2007
Northwestern Vancouver I.	Kyuquot (7)	50.033	-127.367	2005		Gillespie et al. 2007
Barkley Sound	Pipestem Inlet (8)	49.038	-125.203	2005		Gillespie et al. 2007
Barkley Sound	Mayne Bay (9)	48.983	-125.317	2006		Gillespie et al. 2007
West coast Vancouver I.	Pacific Rim National Park (10)	48.918	-125.317	2006		Gillespie et al. 2007
Barkley Sound	Vernon Bay (11)	49.008	-125.143	2006		Gillespie et al. 2007
Clayoquot Sound	Cypress Bay (12)	49.275	-125.905	2006		Gillespie et al. 2007
Clayoquot Sound	Warn Bay (13)	49.255	-125.732	2006	Moult only	Gillespie et al. 2007
Clayoquot Sound	Whitepine Cove (14)	49.303	-125.948	2006		Gillespie et al. 2007
Clayoquot Sound	Whiskey Jenny Beach (15)	49.398	-126.168	2006		Gillespie et al. 2007

Region	Site (and number for Fig. 3)	Latitude	Longitude	Year reported	Notes	Reference
Clayoquot Sound	Pretty Girl Cove (16)	49.473	-126.235	2006		Gillespie et al. 2007
Nootka/Esperanza	Mooyah Bay (17)	49.630	-126.450	2006		Gillespie et al. 2007
Nootka/Esperanza	Zeballos (18)	49.982	-126.852	2006		Gillespie et al. 2007
Nootka/Esperanza	Little Espinosa Inlet (19)	49.948	-126.907	2006		Gillespie et al. 2007
Nootka/Esperanza	Espinosa Inlet (20)	49.968	-126.943	2006		Gillespie et al. 2007
Nootka/Esperanza	Queen Cove (21)	49.883	-126.983	2006		Gillespie et al. 2007
Barkley Sound	Hillier Island (22)	49.033	-125.333	2006	Moults only	Gillespie et al. 2007
Brooks Bay	Klaskino Inlet (23)	50.300	-127.833	2007		G. Gillespie, pers. comm.
Quatsino Sound	Quatsino Sound (24)	50.500	-127.583	2007		G. Gillespie, pers. comm.
Quatsino Sound	Winter Harbour (25)	50.533	-128.000	2007		G. Gillespie, pers. comm.

3. Biology and natural history

3.1. Life history

The life cycle of green crab alternates between benthic adult and planktonic larval stages. One or two clutches of eggs are produced annually. Females can spawn up to 185,000 eggs at a time (Cohen and Carlton 1995). Four zoeal and a megalopal larval stage develop in coastal waters for upward of 50 days, to a maximum of 82 days in laboratory experiments (Williams 1967, DeRivera et al. 2006). Zoeae perform active vertical migrations that enhance their export from estuaries (Quieroga et al. 1997). Megalopae utilize selective tidal stream transport to return inshore and to estuaries in order to settle and metamorphose into juvenile crabs (Quieroga 1998).

Mating takes place when the female has just molted and is still soft (Broekhuysen 1936). The male locates the female by pheromones she releases just before molting, and may carry her around with him for several days until she molts (amplexus). The male deposits spermatophores into paired organs called copulatory pouches, located near the openings of the oviducts (Broekhuysen 1936). Spermatophores may remain viable in these pouches for upwards of 4.5 months, perhaps as long as 10 or 12 months (Broekhuysen 1936). The female carries the eggs on her swimmerets for up to several months, until eggs hatch as free-swimming zoeae. The seasonal timing of these events in the life cycle of green crab is quite variable in different areas. In Basin Head Lagoon, PEI, females were ovigerous from early July to mid-September. Moulting and mating occurred after larvae were released, from August-December, with the peak in September (Sharp et al. 2003). Ovigerous females were present in northern Nova Scotia in June-October. First-stage zoeae were in the water column from June-August. Megalopae were present August-October. Newly settled juveniles were found in the summer (Atlantic coastal site) and autumn (Bras d'Or Lakes) (Cameron and Metaxas 2005). Along the central coast of Maine, most females extruded their eggs in spring (May-June). Mating took place in July to October during the female molt (the male molt was completed by the end of July). Megalopae settled in late August to early October (Berrill 1982). These patterns of reproduction in northeastern North America were very different from those found in the native range of green crab in the eastern Atlantic, where even at sites in Scotland, England, Norway and The Netherlands, ovigerous females were present throughout the year (although egg production was highest during two periods: November-December and spring-early summer), and settlement of the megalopae occurred by March (Broekhuysen 1936, Baeta et al. 2005). Reproductive cycles in western North America may be more similar to those in most of the European range. Nearshore water temperatures from northern California to British Columbia are generally comparable to those off the Atlantic coast of Nova Scotia in summer (i.e., 12-16˚C), but are warmer in the winter (i.e., 8-10˚C rather than 0-2˚C); estuaries may stay warm for an extended period of time. Therefore, more than one green crab spawning is possible each year, allowing for a longer time period of settlement than occurs with native crab species (Jamieson 2000). Little is known of the life cycle of green crabs in British Columbia, but ovigerous females have been collected in April and May, spent females in May, and mating pairs in July (Gillespie et al. 2007, G. Gillespie pers. comm.). In Belgium, ovigerous females were present from December to August; the largest females were thought to breed two or three times each year (winter, spring, and sometimes at the beginning of summer) while small females bred only once, in spring (d'Udekem d'Acoz 1993).

3.2. Larval development

Planktonic larval abundances up to ~150 individuals/m^3 have been recorded, with highest peaks reported in outer estuaries or coastal areas adjacent to estuaries, during nocturnal neap ebb tides (Queiroga et al. 1994). Newly hatched zoea larvae exhibited marked vertical migration patterns of circatidal periodicity, which enhanced their export from estuaries (where many of the adults live) to coastal waters (which are required for larval survival) (Zeng and Naylor 1996, Queiroga et al. 1997). Combining all larval stages, larvae were typically found in coastal waters at depths of 20-25 m during the day and 30-45 m at twilight (Quieroga 1996). Off Portugal, the distribution of larvae was restricted to coastal waters of the inner and middle shelf, with the older zoeal stages occurring furthest offshore, mainly about 15-20 km from the shore (Queiroga 1996). Maximum distance from shore of the larvae was 45 km.

In seawater ($32^{o}/_{oo}$), and average temperatures of 18˚C, larval development required about 4-5 days in each of the four zoeal instars and 12 days in the megalopa (Dawirs et al. 1986). Further details of temperature and salinity requirements are presented in Section 3.5.

Starvation delayed development and could double the duration of the zoeal stage (Dawirs 1984). Larvae were reasonably well adapted to natural shortages of food. Limited access to prey had little effect on survival through the zoea-I stage (Gimenez and Anger 2005), but some feeding was required early in stage I to initiate development (Dawirs 1984). Larvae could not develop to zoea-II if starved for the first half of the normal stage-I duration time, even if then fed (Dawirs 1984). Larvae could molt to zoea-II only if they had fed for at least 20% of the normal stage-I duration time (Dawirs 1984).

3.3. Age and post-settlement growth

The life span of green crabs was reported as 6 years in Maine, 5-7 years in Europe, but only 3-4 years in Oregon, perhaps related to higher growth rate along the west coast of North America as compared to the native environment or New England (Berrill 1982, Lützen 1984, Grosholz and Ruiz 1996, Behrens Yamada et al. 2001b). Adult molting occurred on average once a year (with frequency being inversely proportional to age). Molting, and consequently growth, was also affected by food availability and seasonal temperature fluctuation with 10^{o}C indicated as an important thermal barrier (see Section 3.5.1).

Size is generally measured as carapace width. Most carapace widths have been measured point-to-point, however, Gillespie et al. (2007) cautioned that carapace width may be measured differently by different agencies. The Pacific Canadian standard for research is notch-to-notch (Gillespie et al. 2007), whereas American agencies, Atlantic Canadian researchers, and Canadian regulations for legal fishing size of crabs, use point-to-point measurements of carapace width. Gillespie et al. (2007) determined the relationship between carapace width measured notch-to-notch (CW_N) and point-to-point (CW_P) as:

$$CW_N = 0.9095 (CW_P) + 0.4816 \qquad R^2 = 0.9954$$

Newly settled juveniles (young of the year) in Nova Scotia had carapace width in the range of 1-6 mm in the summer (Atlantic coastal site) and autumn (Bras d'Or Lakes) (Cameron and Metaxas 2005). In Maine, megalopae settled in late August through October, growing to a mean CW of 5.5 mm by winter. The absence of exuviae until mid-May suggested cessation of growth for at least seven months. The young crabs grew to 13-25 mm CW by the second winter (Berrill 1982). Growth rates in Maine and Nova Scotia resembled those observed in the Gullmar Fjord, Sweden, where green crabs reached ~9.5 mm CW by the end of their first winter and ~25 mm by the end of their second winter (Eriksson and Edlund 1977). Growth was much more rapid in the western USA. Newly settled crabs molted as frequently as once a week, reaching adult size (2-3 cm) by mid-summer of the first year (Behrens Yamada et al. 2005).

In Maine, the smallest ovigerous female was 34 mm CW (Berrill 1982). Females in this population matured at age 2-3, and bred 2-3 times in their lifetime (Berrill 1982). In Sweden, females also matured in two years (Eriksson and Edlund 1977). In Oregon, sexual maturity in females was usually at about 1 year of age and at a size of approximately 3 cm (Behrens Yamada et al. 2005). Likewise, maturity was reached in less than one year in the southern North Sea and English Channel (Eriksson and Edlund 1977).

Ovigerous females in Bras d'Or Lakes and eastern Nova Scotia were 40-60 mm CW (Tremblay et al. 2006). Mean size at maturity for females in Basin Head, PEI, was 43.67 ± 3.98 mm CW (Sharp et al. 2003).

Size at maturity for males in Basin Head was 49.25 ± 1.85 mm CW (Sharp et al. 2003). The maximum size recorded for males, which are usually bigger than females, was 90-100 mm CW in Oregon (Behrens Yamada et al. 2001). Males of age 2 were larger than 92 mm CW (Grosholz and Ruiz 1996). Males grew to 86 mm CW in Europe (Grosholz and Ruiz 1996). Typically, introduced populations of green crab grew to larger sizes than native populations in Europe (Table 3).

Table 3. Summary of size relationships (carapace width) of green crabs in different locations. Male and female sizes are pooled for Eastern North America. After Grosholz and Ruiz 1996.

Location	Male		Female	
	Modal size (mm)	Size class range (mm)	Modal size (mm)	Size class range (mm)
Europe	45-55	15-75	45-55	15-75
Eastern North America	50-60 (M&F)	5-80 (M&F)	Combined with male.	
Western North America	65-75	45-95	50-60	40-75
South Africa	55-65	15-75	45-55	15-75

Male reproductive success was related to size. As a reproductive strategy, some males retarded molting and entered an anecdysis phase (in which further growth is suspended to increase reproductive output). This is the basis of the colour morph distinction between green and red (males in anecdysis) phases (Styrishave et al. 2004). These red males were larger, more aggressive with thicker carapace and larger master claw, but they were physiologically compromised and were less able to tolerate environmental stressors such as low salinity.

Menge (1983) provided an equation for conversion from carapace width (CW in cm) to wet weight (WW in g):

$$WW = 0.26\ (CW)^{2.92} \qquad R^2 = 0.99$$

3.4. Habitat

Green crab was found in a variety of habitats including hard substrates of the outer coast and hard and soft substrates in protected embayments (Grosholz and Ruiz 1996). Green crab inhabited a wide range of habitats in sheltered areas including rocky intertidal, unvegetated intertidal, subtidal mud and sand, saltmarshes and seagrasses (Ray 2005). The highest abundances, especially of juveniles, often occurred in seagrass beds (Polte et al. 2005). Juvenile green crab also utilized rocks, shell hash and other cover in the intertidal zone (Jensen et al. 2002). In Europe, numbers of juvenile green crab dramatically increased following the addition of shell to a beach (Thiel and Dernedde 1994). Indeed, Thiel and Dernedde (1994) suggested that the increased abundance of mussel clumps on tidal flats, following the intensified efforts in mussel culturing in the Wadden Sea, had improved habitat availability for green crabs. In the Bras d'Or Lakes, green crab mainly occurred on bottoms consisting of mud or sand mixed with gravel and cobble, rather than in boulder type habitat (Tremblay et al. 2005).

There were clear ontogenetic differences in habitat preference. Active habitat selection at the time of settlement resulted in higher densities of juvenile green crabs on subtidal mussel beds, shell debris, eelgrass and filamentous algal patches (*Cladophora, Enteromorpha, Dictyosiphon*) as compared to open sand without shelter (Moksnes 2002, Baeta et al. 2005, Polte et al. 2005). Densities of megalopae and first instar juveniles (settlers) averaged 114-232 crabs/m^2 in mussel beds, eelgrass and filamentous algal patches versus 4 crabs/m^2 on sand. Older juveniles (2^{nd} to 9^{th} instar) were concentrated in mussel beds in significantly higher densities than in eelgrass and algal habitats, following migrations by young juveniles that could take them 20 m or more, even over open sand (Moksnes 2002). Notwithstanding the preferences described above, green crabs have been extremely adaptable to less suitable habitat. In Maine, 97% of juvenile green crabs were found beneath rocks, but the coarseness of substrate underlying rocks in many areas of New England prevented green crabs from digging in and sheltering there; in those cases, juvenile green crabs could be found among dense coverings of *Fucus* on the sides and tops of rocks and concrete slabs (Jensen et al. 2002). West coast populations appeared to be limited to *Spartina* beds, high intertidal areas and low-salinity refuges. Recruitment of green crab into intertidal oyster shell habitat may have been limited by *Hemigrapsus oregonensis* (McDonald et al. 1998).

In all regions where green crabs have been found, they were more abundant in protected embayments. Green crabs have been successful invaders of warm, sheltered coastal and estuarine habitats throughout the world. Crothers (1970) found that among six crab species studied, only green crabs reached maximum abundance on the most sheltered shores.

Griffiths et al. (1992) suggested that green crabs invading South African shores were unable to colonize wave-swept shores. They were however found on the outer coast in areas with less wave energy. Lohrer and Whitlatch (1997) found few or no green crabs in the eastern US at high-energy sites where the beach consisted only of rock or gravel. In the southern Gulf of St. Lawrence, green crabs initially established populations in sheltered estuaries; limited colonization of coastal waters has occurred only in the eastern portion of the southern Gulf where populations had been established for at least several years and estuarine population densities were higher than those at the northwestern "front" of dispersal (Locke, pers. obs.). In western North America, green crab colonized protected embayments but was not found in rocky habitats, even in areas of transitional wave energy, a habitat type where it is typically found on the European coast (Grosholz and Ruiz 1996). Grosholz and Ruiz (1996) stated that the factors apparently preventing green crabs from occupying protected rocky shores in the western USA were unclear. Hunt and Behrens Yamada (2003) indicated that predation pressure by red rock crab, *Cancer productus*, may contribute to the perceived habitat preference. In the rocky low to mid-intertidal zone of northern New England, feeding rates more than doubled and in some sites more than tripled in wave-protected as compared to wave-exposed sites (Menge 1983).

McKnight et al. (2000) showed that distribution in coastal and estuarine habitats differed significantly between the larger, more aggressive red phase and the smaller green phase. The green phase was found to be consistently more tolerant of temperature and salinity stresses and thus a more efficient invader in estuarine habitats (Baeta et al. 2005, Todd et al. 2005).

In South Australia the crabs became established only in degraded habitats, implying that invasibility was enhanced by habitat degradation (Zeidler 1997). In California, green crab invasions were also more likely to occur in habitats that were recently or persistently disturbed by human activity (Wasson et al. 2005).

3.5. Physiological tolerances

3.5.1. Temperature

Green crabs are poikilotherms, thus physiology and behaviour are affected by daily and seasonal temperature variations. Adult green crabs were eurythermic and survived <0°C to >35°C (Eriksson and Edlund 1977, Hidalgo et al. 2005) but preferred temperatures between 3°C and 26°C (Grosholz and Ruiz 2002). Spaargaren (1984) detemined that green crabs did not freeze at winter temperatures in sublittoral habitats (-2 °C), despite the absence of “biological antifreezes” in the blood. Growth was suppressed and molting did not occur at temperatures below 10°C (Eriksson and Edlund 1977, Berrill 1982, Behrens Yamada et al. 2005). Feeding has been reported as normal down to 6-7 °C, but ceasing somewhere between 2 °C and 7 °C (Eriksson and Edlund 1977, Cohen et al. 1995). In PEI, activity ceased in autumn at temperatures between 2°C and 6°C, and resumed in spring when temperature reached 10°C (Sharp et al. 2003).

Green crabs held out of water tolerated elevated temperatures through heat loss by evaporation (Ahsanullah and Newell 1977). For example, at 21°C and relative humidity of 60%, green crab body temperature was several degrees below ambient due to passive water loss across the gills.

The distribution of green crabs was limited by the temperature required for successful reproduction. While green crab could produce eggs at temperatures up to 26°C (Cohen and Carton 1995), larval development was limited to a narrower range. In the laboratory, larvae were successfully reared from hatching through metamorphosis to the juvenile (C1) stage at 9-22.5°C (Dawirs et al. 1986, DeRivera et al. 2006). Larval stages were found off southern Nova Scotia at temperatures ranging from 5 to 18°C (Roff et al. 1984), but it is unknown whether development was occurring in the lower temperature range. Gray Hitchcock et al. (2003) suggested that rate of larval development may be determined by temperature experienced in the first 30 d of life. Duration of larval development (zoeal stages) varied from 25.4 days at 20 °C to 51.9 days at 10 °C (Nagaraj 1993), but it is important to note that these were well-fed larvae. Development time can double with starvation (Dawirs 1984). Temperature affected not only stage duration but metabolic efficiency. Zoeal stages accumulated energy and biomass more efficiently at 18 °C than 12 °C, but the reverse seemed to be the case for megalopae (Dawirs et al. 1986).

Table 4. Effects of temperature and salinity on the development time of *C. maenas* larvae (zoeal stages). Summarized from Nagaraj (1993).

Temperature (^oC)	Salinity ($^o/_{oo}$)	Larval duration (days)	Mean duration (days) at temperature
10	20	54.9	51.9
	25	50.5	
	30	49.1	
	35	53.2	
15	20	46.5	40.1
	25	39.4	
	30	38.2	
	35	36.4	
20	20	37.2	30.5
	25	32.1	
	30	25.4	
	35	27.4	
25	20	24.3	25.4
	25	25.0	
	30	24.8	
	35	27.3	

Green crab predation pressure on soft-shell clams (*Mya arenaria*) decreased with decreasing temperature (Elner 1980, Miron et al. 2002). In experiments conducted in PEI, predation was highest at 20^{o}C, decreased at 10^{o}C and ceased at 0^{o}C, suggesting that the degree of damage to bivalve populations would be highly dependent on seasonal temperature variation (Miron et al. 2002).

In Maine, high overwintering mortality was associated with cold winters (Welch 1968). Developing egg masses attached to overwintering females were most vulnerable to cold, so reduction of predation pressure on soft-shell clams would not be expected until two or three years later, when the juvenile crabs would have been large enough to feed on clams (Lindsay and Savage 1978). Recently, there have been few years cold enough to restrict the growth of green crab populations (Congleton et al. 2005).

3.5.2. Salinity

Green crabs are efficient osmoregulators (McGaw et al. 1999). They were euryhaline as adults, tolerating salinities ranging from 4 to 52$^o/_{oo}$ (Cohen and Carlton 1995). Mesohaline to polyhaline salinities (10-30 $^o/_{oo}$) were preferred (Broekhuysen 1936, Grosholz and Ruiz 2002). Physiology, particularly the ability to adapt to hypoxia, was compromised below 10$^o/_{oo}$ (Legeay and Massabuau 2000a).

Green crabs responded to lowered salinities by an increase in locomotor activity (Taylor and Naylor 1977). This escape response was typically observed at ~9-10$^{o}/_{oo}$ (McGaw et al. 1999). As well, adult green crabs could reduce their apparent water permeability in response to decreases in salinity (Rainbow and Black 2001). Green individuals of the species were generally more tolerant of salinity variation (and other environmental stressors) than red individuals (McKnight et al. 2000).

Larvae were less tolerant of low salinity than the adults. Freshly hatched zoea larvae survived at salinities <15 $^{o}/_{oo,}$ but did not fully develop through the life cycle, while metamorphosis to the megalopa stage required salinities ≥20$^{o}/_{oo}$ (Anger et al. 1998). Even transitory exposure to salinities <20$^{o}/_{oo}$ delayed later development and increased mortality during later molts. Anger et al. (1998) found that development was significantly delayed and mortality increased at 20$^{o}/_{oo}$ as compared with 25 and 32$^{o}/_{oo}$. Rates of growth and respiration decreased during exposure to salinities ≤25$^{o}/_{oo}$ (Anger et al. 1998). Nagaraj (1993) found that salinities from 20 to 35$^{o}/_{oo}$ did not affect development rates (see Table 4). While the upper limit of salinity for larval development has rarely been investigated, Broekhuysen (1936) indicated that normal development could occur at >40$^{o}/_{oo}$ with temperature of 16^{o}C, but the upper limit decreased to 26$^{o}/_{oo}$ at temperatures around 10^{o}C.

The timing of larval release during ebb tides ensured a rapid export of pelagic larvae to coastal marine waters with higher salinity than the estuaries in which many adult populations live (Quieroga et al. 1997).

The changes in salinity tolerance outlined above reflected an ontogenetic progression in the ability of green crabs to osmoregulate; zoeal stages were osmoconformers, megalopae were weak osmoregulators, while adults were hyper-regulatory (Torres et al. 2002, Cieluch 2004). Adults shifted from osmoconforming to osmoregulating below a critical salinity of 22$^{o}/_{oo}$ (Henry et al. 2003).

There appeared to be a genetic component to the ability to osmoregulate. Adult crabs from the Baltic Sea (Theede 1969 cited in Anger et al. 1998) were more capable of hyper-osmoregulation (i.e., tolerated lower salinities) than conspecifics from the North Sea. The difference was not fully reversible by adaptation.

3.5.3. Oxygen

Green crabs are considered reasonably tolerant of oxygen stresses. Sensitivity to hypoxia was affected by both salinity and temperature. Hypoxia tolerance was greater at higher salinities. Green crabs could tolerate Po_2 levels as low as 3kPa at salinities >10$^{o}/_{oo}$ (Legeay and Massabuau 2000a). Below 10$^{o}/_{oo}$, crabs tended to suffer mortality from hypoxia. Legeay and Massabuau (2000a) concluded that there was a causal relationship between hypoxia events and distribution of crabs along salinity gradients. Green crab was most sensitive to hypoxia in winter. In winter, cellular O_2 supply was affected at ambient Po_2 >6 kPa, whereas during summer similar effects were found at Po_2 levels as low as 2-3 kPa (Legeay and Massabuau 2000b).

Hypoxia affected the behaviour of crabs. For example, Sneddon et al. (1999) reported a correlation between hypoxia events and crab fighting ability. Fights were shorter at water Po_2 levels of 6.7 kPa and significantly reduced below 2 kPa. Males and non-ovigerous females stranded in warm, oxygen-depleted tide pools exhibited an "emersion" response, where they reversed the normal direction of respiration in order to use atmospheric oxygen (Wheatly 1981). The crab raised itself onto the back of its abdomen and reversed the direction of its scaphognathite beat, causing air to enter the branchial chamber via the normally exhalent openings and stream from the normally inhalant Milne-Edwards openings at the base of the chelae. Berried females in hypoxic water have long been known to aerate the eggs by balancing on two pereiopods while using the remaining pereiopods and the chelae to pierce the egg mass and agitate the eggs, accompanied by flapping movements of the abdomen (Broekhuysen 1936). Wheatly (1981) observed a second hypoxia-induced behaviour of berried females. Instead of the typical "emersion response", the females alternated between normal ventilation, which directed air bubbles from the exhalent openings toward the anterior of the egg mass, and reverse ventilation, which directed a stream of bubbles out of the openings at the base of the posteriormost pair of walking legs and over the posterior of the developing egg mass. The net result was the formation of a large accumulation of air bubbles around the egg mass. Females could defer the release of larvae until they were returned to well-aerated water (Wheatly 1981).

Green crab could readily survive at least five days out of water (Darbyson 2006), which has implications for their likelihood of being moved around on trailered boats, gear stored on the deck of vessels, and similar vectors. As mentioned above in section 3.1.1., the temperature tolerance of green crabs actually increased when they were out of water and able to employ evaporative cooling (Ahsanullah and Newell 1977).

3.5.4. Depth

Green crabs have most commonly been reported from the high tide level to depths of 5-6 m, but there are records from waters as deep as 60 m (Crothers 1968 cited in Cohen et al. 1995, Elner 1981, Proctor 1997). In estuaries and coastal areas of the southern Gulf of St. Lawrence, green crabs have routinely been trapped at 2-5 m depth (Williams et al. 2006) and captured by beach seine in ~1 m depths (Locke et al. unpub. data). In Denmark, green crabs were rarely found at depths > 10 m (Munch-Petersen et al. 1982). In Chedabucto Bay, Nova Scotia, lobster fishermen have often caught green crabs in lobster traps set at depths of up to 12 m (Williams et al. 2006).

3.5.5. Metals

Green crab was recommended as an indicator species or biomarker for the monitoring of heavy metal contamination (Martin-Diaz et al. 2004, 2005, Brian 2005, Stentiford and Feist 2005, Moreira et al. 2006). Heavy metal pollution has been associated with respiratory failure in crabs. Copper salts negatively affected crab respiration (Kerkut and Munday 1962), but this effect may be reversible (Depledge 1984). Exposure to mercury resulted in 100% mortality within two days (Depledge 1984). Toxicity increased at higher temperatures.

3.6. Behaviour

3.6.1. Migrations

Adults migrated inshore-offshore with the tides. On gravelly shores, newly recruited early juveniles were most abundant in the high intertidal zone and did not undertake up- and down-shore migrations (Zeng et al. 1999). Hunter and Naylor (1993) investigated intertidal migration using traps oriented with, against and at right angle to tidal flow. More crabs were taken in traps facing tidal flow. Males in the green phase predominated in the catches, implying that migration dynamics within a population were complicated by gender and age/colour phase.

An offshore overwintering migration was typical of most estuarine populations. Green crabs moved out of estuaries to deeper, warmer, coastal waters in winter (Broekhuysen 1936), and buried in the bottom (Welch 1968). Females were normally collected in deeper waters than the males. In The Netherlands, the winter offshore migration occurred when water temperature fell below 8.5^{o}C in November-December (Broekhuysen 1936). For ovigerous females, the offshore migration in winter optimized the temperature and salinity conditions required for egg development. In summer temperatures of 17 ^{o}C, eggs developed normally at approximately 20$^{o}/_{oo}$ or above, and females positioned themselves appropriately in the estuary. However, the lower limit of egg development at 10 ^{o}C was 26$^{o}/_{oo}$, which was only available offshore. About 60-70% of the females were ovigerous over winter in The Netherlands (Broekhuysen 1936). In summer, the berried females were the first to reinvade inshore waters, to enable hatching of the eggs in shallow water where the increased temperature aided the development of the eggs (Wheatly 1981). Offshore migration has not been directly observed in Canadian estuarine populations, but observations from Basin Head Lagoon, PEI, were consistent with an overwintering migration to deeper coastal waters of the southern Gulf of St. Lawrence. In fall, large numbers of males and females were trapped near the lagoon entrance while few remained in the main basin of the estuarine lagoon where they had been plentiful in summer (Sharp et al. 2003).

An offshore overwintering migration was observed even in Portugal, where the lowest annual temperature in the Ria de Aveiro lagoon was 10 ^{o}C (Gomes 1991). Salinity in the lagoon, however, declined at some stations from $34^{o}/_{oo}$ in August to $0.3^{o}/_{oo}$ in February. The lowest salinity and temperature where green crabs were found offshore in winter were $17^{o}/_{oo}$ and 13 °C, respectively. Some crabs migrated a distance of 15 km to the overwintering areas (Gomes 1991).

Coastal populations living at or near full salinity may not undertake offshore overwintering migrations, or at least not to the same extent. A green crab population from the coast of Wales was found intertidally year-round (Naylor 1962). Small crabs (CW<30-35 mm) were present on the shore in all months of the year, although from December through March their distribution shifted lower on the shore. During winter, they actively foraged in the middle of the intertidal zone at high tide and descended to just below the low water level at low tide. Males ranged higher up the shore than females. In the coldest months, larger crabs moved offshore to a depth of at least 6 m (Naylor 1962).

In the salt marshes of Wells, Maine, green crabs overwintered intertidally in burrows in banks of *Spartina* sod (Welch 1968). Dow and Wallace (1952) recorded large concentrations of green crabs in marsh burrows in Maine during late fall; 40 green crabs were found grouped together in one burrow, and at another location, 300 green crabs were unearthed by removing only three or four clam forkfuls of marsh sod.

3.6.2. Competition

Competition between green crabs and other taxa may be either exploitative or behavioural in nature, and may involve either food or habitat (space). Green crabs utilize such a wide range of food resources that it seems almost inevitable that their diet will overlap with that of other taxa, and that exploitation competition will occur in situations where food supply is limiting. Likewise, there is considerable overlap in habitat among crab species.

3.6.2.1. Competition for food

Several experimenters have identified the potential for food competition due to overlap in the diet of green crabs and native decapods, but none have demonstrated that competition actually occurs in the environment. This would require that green crabs and native species coexist in the wild and compete for a limiting food resource, a situation which has not yet been supported by convincing evidence.

Ropes (1989) found that three species of portunid crabs from eastern North America (green, blue (*Callinectes sapidus*) and lady (*Ocellatus ovalipes*) crabs) have similar food preferences, thus the expectation is that there is potential for competition for resources between green crab and the other two species. Green crab distribution would potentially overlap with blue crab inside estuaries, and with lady crab in the outer portions of estuaries (> $22^{o}/_{oo}$) and open coastal (sandy) habitats.

Green crabs and grapsid crabs (*Hemigrapsus oregonensis* and *H. sanguineus*) competed for food in the laboratory (Jensen et al. 2002). Green crab outcompeted *H. oregonensis*, native to the west coast of the USA, for mussels. However, in nature there was relatively little dietary overlap between green crabs and *H. oregonensis*, which fed mainly on diatoms and algae, and only the smallest snails and newly settled bivalves. There is, however, substantial diet overlap between green crabs and Asian shore crabs, which fed on plant material, mussels and barnacles. When competing for food against *H. sanguineus*, a recent invader of the east coast of the USA, green crab was usually the first to find the bait, but was almost invariably dislodged immediately from the food by the Asian shore crab. (Note, however, that in natural situations the green crab might have the option of fleeing with the prey, which in these experiments were attached to the bottom.) Approaching green crabs were fended off with kicks from the walking legs of Asian shore crabs, while the chelae continued to be used for feeding. Green crab from Maine, where there were no Asian shore crab, were more persistent in their unsuccessful efforts to displace Asian shore crab than those from Delaware, where the two species coexisted, suggesting that the Delaware green crabs have learned that Asian shore crab is the dominant competitor (Jensen et al. 2002). Green crabs were able to open the bivalves more quickly than either species of *Hemigrapsus*, and were able to open larger mussels than comparably sized Asian shore crabs (McDermott 1999).

Juvenile green crab dominated equal-sized Dungeness crab (*Cancer magister)* when competing for food, but do not currently share habitat (McDonald et al. 2001). Jamieson et al. (1998) predicted that the two species would interact on the large tidal flats in the Strait of Georgia.

Green crab diet, particularly the consumption of bivalves, gastropods, polychaetes and crustaceans, overlapped that of *Cancer* crabs and adult American lobster in waters of southeastern Nova Scotia (Elner 1981). Elner (1981) suggested that these species probably would compete for food in food-limiting situations, and speculated that high abundances of green crabs in inshore habitat might reduce the resources available to the other species. In laboratory experiments, adult green crabs (63-75 mm CW) beat juvenile (28-57 mm CL) and sub-adult lobsters (55-70 mm CL) to a food source, and in almost all trials retained possession of the food source (Rossong et al. 2006, Williams et al. 2006). In trials where the sub-adult lobsters were allowed to initiate feeding before the release of the green crabs, lobsters were able to defend the food from green crabs (Williams et al. 2006).

3.6.2.2. Competition for habitat

Green crabs and grapsid crabs (*Hemigrapsus oregonensis* and *H. sanguineus*) used similar habitat, especially intertidal shelter, and habitat utilization by green crabs was strongly affected by the presence of *Hemigrapsus* spp. (Jensen et al. 2002). Both *Hemigrapsus* species consistently dominated green crab in contests for shelter, and habitat utilization by green crab was altered by the presence of the grapsids. Adult Asian shore crab excluded most juvenile green crabs of similar size (carapace width 14-20 mm) from rocks and bivalve shells used as shelters in intertidal habitat in New England, where >97% of the green crabs were found under rocks in the absence of grapsids. Jensen et al. (2002) suggested that these competitive interactions could limit the ultimate distribution and impact of green crabs in the northeastern Pacific, as a shortage of appropriate refuge space could result in a bottleneck to population growth. Competitive displacement from preferred areas may result in increased risk of predation and reduced access to food.

Juvenile Dungeness crabs (*Cancer magister*) emigrated from oyster shell habitat as a result of competition and predation by green crabs. Depending on the extent to which Dungeness and green crabs overlap, there could be a negative effect on Dungeness crab that could reduce recruitment to the fishery. Currently, the distribution of green crab in Washington state does not overlap the nursery areas of Dungeness crab (McDonald et al. 2001).

Higher levels of limb autotomy of green crab were found in areas of Bodega Bay, California, inhabited by red rock crab *Cancer productus* and brown rock crab *C. antennarius*, than in areas lacking *Cancer* spp. (McDonald et al. 1998). This could indicate that green crabs were being injured by interactions with the rock crabs, or that they were being driven out of protected habitats into locations where they were being damaged by predators. Gillespie et al. (2007) observed higher rates of autotomy within the green crab population with increased density of green crabs in British Columbia, which they attributed to intraspecific agonistic behaviours.

The mud crab *Neopanope sayi* and grass shrimp *Palaemonetes* spp. fled from enclosures where they were able to physically interact with green crabs, but did not respond to chemical cues (Thompson 2007). Mud crab abundance in eelgrass habitat was reduced from 2 crabs/m^2 to 0 mud crabs in the enclosures with green crabs.

In the Bras d'Or Lakes, direct competition between green crabs and other decapods was not assessed, but habitat overlap was common. Green crab (20-79 mm CW) co-occurred with rock crab (*Cancer irroratus*) in 15 of 32 dive transects and with American lobster (15-139 mm CL) in 9 transects (Tremblay et al. 2005). On some transects, the green and rock crabs were in close proximity, within 1 m. Green crab overlapped in habitat usage and depth distribution with rock crab but only rarely with American lobster. Green and rock crabs were generally found on mud or sand mixed with gravel and cobble, whereas most lobsters were found on boulder habitat. The most common depth range of rock crab (3-9 m) overlapped with both green crab (3-6 m) and lobster (6-9 m) but there was little overlap in the depth distribution of green crab and lobster in the Bras d'Or Lakes. In contrast, 89% of the members of the Guysborough County Fishermen's Association (eastern shore of Nova Scotia) reported encountering green crabs in their lobster traps, and anecdotal reports of green crabs in lobster traps exist from the area between Inverness and Cheticamp, NS, as well as a single observation from Lobster Point, near Souris, PEI (JCG Resource Consultants 2002).

3.6.3. Predation

3.6.3.1. Predation on green crab

High mortality from predation during settlement and early post-settlement was recorded in all habitats in Sweden. Predation by cannibalistic juvenile green crabs in the 4^{th} to 9^{th} instar (age 1; 5-10 mm carapace width; present at densities of ~ 12 crabs/m^2; and age 0; 3.5-10 mm at the end of the recruitment season) and shrimps (brown shrimp *Crangon crangon*, grass shrimp *Palaemon elegans)* caused average mortality of 22% and 64% of the settling crabs/3 days, respectively (Moksnes 2002). By fall, juvenile crabs made up over 90% of the predators.

Predation by other decapods on green crab appeared to be relatively common. European reports of predation included another by the brown shrimp *Crangon crangon* (Pihl and Rosenberg 1984), as well as velvet swimming crabs *Liocarcinus puber* (Rheinallt 1986). Adult rock crabs *Cancer irroratus* preyed on adult green crabs in the laboratory (Elner 1981). Predation pressure by native rock crabs *Cancer* spp. may influence habitat preference in green crabs on the Pacific coast (Hunt and Behrens Yamada 2003). The blue crab *Callinectes sapidus* may limit both abundance and geographic range of green crabs on the Atlantic coast (DeRivera et al. 2005). Adult American lobsters *Homarus americanus* in aquaria readily consume green crabs (Elner 1981, Locke pers. obs.).

Cuttlefish were predators of green crabs in Brittany (Le Calvez 1987).

Many fish eat green crabs. Kelley (1987) reported green crabs as a dominant food of the European sea bass *Dicentrarchus labrax* off the UK coast. In North America, they were frequently eaten by striped bass *Morone saxatilis* (Nelson et al. 2003). Cohen et al. (1995) reviewed literature listing, in addition, two sculpins, three gobies, various gadids and flatfish, a ray and a shark as predators of green crab in the Atlantic. Fish preying on green crabs in San Francisco Bay included staghorn sculpin *Leptocottus armatus*, Pacific tomcod *Microgadus proximus*, starry flounder *Platichthys stellatus*, English sole *Parophrys vetulus*, Pacific sanddab *Citharichthys sordidus*, pile perch *Damalicthys vacca*, white surfperch *Phanerodon furcatus*, rubberlip surfperch *Rhacochilus toxotes*, striped bass *Morone saxatilis*, white croaker *Genyonemus lineatus*, white sturgeon *Acipenser transmontanus*, green sturgeon *A. medirostris*, bat ray *Myliobatis californica*, big skate *Raja binoculata*, leopard shark *Triakis semifasciata*, and brown smoothhound shark *Mustelus henlei* (Cohen et al. 1995).

Birds are major predators of green crabs. About a dozen bird species feed on green crabs in Portugal (Moreira 1999). In North America, sandpipers, sanderling, curlew, the great blue heron *Ardea herodias*, cormorants, ducks including the mallard *Anas platyrhyncha*, and gulls, feed on green crabs (Cohen et al. 1995). Ellis et al. (2005) found that crabs in the Gulf of Maine were preyed on by Great Black-backed Gulls but were not a preferred food item. However, green crab was a major prey of herring gulls

Larus argentatus in the UK (Sibly and MacCleery 1982, Dumas and Witman 1993). In the Dutch Wadden Sea, Camphuysen et al. (2002) observed mass mortalities of common eider ducks, attributed in part to transmission of the acanthocephalan parasite *Polymorphus* (*Profilicollis) botulis* for which the green crab is an intermediate host.

Green crabs were a dominant food in the diet of coastal populations of mink *Mustela vison* and otters *Lutra lutra* (Dunstone and Birks 1987, Mason and MacDonald 1980). They were also consumed by harbour seal *Phoca vitulina* (Sergeant 1951 cited in Cohen et al. 1995).

Hogarth (1975) attributed the high degree of colour polymorphism in green crabs to predator avoidance mechanisms.

3.6.3.2. Predation by green crab

Planktonic larvae are filter-feeders, early stage juveniles feed primarily on detritus then switch to infauna as they get older, and adults prefer to prey on bivalves (Pihl 1985).

Little is reported on feeding of larval stages. Larvae could ingest particles in the size range of bacteria, small algal cells and organically enriched detrital particles (Factor and Dexter 1993).

Juvenile and adult green crabs preyed on a variety of marine organisms including species from at least 104 families and 158 genera, in 5 plant and protist and 14 animal phyla (Cohen et al. 1995). The wide range of types of prey is evident from the information summarized in Table 5.

Table 5. List of prey taxa consumed by adult and juvenile green crabs. Summarized from Cohen et al. (1995).

Algae
- Phytoplankton
- Chlorophyta
- Phaeophyta
- Rhodophyta

Spermatophyta

Protista
- Foraminifera
- Rotifera

Animalia

Hydrozoa	Anostraca	Natantia	Gastropoda
Nemertea	Ostracoda	Astacura	Bivalvia
Nematoda	Copepoda	Anomura	Bryozoa
Turbellaria	Cirripedia	Brachyura	Phoronida
Oligochaeta	Mysidacea	Insecta	Asteroidea
Polychaeta	Isopoda	Cephalopoda	Echinoidea
Chelicerata	Amphipoda	Polyplacophora	Urochordata
			Osteichthyes

Green crabs have definite dietary preferences, which were consistent in diets compared among populations in Europe, eastern and western North America, and South Africa. Mollusca were preferred prey, followed by Crustacea, Annelida and Chlorophyta, in that order. Echinodermata were consistently rejected as prey (Grosholz and Ruiz 1996). Meiofauna in general were also apparently exempt from green crab predation (Feller 2006).

Studies have specifically addressed adult green crab predation on a wide variety of prey taxa:

- fishes such as juvenile winter flounder (Breves and Specker 2005, Taylor 2005), plaice (Wennhage 2002), stickleback eggs (Őstlund-Nilsson 2000);

- crustaceans such as juvenile lobsters (observed in the laboratory by Rossong et al. 2006, but not recorded from the field), hermit crabs (Rotjan et al. 2004), *Hemigrapsus* sp. (Grosholz et al. 2000), barnacles (Rangely and Thomas 1987);

- bivalves such as scallops (Wong et al. 2005), *Macoma* spp. (Richards et al. 2002, Hiddink et al. 2002a, 2002b, Palacios and Ferraro 2003, Griffiths and

Richardson 2006), blue mussels (Frandsen and Dolmer 2002), venerid clams (Walton et al. 2002, Palacios and Ferraro 2003), surf clams (Scattergood 1952, Hart 1955), soft-shelled clams (Palacios and Ferraro 2003, Floyd and Williams 2004), Olympia oysters (Palacios and Ferraro 2003), American oysters and quahaugs (Hart 1955, Mascaró and Seed 2001); *Nutricola* spp. (Grosholz et al. 2000);

- gastropods such as *Littorina* spp. (Ekendahl 1998, Trussell et al. 2004), *Ilyanassa obsolete* (Ashkenas and Atema 1978), dogwhelks *Nucella lapillus* (Hughes and Elner 1979);

- nematodes (Schratzberger and Warwick 1999);

- polychaetes such as *Spirorbis* sp. (Tyrell et al. 2006).

The effects of green crab on many prey species extended beyond simply causing mortality of the portion of the prey population that was consumed, to adaptive responses that diverted energy from production to anti-predator strategies (e.g., cryptic behaviours, displacement to different habitat, shell thickening, stronger byssal attachments) (e.g., Hughes and Elner 1979, Johanneson 1986, Freeman and Byers 2006).

Selective predation by green crabs can shift the composition of marine communities. On the west coast of the US, many changes that have occurred in the soft-sediment community (e.g., Bodega Bay) appear to be the result of green crab predation (Ruiz et al. 1998). Effects on soft-sediment communities have not been as thoroughly investigated on the east coast, but green crabs in the southern Gulf of St. Lawrence could affect densities of key species in eelgrass *Zostera marina* beds (Locke et al. 2007, Thompson 2007, Locke et al. unpub. data) and on mudflats (Floyd and Williams 2004). Thompson (2007) found a 53% reduction in total biomass of 19 studied taxa in eelgrass beds enclosed with 5 green crabs/m^2 relative to crab exclosures. Statistically significant reductions in biomass and abundance ranging from 35% to 100% were attributed wholly or partially to predation on the gastropods *Astyris lunata*, *Actiocina canaliculata*, *Euspira triserata* and *Nassarius trivittata*, and the polychaetes *Pectinaria gouldii* and family Polynoidae. Non-significant reductions were observed in the gastropods *Turbonilla* sp. and *Littorina littorea*, and the bivalves *Tellina* sp. and *Macoma* sp. (Thompson 2007). On a British estuarine mudflat, adult green crabs caused a relative increase of the oligochaete component of the benthic macrofauna; juvenile green crabs significantly reduced the abundance of small annelids, especially polychaetes (Gee et al. 1985). Direct and indirect effects of green crabs on rocky shore communities of New England have been well documented (Menge 1983, 1995). Green crab had minor effects on the communities of exposed coastal rocky shores in northern New England, even at densities in the range of 3-4 crabs/m^2 (Menge 1976). Indeed, nowhere in their native or introduced ranges do they have a major ecological impact in exposed habitats (Grosholz and Ruiz 1996). In its native range, green crab increasingly influenced the distribution of the blue mussel *Mytilus edulis* and the snail *Nucella lapillus* with decreasing wave exposure (Grosholz and Ruiz 1996).

3.7. Parasites/diseases

Two issues are relevant when considering parasites in relation to invasions: the invader's responses to native parasites and the effect of introduced parasites on native hosts.

Green crabs in their native range were infected with a variety of parasites and symbionts. Green crabs were also host to so far unidentified viral strains similar to viruses found in a variety of crustacean and fish species (Montanie et al. 1993, Owens 1993).

Green crabs from Atlantic Canada lacked most of the parasites and symbionts found associated with green crabs in Europe (Brattey et al. 1985). The difference in parasite load may account for the larger size of green crabs in invaded versus native habitat. Torchin et al. (2001) found that parasite load on green crabs was significantly higher in their native habitat than in invaded habitats (prevalences of 96% versus 8%, respectively).

Green crabs in the Maritimes were infected with the parasites *Polymorphus* sp. (Acanthocephala, Palaeacanthocephala) and *Microphallus* sp. (Platyhelminthes, Digenea) (Brattey et al. 1985). These taxa were also found in *Cancer irroratus*, but at lower rates of prevalence (frequency). Crabs are the intermediate hosts of these parasites, for which the definitive hosts are native bird species. For the digenean *Microphallus*, seabirds such as gulls *Larus argentatus* and terns *Sterna hirundo* are the definitive hosts; in St. Andrews NB, prevalence of *Microphallus* in green crabs (93.5%) was ten times that in rock crabs, potentially resulting in high rates of transmission to seabirds. The prevalence of the acanthocephalan *Polymorphus* sp. was also higher in green crabs than in rock crabs. While the Canadian specimens of *Polymorphus* were not identified to species, the potential for transmission of *Polymorphus (Profilicollis) botulus* would have serious implications for native bird populations, particularly eider ducks *Somateria mollissima* which may experience high mortality (Lafferty and Kuris 1996, Camphuysen et al. 2002).

Green crabs are capable of reducing their exposure to parasites. When faced with mussels infected by the shell boring parasite *Polydora ciliata*, crabs tended to select smaller, non-infested mussels (Ambariyanto and Seed 1991).

At least one green crab parasite appears to have transferred to a native decapod in eastern North America. Newman and Johnson (1975) reported for the first time, from a blue crab *Callinectes sapidus*, a dinoflagellate parasite normally found in *Carcinus* and *Portunus*. As the only representative of those genera in the region was green crab, it is likely to have been the source of the parasite.

Several parasite species have been proposed as potential biological control agents of green crabs, for example *Sacculina carcini* (Minchin 1997), nemertean egg predators

(Kuris 1997), epicaridean parasites (Hoeg et al. 1997), and other parasites (Goggin 1997). The parasitic barnacle *Sacculina carcini* was once considered a promising potential biological control agent but has since been found to infect native crabs in North America and Australia, causing mortality that was significantly higher than for green crabs (Thresher et al. 2000, Goddard et al. 2005). Thus, biological control using *S. carcini* could pose a serious risk to native crabs. The potential dangers of the use of parasites for biocontrol are further emphasized by Secord (2003).

4. Dispersal capabilities

4.1. Natural dispersal

In their native habitat, green crabs have usually expanded their range by only a few kilometers per year punctuated by periodic long-distance expansions associated with unusual oceanographic conditions (Thresher et al. 2003). Larvae have the potential to disperse over considerable distances given that green crab larval stages must develop in open waters for >50 days, and indeed may remain in the water column for >80 days (see Section 3.2). Behrens Yamada et al. (2005) attributed dispersal of green crabs along the Pacific coast to larval transport by ocean currents associated with an unusually intense El Niño effect. Northward-moving coastal currents transported larvae up to 50 km/d during the El Niño of 1998 (Behrens Yamada and Becklund 2004). Oceanographic current changes associated with global climate change are likely to affect the distances and directions of future range expansion (Roman 2006).

Dispersal by adults and juveniles is relatively local in nature. There have been no records of adult or juvenile green crabs at sea on floating algae or logs (Cohen et al. 1995). In western Sweden, most green crabs immigrated to coastal embayments as pelagic megalopae, and there was little post-metamorphosis dispersal by juvenile crabs (Moksnes 2002). It was the opinion of Moksnes that extensive areas of exposed rocky coast separating bays where green crabs were found limited the exchange of juveniles between local populations, and that the local populations were in fact isolated. Genetic patterns also indicated that deep-water barriers have hindered adult green crab dispersal in Europe (Roman and Palumbi 2004).

4.2. Anthropogenic dispersal

The vast majority of green crab invasions throughout the world have been attributed to transport by human agents. Human-mediated dispersal methods include: ballast water, other shipping vectors e.g., seawater pipe systems (sea chests), shipment of commercial shellfish/aquaculture products, bait release, release as a potential food resource, traps and cages, deliberate or accidental release from research/education facilities, marine construction equipment, movement of sediments/sand, and historical vectors such as dry ballast (Cohen et al. 1995, Grosholz and Ruiz 2002).

One of the major vectors for green crab invasions has been shipping (Cohen and Carlton 1995; Cohen et al. 1995). Carlton and Cohen (2003) documented three major episodes of anthropogenic transport of green crabs to North America: around 1800, the 1850's to 1870's and the 1980's to 1990's. The invasions of the 1800's were largely attributable to transport of adult crabs in dry ballast and ships hulls. Subsequent ballast-mediated invasions would have been in water ballast. Those of the 20th and 21st centuries have been due to a greater variety of transport mechanisms (ships hulls, ballast water, drilling platforms, fishery product transport, scientific research, aquarium releases, etc.). They attributed the observed increase in recorded invasions to a world-wide increase in shipping.

Darbyson (2006) suggested that while commercial shipping may have been a factor in the arrival (primary invasion) of green crabs to the southern Gulf of Saint Lawrence, local dispersal (secondary spread) within the Gulf was likely caused by fishing, aquaculture and recreational boating activity. The ability of green crabs to survive for extended periods in the bilges of boats and other apparently unfavourable conditions was well known to fishermen in Maine in the 1950s (Dow and Wallace 1952). Dow and Wallace report having left green crabs in bags of brackish water in the trunk of a car for over 24 hr, transferring them to fresh water for 6 hr, then dumping out the water and leaving the crabs in the damp bags for a further two days until they finally died. Darbyson (2006) found that green crabs could readily survive 5 days out of water in black fish crates in summer. Green crabs may survive 8 days out of water, although the conditions of the test were not reported (JCG Resource Consultants 2002).

Scattergood (1952), discussing the vectors of spread through Maine, wrote: "Undoubtedly, man's activities are partially responsible for the remarkable spread of *Carcinides*. The lobster and sardine fisheries probably provide the principal means by which crabs may be transported from one area to another. Since the crabs can live for several days out of water, it is relatively easy for the crabs to be carried in lobster smacks, lobster-carrying trucks, lobster-fishing boats, sardine carriers, and sardine-fishing boats. I have seen live crabs in crates of live lobsters and have noticed them aboard sardine carriers and fishing boats…For many years, lobsters have been carried about from fishing ground to lobster pound to market, and, in these moves, often covering hundreds of miles, there were many opportunities to spread live green crab over wide areas."

4.3. Rates of range expansion

Rates of range expansion have been quite variable among green crab invasions (Grosholz and Ruiz 1996). In both their native habitat and in invaded locations, green crabs have typically expanded their range slowly, only a few kilometers per year (Thresher et al. 2003). However, the species has an extensive history of long-distance travel resulting in primary invasions. The rare episodes of long-distance and large-scale spread appear to be related to either unusual oceanographic conditions or to human assistance (Thresher et al. 2003).

On the west coast of Canada and the USA, green crabs dispersed northward about 1500 km in 12 yr (Jamieson et al. 2002). The strong recruitment event and major range expansion that took place in 1998 was believed to have been the result of unusually strong northward-moving coastal currents of up to 50 km/day, which occurred between November 1997 and February 1998 (Jamieson et al. 2002, Behrens Yamada and Becklund 2004). In contrast, following its arrival in western North America in 1989, green crab remained limited to San Francisco Bay until 1993, when it spread 80 km northward, and 1994, when it spread 125 km southward (Grosholz and Ruiz 1996). Mean annual range expansion over the five years of 20 km/yr northward and 31 km/yr southward was close to the mean range expansion for marine species generally (Grosholz and Ruiz 1996).

Northward expansion of green crab from New England to Nova Scotia averaged 63 km/yr, but was very episodic (Grosholz and Ruiz 1996). Within the southern Gulf of St. Lawrence, we have observed episodic range expansions of up to 100 km in a year (Locke et al. unpub. data). In South Africa, range expansion averaged 16 km/yr from 1983 to 1992 (Grosholz and Ruiz 1996).

5. Potential distribution in Canada

Worldwide, green crab has a primarily temperate, anti-tropical distribution, falling within equatorial limits of average summer surface temperatures around 22˚C, and polar limits of average winter ocean temperatures of -1˚C to 0˚C, consistent with an upper temperature breeding barrier of 18 to 26˚C and high winter mortalities at sustained temperatures ≤ 0˚C (Cohen et al. 1995). The lower temperature limit of green crab is somewhat uncertain; Spaargaren (1984) determined that animals did not freeze at -2˚C, within the winter temperature range expected in sublittoral conditions.

Models of green crab distribution relative to temperature have predicted that the species should be able to spread north of its present range on both coasts.

In eastern Canada, Chmura et al. (www.geog.mcgill.ca/climatechange/results.htm, accessed 22 Nov 2006) estimated the northern thermal limit, based on mean monthly February temperature (usually the coldest month of the year) and physiological tolerances of green crab determined from the literature, as being about 250 km south of Ungava Bay. If Chmura and colleagues were right, the green crab could spread up the St. Lawrence estuary. They did not model the extent of such spread. In that case, we consider that salinity would limit its spread in the St. Lawrence estuary to areas with salinity in the range of $10^{o}/_{oo}$ or greater, and more likely in the range of $15\text{-}20^{o}/_{oo}$ as the lower limit. Although the green crab can survive salinities as low as $4^{o}/_{oo}$, it is unlikely to be widely distributed at this low salinity (see Section 3.5.2). We predict green crab would extend up the St. Lawrence estuary at least to Mont-Joli, where the lowest annual salinity values (May) vary between $22^{o}/_{oo}$ on the north shore and $15^{o}/_{oo}$ on the south shore (El-Sabh 1979).

Unlike the model of Chmura and colleagues, DeRivera et al.'s (2006) model predicted that Baie-Comeau, which is located across the river from Mont-Joli, would be too cold for larval development. The latter estimate was based on the physiology of crabs from New England; the question is whether the Gulf of St. Lawrence populations are more cold-tolerant, having apparently originated from very near the northern limit of green crab in Europe (Roman 2006). Unfortunately, DeRivera et al. did not evaluate survival at many sites in Atlantic Canada; the only others were the Magdalen Islands and Halifax, both of which were judged suitable by the model. We assume that the temperature regime of Baie-Comeau probably typifies most of the Northern Gulf, which would imply that sites to the northeast of the Gaspé Peninsula would be unsuitable as well, by DeRivera et al.'s model. Assuming that the climate of the Magdalen Islands is typical of the southern Gulf of St. Lawrence, this model implies that green crabs would eventually be distributed along the entire New Brunswick coast and the Quebec shore of Chaleur Bay.

Range limits in western Canada were not explicitly modeled, but Cohen et al. (1995), Gray Hitchcock et al. (2003), Hines et al. (2004), and DeRivera et al. (2006) all predicted that the northern limit of green crab in the northeastern Pacific was in Alaska, thus all models indicate that the entire British Columbia coast would be vulnerable.

6. Impacts or uses of green crab

6.1. Uses of green crab

6.1.1. Fisheries

Green crabs have been fished commercially for a long time in parts of Europe. Soft-shell green crabs are a delicacy in Spain and Portugal, in particular. In fact (ironically), the species has been in decline in Portugal due to over-fishing (Gomes 1991). The commercial fishery for green crabs in France, Portugal and Spain (Atlantic and Mediterranean catches combined) has yielded up to 900 tonnes/year (Svane 1997). Annual landings from the Atlantic fishery by Portugal, Spain, France and England averaged 200 tonnes from 1982 to 1987 (Cohen et al. 1995). Despite the popularity of green crabs in certain cultures, the lack of markets has limited fishing effort on this species in places like the Shetland Islands, Scotland, where commercial catches have been very small and irregular (Napier 2002).

There has been some examination of the potential for commercial fisheries in Atlantic Canada and New England (e.g., chemical analyses of meats and shell, product testing) (Skonberg and Perkins 2002, Naczk et al. 2004, Food Science Centre of the University of Prince Edward Island pers. comm.). We recognize three stumbling blocks in Atlantic Canada: (1) The populations of green crab may not be large enough to sustain commercial fisheries, (2) Representatives of industries potentially affected by green crabs (e.g., eel fisheries, bivalve aquaculture) have expressed concerns that management of a sustainable green crab fishery could take precedence over management of green crab as an invader; furthermore, they are concerned that proponents of a new fishery might intentionally introduce green crabs to new areas, (3) The North American palate is not adapted to green crabs and there is at present no established market.

In the Maritimes Region, a small commercial fishery was planned to take place in 2006 off the Atlantic coast of Nova Scotia, but has been delayed (M.J. Tremblay, DFO Maritimes, pers. comm.). The PEI fisheries industry had also been interested in exploring the option of a commercial fishery (Gillis et al. 2000).

Welch (1968) stated that green crab was of "minor commercial importance" as bait for sport fishermen south of Cape Cod. This market was supplied by a limited fishery in Maine, New Hampshire, and Massachusetts.

6.1.2. Other potential uses

In its native range, green crab is an important scavenging species, especially of commercial fishery discards (Catchpole et al. 2006, Moore and Howarth 1996). Green crab was one of the major species contributing to the removal of 3.4 $kg/m^2/7d$ in dry weight of fish feed pellets from under marine fish farms (Smith et al. 1997).

Green crab may be of use in controlling biofouling on bivalve aquaculture sites. They preyed on mud crabs feeding on bay scallops on spat bags, although green crabs consumed bay scallops as well (Turner et al. 1996). They have been used to remove mussels fouling oyster nets, although they also ate the oysters (Enright et al. 1993). They were also effective in reducing the accumulation of silt and detritus on the nets and oysters. Their utility as an anti-biofouler was greatest when the chelae were neutralized to prevent destruction of the target crop, but this restricted the crabs to feeding only with their mouthparts and therefore only small, recently settled fouling species could be consumed. Overall, green crabs were less effective, and also less appropriate for this purpose, than other species such as hermit, mud or toad crabs, whose smaller chelae did not damage the aquaculture product (Enright et al. 1993). In the Wadden Sea, the combined predation of adult green crabs and juvenile starfish controlled the density of barnacles, important biofoulers of subtidal wild blue mussel beds; the incidence of predation on the mussels themselves was not indicated (Buschbaum 2002).

As potential controls of tunicates on aquacultured mussels in suspension, they may have some limited utility. Green crabs consumed the tunicate *Ciona intestinalis*, a fouling organism causing losses to the mussel aquaculture industry, but were less effective anti-tunicate controls than the rock crab *Cancer irroratus* (Carver et al. 2003). Green crab did not eat golden star tunicate, *Botryllus schlosseri* (Teo and Ryland 1994). Its efficacy against other invasive tunicates now present in Canada has not, to date, been evaluated.

Green crabs consistently rejected echinoderm prey even though these may be readily consumed by resident crabs (Grosholz and Ruiz 1996), therefore they would be ineffective in controlling starfish predators of aquacultured bivalves.

6.2. Impacts associated with introductions

6.2.1. Impacts on flora

Ropes (1968) found that plant foods, found in 30% of sampled guts, were second only to bivalves (frequency ~ 70%) in the diets of green crabs. *Spartina* and algae were particularly common in the diet of intertidal crabs, especially those that lived in salt marsh "caves". Feller (2006) also reported benthic algae in the gut contents of juvenile green crabs. Whether green crab grazing would have any direct or indirect effect on the algae or plants has rarely been studied.

Indirect, trophic cascade effects on flora are likely to be common. For example, removal of grazing snails by predatory green crabs or even the behavioural changes caused by green crab presence indirectly enhanced primary producers such as *Enteromorpha* and *Ulva* spp. by reducing grazing pressure (Trussell et al. 2004). Similarly, in relatively protected low rocky intertidal regions of northern New England, the foraging activities of six species of predators suppressed mussel and barnacle populations which otherwise outcompeted *Chondrus crispus*. At one site, ~80% of the effect was attributed to green crabs. In the presence of the green crabs, *Chondrus* was the dominant occupier of intertidal space (Menge 1983).

In contrast to its enhancing effect on intertidal algae, green crab predation on gastropods might be harmful to eelgrass *Zostera marina*. Thompson (2007) speculated that the removal of gastropods that graze on eelgrass epiphytes, and the consequent proliferation of epiphytes, could in turn lead to reduced light transmission, blocking photosynthesis and reducing growth of eelgrass. No reduction in eelgrass biomass or shoot density was observed during Thompson's enclosure studies with 5 green crabs/m^2, but the longest experiments lasted 35 days which most likely would not be sufficient to detect any long-term effects on eelgrass related to epiphyte growth.

At subtidal sites in the Great Bay Estuary of New Hampshire, bioturbation by green crabs disrupted newly transplanted eelgrass *Zostera marina* until crab exclusion cages were installed (Davis and Short 1997). Green crab density at sites where this occurred was 5.4 crabs/m^2 (Davis et al. 1998). In experiments with 4-15 crabs/m^2, up to 39% of viable shoots were lost within one week of exposure to green crab activities. The highest shoot loss was observed at 4 crabs/m^2. There was very little damage at the lowest crab density, 1 crab/m^2. Damage resulted from the foraging activities of green crabs in the top few cm of sediment, and there was no evidence that green crabs consumed eelgrass shoots (Davis et al. 1998). Thompson's (2007) study in the southern Gulf of St.

Lawrence, by contrast, did not detect any bioturbation effects on eelgrass after 35 days of exposure to 5 green crabs/m^2, but he was working in established rather than newly planted eelgrass beds.

It has been suggested that recently observed eelgrass *Zostera marina* declines in the southern Gulf of St. Lawrence may be exacerbated by the combined adverse effects of green crab and the green alga *Codium fragile* ssp. *tomentosoides*. Recent observations indicated that damage to eelgrass by green crabs, which were observed to dig in the bottom and loosen roots as well as apparently clipping off the shoots, created gaps in eelgrass beds that were subsequently colonized by *Codium* (D. Garbary, St. Francis Xavier University, pers. comm.). Harris and Jones (2005) also implicated green crabs in promoting establishment of the invasive alga *Codium*.

6.2.2. Impacts on fauna

Many potential prey species rely on chemical cues to detect and respond to green crab predation pressure (e.g., Griffiths and Richardson 2006). This poses a particular challenge for native species during initial invasions as potential prey will not have been exposed to such chemical cues.

6.2.2.1. Gastropods

Green crabs have had major effects on the ecology of gastropod populations. *Littorina* species responded to green crab predation in a variety of ways including predator avoidance (crawl-out response) and release of alarm substances (Jacobsen and Stabell 1999). Ekendahl (1998) indicated that visual selective predation may affect colour frequency in *Littorina saxatilis*. In the Gulf of Maine, a latitudinal gradient of shell thickness in *Littorina* populations was correlated with a gradient in claw morphology in green crabs - southern green crabs had significantly larger, stronger chelae than northern populations (Smith 2004). Patterns in claw size and performance strongly suggested trophic responses to geographic differences in prey armor. Trussell (2000) observed the same latitudinal pattern of plasticity in *Littorina* shell morphology but attributed it to predation pressure by green crabs (another example of an 'inducible defence'). Perhaps this is a case of an 'evolutionary arms race' between a native prey and invasive predator.

6.2.2.2. Bivalves

Green crabs are well-documented to suppress the abundance of bivalve prey, including several species that are commercially fished or grown in aquaculture in Canada: blue mussels *Mytilus edulis*, quahogs *Mercenaria mercenaria*, eastern oysters *Crassostrea virginica*, soft-shell clams *Mya arenaria,* and bay scallop *Argopecten* *irradians irradians* (Clark et al. 2004, Gardner and Thomas 1987, Floyd and Williams 2004, Miron et al. 2005).

The northern expansion of green crabs through Maine and the Bay of Fundy was correlated with declines in the abundance and fishery landings of the clam *Mya arenaria*. While harvesting by humans removed much of the adult clam resource, circumstantial evidence strongly implicated the green crab in several successive years of recruitment failures, when the crabs consumed young clams before they could grow to harvestable size (Lindsay and Savage 1978). Glude (1955) documented a 50% decline of clam abundance at one site in four years, during which there was minimal fishing pressure. MacPhail et al. (1953) reported mortalities of planted soft shell clams as high as 57% over a three-day period following the arrival of green crabs, compared to estimated former mortalities of 10%/month. Smith et al. (1955) demonstrated survival of 355-409 clams/m^2 in plots protected from green crabs after 6 months, while no clams remained in uncaged plots. MacPhail et al. (1953) stated:

"It must be concluded that the green crab is one of the worst, if not the worst, clam predators we know. Its ability to multiply rapidly, to feed on many varieties of shellfish other than commercial species, and its large appetite for commercially important shellfish, all suggest that it can do enormous damage."

Effects are likely to be most obvious immediately following the introduction of green crabs. Enclosure with green crab in Barnstable Harbor, MA, where green crabs and soft-shell clams had co-existed for more than a century, changed the size distribution of the clam population but did not significantly affect abundance. Juvenile clams of shell length > 2 mm were disproportionately affected by green crab predation (Hunt and Mullineaux 2002). Green crabs at ambient density (1.2 crab/m^2) removed ~80% of soft-shell clams (*Mya arenaria*) <17 mm in field experiments on a mudflat in Pomquet Harbour, NS (Floyd and Williams 2004). Similar removal rates were seen at a higher density (6 crabs/m^2), which reflected published density of green crabs in New England (e.g., Davis and Short 1997). The rate of consumption at was 14.5 – 21.8 clams/crab/day at 1.2 crabs/m^2, and 3.1-8.5 clams/crab/day at 6 crabs/m^2. There was no effect on clams > 17 mm. Floyd and Williams (2004) attributed this to a depth refuge, as the literature says the crabs should readily have been able to prey on clams this size. The crabs were males ranging from 44 to 65 mm CW, and the experiment ran from May 23 to August 21-23. Overwinter mortality (between August and May) of small soft-shell clams was 90%, but could not be partitioned between green crabs and other potential causes (Floyd and Williams 2004). Ropes (1968) found crabs as small as 10 mm to be eating soft-shell clams of about the same size as the crabs.

Intense predation on scallops *Argopecten irradians* in Connecticut between August and October was attributed in part to green crab, which preyed on released scallops of size < 50 mm (Morgan et al. 1980). Green crabs were believed to limit local fisheries on scallops in Massachusetts (Ruiz et al. 1998). Scallops seeded in Atlantic Canada also attracted potential predators including green crabs, but minimal predator aggregation was observed (Wong et al. 2005).

On Martha's Vineyard, Massachusetts, green crabs were considered to be the major cause of mortality and poor fishery performance for quahogs *Mercenaria mercenaria* (Ruiz et al. 1998).

Green crab size-selectively preyed on *Macoma* spp., which was most susceptible to predation during spring and winter migrations (Hiddink et al. 2002a, 2002b). *Macoma* reacted to green crab chemical cues by increasing burrowing depth (Griffiths and Richardson 2006). Density-dependent predation by green crabs determined recruitment and adult-juvenile interactions in *Macoma* (Richards et al. 2002).

Mackinnon (1997) observed that green crab presence resulted in 75% mortality in blue mussel *Mytilus edulis* populations. Medium-sized (shell length 2.25 cm) mussels were preferred as prey, at least by male crabs of CW 70-75 mm (Jubb et al. 1983). Predation on blue mussels appeared to be affected by habitat complexity. Mussels in complex substrates tended to be preyed on less, but suffered from increased competition for resources. Mussels on more uniform substrates were subjected to increased predation pressure. These mussels reacted by increasing shell thickness and size of the posterior adductor muscle (Frandsen and Dolmer 2002, Freeman and Byers 2006, Freeman 2007).

In multiple-prey choice laboratory experiments in PEI, male inter-molt (red or orange) green crabs ate 83% of mussels < 25 mm, 75% of oysters < 25 mm, and 58% of soft-shell clams < 15 mm, in 4 days (Miron et al. 2002, Miron et al. 2005). Small quahogs were also consumed. In New England, laboratory and field experiments with a duration up to 2 d found the mortalities of mussels to be between 75% (no control) and 44% (compared to 25% in the control) (Tyrrell et al. 2006).

Nutricola spp. in California experienced a five to ten-fold decline in abundance within three years of green crab introduction (Grosholz et al. 2000). These bivalves were a major food source for shorebirds. A population collapse of *Nutricola* in Bodega Bay in 1985, unrelated to green crabs, resulted in a significant decline in shorebird abundance and physiological condition (Ruiz et al. 1998).

Finger (1998 abstract, cited in Ruiz et al. 1998) reported losses of cultured Manila clams *Venerupis philippinarum* as high as 50% in Tomales Bay, California, attributed to green crab. Manila clam is itself an introduced species in the Pacific Northwest. Venerid clams in Tasmania were subject to both size selective and density-dependent predation (Walton et al. 2002).

6.2.2.3. Crustacea

The net effect on lobster population structure is still unknown, but green crabs were reported to have a significant agonistic effect on juvenile American lobster *Homarus americanus* in laboratory experiments (Rossong et al. 2006). Elner (1981) found no evidence of green crab predation on American lobster, based on field-collected green crab stomachs from southwestern Nova Scotia, but adult green crabs fed on juvenile lobsters in the laboratory. Off southwestern Nova Scotia, lobsters and green crabs coexisted in the same habitat; lobsters were trapped commercially in depths as shallow as 3 m (Elner 1981). Predation by green crabs on settling postlarval lobsters has been observed but is affected by substrate type (Barshaw et al. 1994). Cobble appeared to provide the greatest protection from crabs, with peat next and sand the least favourable substrate.

Elner (1981) found the remains of *Cancer* crabs (*C. irroratus* or *C. borealis*) in green crab stomachs from Port Hebert, NS. On the west coast of North America, juvenile Dungeness crab *Cancer magister* was highly vulnerable to green crab predation (Ruiz et al. 1998).

Hemigrapsus sp., on the Pacific coast of North America, showed a five to ten-fold decline in abundance within three years of green crab introduction (Grosholz et al. 2000), yet *Hemigrapsus sanguineus* appeared to outcompete green crab on the Atlantic coast of North America (McDermott 1999).

Hermit crabs responded to green crab predation by altering shell choice behaviour, favouring intact shells (Rotjan et al. 2004).

Rangely and Thomas (1987) found that juvenile green crabs (carapace width 21-29 mm) in the Bay of Fundy selectively preyed on rock barnacles (*Semibalanus balanoides*) and suggested that small crabs could be an important factor for barnacle mortality. Buschbaum (2002) found no significant effect on *Semibalanus balanoides* densities in the intertidal zone, whereas predation by adult green crabs (in combination with juvenile starfish) significantly reduced subtidal densities of the barnacle *Balanus crenatus*. The predation effect of small crabs (CW 15-30 mm), which were three times more abundant in the intertidal than the subtidal, was undetectable. Predation determined barnacle abundance on subtidal mussel (*Mytilus edulis*) beds; in turn, barnacles fouled and affected the growth of the mussels. Buschbaum did not quantify the relative importance of green crabs vs. starfish in this process, but noted that groups of barnacles were often totally crushed and scraped off from the shells of the mussels, a feeding mark typical of large green crabs.

6.2.2.4. Fishes

Green crabs were reported to have a potentially significant impact on juvenile winter flounder, consuming up to >30% of a year class (Taylor 2005).

No evidence of nest predation on fish eggs has been reported from Canadian waters, but this was common in the native range of green crab. Ostlund-Nilsson (2000) reported green crab predation on the eggs of the fifteen-spined stickleback *Spinachia spinachia*. Apparently, this affected mate selection, as females tended to prefer males who built "high-location" nests that appeared safer from nest predation. Green crab predation may also indirectly reduce egg hatching rates of fishes. Female common gobies *Pomatoschistus microps* prefer to spawn in nests with the most sand on top and the smallest entrance, which are less vulnerable to detection by an egg predator, the green crab. However, these small entrances may reduce oxygenation of eggs (Jones and Reynolds 1999).

6.2.2.5. Other

Green crabs appeared to have the potential to negatively affect the recruitment and settlement of a large number of intertidal and subtidal invertebrate taxa (Enderlein and Wahl 2004). Population dynamics of infaunal organisms were reportedly affected by a combination of predation pressure and substrate disturbance (Le Calvez 1987). Nematodes in organic-poor sediments were mainly affected by predation pressure, those in organic-rich sediments mainly indirectly by disturbance of the sediment (Schratzberger and Warwick 1999). Trussell et al. (2004) indicated that predation pressure by green crab could have trophic cascade-type effects. For example, Grosholz et al. (2000) showed that certain infaunal populations increased significantly as a side effect of green crab predation. Obviously the net effect of green crab establishment will result from the sum of direct and indirect effects on an ecosystem, which is going to be a complex effect given the many kinds of interactions that green crabs may have with biota and habitat. Potential cascade effects must be considered when investigating the impact of invasive green crabs.

6.2.3. Effects on habitat/ecosystem

Green crabs have had similar and predictable ecological impacts in their native range and in introductions, even though their habitat use may vary between areas. This is because the ecological impacts of green crabs are strongest and most predictable in protected embayments which are uniformly occupied by green crabs in all regions. Green crabs have been less predictable in colonizing outer coast areas but have not been documented to have a significant impact in such areas (Grosholz and Ruiz 1996).

Extensive pitting of the bottom in late fall and winter is attributed to green crab foraging (Floyd and Williams 2004). Green crabs routinely burrow and dig pits to a depth of 15 cm (Ropes 1968, Lindsay and Savage 1978). Dow and Wallace (1952) documented burrows to a depth of 23 cm in sandy sediments with sufficient clay-silt content to serve as a binder. Burrows were consistently shallower in sand, and were not observed in pebbles, cobble or coarse gravel.

6.2.4. Adverse effects on human uses of water body

6.2.4.1. Aquaculture

Among species aquacultured in Canada, bivalves are most likely to be affected by the green crab. On the east coast, species that could be affected include: blue mussels *Mytilus edulis*, quahogs *Mercenaria mercenaria*, eastern oysters *Crassostrea virginica*, soft-shell clams *Mya arenaria,* and bay scallop *Argopecten irradians irradians* (Clark et al. 2004, Gardner and Thomas 1987, Floyd and Williams 2004, Miron et al. 2005). In western North America, green crabs affect cultured Manila clam *Venerupis philippinarum* (Ruiz et al. 1998). The effects have been discussed above in Section 6.2.2.2.

One aspect of green crab impacts on bivalves that has not been previously discussed in this document is the effect on stock enhancement programs for infaunal bivalves. Stock enhancement of the soft-shell clam (*Mya arenaria*) was attempted throughout New England as a response to declining catches, but would have required protection of clams < 50 mm long from green crab predation, using chicken wire fences during two summers of growth to market size. Fences were expensive and often failed to exclude green crabs, which were observed swimming over the fences at high tide (Smith et al. 1955). There were, however, enough instances where soft-shell clam or blue mussel populations increased following the use of fences that, in 1976, the state of Maine established a program of matching funds to help coastal towns erect fences around clam beds (Lindsay and Savage 1978). Walton and Walton (2001) observed that green crabs were considered the most significant threat to quahog (*Mercenaria mercenaria*) stock enhancement programs in New England. Producers scored the damage done by green crabs at a mean value of 8.3 on a scale of 1 (lowest) to 10 (highest). They found that green crabs significantly reduced the efficiency of seeding programs.

Shellfish growers in Washington state were initially concerned about the potential effects on aquaculture, but the level of concern was low in 1999, a couple of years after the initial discovery of green crabs, due to lack of observed effects on their product to date with crabs at low densities (0.002-0.006 crab/trap/hr) (Carr and Dumbauld 2000).

6.2.4.2. Fisheries

The most widely known example of green crab impact on a commercial fishery is the example of the soft-shell clam fishery in Maine and Atlantic Canada. Soft-shell clam production in Maine decreased from > 8.5 million pounds to slightly over 0.6 million pounds during an eight year period in the 1940's concurrent with the green crab invasion (Glude 1954). Floyd and Williams (2004) observed that although large soft-shell clams likely have a depth refuge from green crab predation, crabs have the potential for decimating stocks of small clams, thus significantly affecting recruitment. Hoagland and Jin (2006) question whether the responsibility of the green crab for the demise of the soft-shell fishery in New England (as attributed by Pimentel 2000) was overstated – while this may have been the case, our own view is that a combination of fishing pressure and recruitment limitation by green crab was responsible. The clam population was clearly unable to sustain historical fishing levels under the heavy additional pressure imposed by green crabs. Early accounts of the rapid and catastrophic loss of softshell crabs from research plots are consistent with green crab limitation of the fishery (e.g., Smith et al. 1955).

Green crabs have also been implicated in adversely affecting other bivalve fisheries, e.g., bay scallops, and surf clams (Walton 1997). Walton et al. (2002) found that green crabs significantly impacted a fledgling fishery for venerid clams in Tasmania. They observed that green crab predation rates were significantly higher than any native crustaceans; that predation was density-dependent and that green crabs preferred juvenile venerid clams (<13 mm shell length). Walton observed that green crabs had a significant impact on the fishery of Tasmanian clams.

In commercial fisheries of Atlantic Canada, the trappability of rock crabs (*Cancer irroratus*) is unlikely to be affected by green crabs, based on laboratory experiments (Miller and Addison 1995).

In Pacific Canada, green crabs are unlikely to affect the trappability of Dungeness crabs (*Cancer magister*), as the fishery occurs at depths that are not frequented by green crabs (G. Gillespie, pers. comm.). This does not discount the potential for green crabs to affect to affect recruitment of Dungeness crabs, which typically settle in shallow water in estuarine habitats, the same areas that could support high densities of green crabs (G. Gillespie, pers. comm.).

Green crabs compete with and prey on juvenile American lobster (*Homarus americanus*) in the laboratory (Rossong et al. 2006). To date there is no clear evidence that this would have any impact on the commercial lobster fishery, but given that predation by green crab has the potential to affect lobster recruitment, this may warrant further study. JCG Resource Consultants (2002) cited an anecdotal account of lobster larvae in the stomach contents of green crab from Cape Breton Island. It should be noted, however, that increased lobster recruitment, attributed to warmer temperatures, occurred in several areas of Atlantic Canada shortly after the establishment of green crabs (Campbell et al. 1991).

In PEI, green crabs are a major nuisance species in the American eel *Anguilla rostrata* fishery, as green crabs either prevent the entry of eels to fyke nets, or damage eels captured in the nets so that they are unmarketable (Locke pers. obs.).

6.2.4.3. Marine transportation

There are no known effects of green crabs on marine transportation.

6.2.5. Impacts on human health

Green crabs can concentrate marine biotoxins consumed by bivalve prey. Esters of okadaic acid in razor clams (*Solen marginalis*) in a Portugese lagoon led to at least one case of human Diarrheic Shellfish Poisoning after ingestion of a large number of green crabs contaminated with okadaic acid (>32 mg/100g in a remaining sample of the meal). Domoic acid (the compound responsible for Amnesic Shellfish Poisoning) was also present in the crabs (Vale and Sampayo 2002).

7. Management

7.1. Patterns in population abundance following establishment

Following the detection of green crabs in a new location, populations often built up to high numbers within two or three years, which is consistent with the generation time of the species. In California, overnight trap sets captured hundreds of crabs after only two years (Cohen et al. 1995). In the Bay of Fundy, catches reached comparable levels in about three years (Medcof 1958). In eastern Prince Edward Island, catch per unit effort in traps increased about three-fold between 2001 and 2002, about five or six years after initial introduction (JCG Resource Consultants 2002).

Green crabs in Atlantic Canada followed a "boom and bust" cycle in the early years following invasion, such as has been described for some other invasive species. In the Bay of Fundy, green crab catch rates declined from >300 crabs/trap in 1954, three years after the invasion, to 65 crabs/trap in 1957 (Medcof 1958). The catch rate of green crabs in traps in the Bras d'Or Lakes decreased between 1999-2000 and 2005 (Tremblay et al. 2006), about 10 to 15 years after the likely establishment of green crabs (Audet et al. 2003). No change was seen over the same time period in eastern Nova Scotia sites where green crab had been established longer (Tremblay et al. 2006). Green crab abundance in Nova Scotian estuaries of the southern Gulf of St. Lawrence had also apparently declined in 2003 and 2004 (Rossong et al. 2006), about a decade after green crab first established there.

Densities of adult crabs in the native range or in areas where invasions have been long established tend to be around 5 crabs/m^2 or lower. Munch-Petersen et al. (1982) reported 0.001-5 crabs/m^2 in depths of 0-10 m, in the Kattegat, Denmark. Muus (1967, cited in Munch-Petersen et al. 1982) found densities of 0.2-0.5 crabs/m^2 in Danish waters. In the low rocky intertidal zone of northern New England, crab densities (adult and juveniles combined) ranged from 0.08-12.4 crabs/ m^2 (Menge 1983). In soft-bottom subtidal waters of the Great Bay Estuary, New Hampshire, density was 5.4 crabs/ (Davis et al. 1998). Young et al. (1999) found crabs at densities up to 5 crabs/ m^2 in salt marsh creeks in New England. On most rocky shores studied in Maine and Massachusetts, there were fewer than 0.5 crabs/m^2 in the high- and mid-intertidal zones, except for one site which had 3 crabs/m^2 in the mid-intertidal and 4 crabs/m^2 in the high intertidal (Menge 1976). Ambient density was 1.2 crab/m^2 on a mudflat in Pomquet Harbour, NS, almost a decade after green crab establishment (Floyd and Williams 2004). Tremblay et al. (2005) observed densities of 0.009 crab/m^2 in diving surveys off Crammond Islands, in the West Bay of the Bras d'Or Lakes, but noted that the depths and habitat types surveyed were probably not optimal for green crabs. Densities were about 17 times lower in the East Bay, around 0.009 crab/m^2, but again not in optimal habitats.

7.2. Control strategies

Management strategies can be categorized as prevention, eradication, and control.

Prevention would involve blocking anthropogenic pathways; although natural transport probably plays a major role in green crab dispersal in relatively local areas, vectors such as ballast water accelerate the transport of populations into areas that they might not have reached by natural dispersal for many years. Slowed expansion times can provide significant economic benefits. Green crab is a target pest species identified by the Australian Ballast Water Management Advisory Council, which aims to block the ballast water vector (Currie et al. 1998). The relative importance of the various potential vectors of green crabs, described in Section 4, have not been quantified. Understanding the role of vectors is a requirement for informed management of pathways.

Eradication, the second option for management, is generally considered intractable due to the ready supply of planktonic larvae (Ruiz et al. 1998). This conclusion might not be appropriate in situations where a new invasion has occurred far from existing populations, the only likely vectors are anthropogenic and can be controlled, and early detection/rapid response is feasible.

The third option, control, essentially involves suppressing the population of green crabs below an economic or ecologic threshold, or excluding it from sensitive areas. Control methods that have been considered or attempted for green crabs include sound pulses, air exposure/desiccation, chemical control, biological control ("guarding" bivalve seed with toadfish *Opanus tau*), genetic manipulations, local physical barriers (nets, fences, rafts), altered fishery practices (overwintering seed so it is larger when planted, closed areas), manual removal, commercial harvesting, trapping, and parasitic castrators (Walton 2000, Walton and Walton 2001, McEnnulty et al. 2001). Selective harvest to maintain green crabs below a threshold, and control measures to exclude green crabs from aquaculture sites, have already been implemented or attempted in many areas.

Selective harvest programs as typically carried out in New England did not seem to reduce abundance, but abundance may be controlled by intensive and frequent trapping within restricted embayments (Walton 2000). A great deal of effort may be required to achieve this. For example, the town of Edgartown on Martha's Vineyard, Massachusetts, removed an estimated 10 tonnes of green crabs from local ponds in 1995, but unfortunately the effect on clam and scallop survival was not assessed (Ruiz et al. 1998).

However, overfishing is probably responsible for the decline of the commercial fishery on green crabs in Portugal (Gomes 1991), so clearly with enough effort it is possible to suppress green crabs.

JCG Resource Consultants (2002) conducted a study of the potential of harvesting to control green crabs in eastern Prince Edward Island as well as to supply crabs for seafood product development. In 14 fishing days, approximately 15,000 green crabs were caught. Catch rates exceeded 100 crabs/trap (>7 kg of crabs/trap) using modified lobster traps. There was no bycatch of other nearshore species. The mean size of green crabs caught in the modified lobster traps baited with frozen herring was 75 mm (CW); in unbaited eel traps the mean size was ~50 mm (CW). Approximately 85% of the captured green crabs were male.

Management strategies for aquaculture include the timing of seed placement, the size and density of seed plots, the density of seed within plots, the physical substrate type and the use of physical barriers (cages, racks or bags) (Ruiz et al. 1998). Davies et al. (1980) presented designs, costs and benefits of appropriate fences to protect seed mussels. Protecting mussels for the first year of cultivation led to an eight-fold increase in final yield (Dare et al. 1983). In North Wales, it was recommended that Pacific oyster (*Crassostrea gigas*) be protected until at least 5 g and preferably 8-10 g in size (Dare et al. 1983). Exclusion of green crabs from sites seeded with soft-shell clams in Massachusetts was apparently successful, using 4-mm plastic webbing (Buttner et al. 2004). However, lease sites were quite large, in the range of 0.4-2 hectares (Buttner et al. 2004), which must have made exclusion quite difficult. Fences have also been used extensively in Maine to protect soft-shell clams; fences were put out in spring before the crabs become active; the fences were imbedded several cm into the sediment to prevent crabs from digging underneath; a typical fence was about 45 cm high; traps designed to catch green crabs were placed inside the fence; because the fences are susceptible to ice damage, they were removed before winter (Lindsay and Savage 1978). Most (85% of) quahog growers in New England who took measures to protect newly planted seed from predation used nets and fences. About 65% were currently using or had tried traps (Walton and Walton 2001). Just over half of these growers found trapping was effective. However, almost half of the survey respondents had tried and given up on methods of protecting seed. New England quahog growers who supported trapping noted reductions in green crab density, however others considered it to be ineffective, or otherwise had issues with attraction of predators to the area, the large acreage involved, and negative effects on nontarget species including endangered species (Walton and Walton 2001). Control strategies often rely on baited traps, but these have little effect on propagule pressure because ovigerous females are less mobile and unresponsive to bait. Therefore trapping primarily captures males, which is of little consequence in suppressing populations (Munch-Petersen et al. 1982, Lützen 1984, McDonald et al. 2004).

Delayed outplant was recommended as a strategy to reduce losses to green crab predation in commercial production of Manila clams (*Venerupis philippinarum*) (Grosholz et al. 2001). Similarly, modifications of timing, size and density of seeding of quahog *Mercenaria mercenaria* in Martha's Vineyard have been tried, in order to develop an optimum seeding strategy to minimize predation (Walton et al. 1999).

Biological control by parasites, particularly the castrating barnacle *Sacculina carcini* has been proposed, but the parasite is not specific to the green crab, poses an unacceptable risk to native crab populations, and is relatively ineffective as a control measure (Thresher et al. 2000, Goddard 2001). All infected *Cancer magister* died within 97 days, whereas green crabs survived up to 355 days (Goddard 2001). More than one-third of the green crabs settled on by *S. carcini* did not develop infections or any detectable host response (Goddard 2001).

8. Summary

The green crab is considered one of the 100 'worst alien invasive species'. A native of coastal and estuarine waters of Europe and Northern Africa, it has invaded waters of both Atlantic and Pacific coasts of North America, South Africa, Australia, South America, and Asia. Green crabs were first observed on the east coast of North America in Massachusetts in 1817, and now extend from Prince Edward Island to Virginia and from British Columbia to California. Green crabs are successful invaders of warm, sheltered coastal and estuarine habitats throughout the world and of semi-exposed rocky coasts in some areas.

The green crab is a voracious omnivore with a wide tolerance for salinity variation and habitat types. It is commonly found from the high tide level to depths exceeding 5 m, sometimes even as deep as 60 m. It is eurythermic, being able to survive temperatures from 0 to over 35^{o}C and reproduce at temperatures up to 18 to 26^{o}C. It is euryhaline, tolerating salinities from 4 to 52$^{o}/_{oo}$. It is reasonably tolerant of oxygen stresses.

Green crabs live 4-7 years and can reach a maximum size of 9-10 cm (carapace width). Recruitment strength appears to be positively correlated with the previous winter temperatures, with mean monthly temperatures above 10^{o}C needed for at least part of the winter. The life cycle alternates between benthic adults and planktonic larvae. Females can spawn up to 185,000 eggs at a time. Four zoeal and a megalopa larval stage develop in open waters for upward of 50 days, possibly as long as 90 days, and undertake vertical migrations enhancing their export from estuaries, making green crabs extraordinarily efficient larval dispersers. Planktonic larval abundances can reach ~150 individuals/m^3.

The vast majority of green crab invasions throughout the world are attributable to transport by human agents. At least three major episodes of anthropogenic transport of green crabs to North America have been identified: around 1800, the 1850's to 1870's and the 1980's to 1990's. Along the Atlantic coast it is believed that expansion may be related to a combination of temperature changes associated with global climate change and a series of passive transport events including: ballast water, movement of commercial shellfish/aquaculture products, bait release, traps and cages, research/education facilities, marine construction equipment, movement of sediments/sand and historical vectors. Episodic dispersals are an important factor in understanding green crab distribution and are apparently associated with increased shipping. Anthropogenic disturbances in coastal and estuarine waters may enhance invasive success.

Green crabs prey on a variety of marine organisms including species from at least 104 families, 158 genera, in 5 plant and protist and 14 animal phyla. Chief among these are (in order of importance) bivalves, gastropods, crustaceans and fishes. Green crabs may prey on commercially important bivalves, gastropods, decapods and fishes. Patterns of predation are quite similar worldwide. Impacts on prey are greater in soft-bottom habitat and in environments sheltered from strong wave action. In addition to the direct effect on the mortality of prey species, behavioural and physiological responses to green crab predation include a variety of 'inducible defense' mechanisms such as predator avoidance (e.g., crawl-out response), increasing shell thickness, change of colour frequency, and release of alarm substances. Predation pressure by green crab is thought to have trophic cascade-type effects resulting in changes to native trophic structure as well as facilitating introduction of other invasive species.

Given the omnivorous and very diverse nature of green crab diets, it is likely that they may compete for food with many other predators. The potential for competition for food or habitat has been identified for several commercially fished decapods.

The predominant natural predators of green crabs include fish and bird species, as well as larger decapods.

Habitat characteristics may be affected by the activities of green crab, especially digging in soft sediment, which may displace rooted macrophytes such as eelgrass.

Introductions and active dispersal of green crabs have been of particular concern to shellfish culture industries, shellfish lease holders and commercial inshore clam fisheries as well as eel fisheries. Green crabs have been implicated in affecting fisheries for fishes, softshell clams, bay scallops, venerid clams and surf clams. It is increasingly important to treat the effects of invasive species, not as isolated events, but as aspects of a whole-ecosystem view toward the influence of invasive species on fisheries management. Control efforts have included fencing, trapping and poisoning, with varying success. Early efforts at eradication through physical removal in Massachusetts have proven inconclusive. Additionally, parasites have been proposed as biocontrol agents, but introducing the parasitic castrator *Sacculina carcini* (the most promising candidate) could pose an unacceptable risk to native crabs.

Not all effects of green crabs invasions appear to be negative. There is a strong market for commercial fisheries in its native range. Green crabs may be good indicator species for the monitoring of heavy metal contamination. Green crabs have potential as control agents for biofouling (e.g. fouling by invasive tunicates). They may also be useful as agents for the removal of at least some forms of organic pollution at aquaculture sites.

9. Acknowledgements

We thank DFO's Centre of Expertise in Aquatic Risk Assessment for funding, and M. Koops and T. Landry for their encouragement to undertake this project. We also appreciate comments on the manuscript by G. Gillespie, M. Hanson, and an anonymous reviewer, and the contribution of unpublished observations or manuscripts in press by C. McKenzie, N. MacNair, N. Simard, J. Tremblay, J. Thompson, R. Hart, L. Gendron, D. Brickman, M. Dadswell and G. Gillespie.

10. Literature cited

Ahyong, S.T. 2005. Range extension of two invasive crab species in eastern Australia: *Carcinus maenas* (Linnaeus) and *Pyromaia tuberculata* (Lockington). Mar. Poll. Bull. 50: 460-462.

Ahsanullah, M. and R.C. Newell. 1977. The effects of humidity and temperature on water loss in *Carcinus maenas* (L) and *Portunus marmoreus* (Leach). Comp. Biochem. Physiol. A 56: 593-601.

Ambariyanto, S.R. and R. Seed. 1991. The infestation of *Mytilus edulis* Linnaeus by *Polydora ciliate* (Johnston) in the Conwy Estuary, North Wales. J. Molluscan Stud. 57: 413-424.

Anger, K., E. Spivak and T. Luppi. 1998. Effects of reduced salinities on development and bioenergetics of early larval shore crab, *Carcinus maenas*. J. Exp. Mar. Biol. Ecol. 220: 287-304.

Anon. 1961. Annual report of the Fisheries Research Board of Canada, 1960-61. p. 54.

Ashkenas, L.R. and J. Atema. 1978. A salt marsh predator-prey relationship: attack behavior of *Carcinus maenas* (L.) and defenses of *Ilyanassa obsoleta* (Say). Biol. Bull. 155: 426.

Audet, D., D.S. Davis, G. Miron, M. Moriyasu, K. Benhalima and R. Campbell. 2003. Geographical expansion of a nonindigenous crab, *Carcinus maenas* (L.), along the Nova Scotian shore into the southeastern Gulf of St. Lawrence, Canada. J. Shellfish Res. 22: 255-262.

Baeta, A., H.N. Cabral, J.M. Neto, J.C. Marques and M.A. Pardal. 2005. Biology, population dynamics and secondary production of the green crab *Carcinus maenas* (L.) in a temperate estuary. Est. Coast. Shelf Sci. 65: 43-52.

Bagley, M.J. and J.B. Geller. 1999. Microsatellite DNA analysis of native and invading populations of European green crabs. First National Conference on Marine Bioinvasions, January 24-27 1999. Cambridge, MA.

Barshaw, D.E., K.W. Able and K.L. Heck. 1994. Salt marsh peat reefs as protection for postlarval lobsters *Homarus americanus* from fish and crab predators: Comparisons with other substrates. Mar. Ecol. Prog. Ser. 106: 203-206.

Behrens Yamada, S. and M. Becklund. 2004. Status of the European green crab invasion. J. Shellfish Res. 23: 651.

Behrens Yamada, S., B.R. Dumbauld, A. Kalin, C.E. Hunt, R. Figlar-Barnes and A. Randall. 2005. Growth and persistence of a recent invader *Carcinus maenas* in estuaries of the northeastern Pacific. Biol. Invas. 7: 309-321.

Behrens Yamada, S. and L. Hauck. 2001a. Field identification of the European green crab species: *Carcinus maenas* and *Carcinus aestuarii*. J. Shellfish Res. 20: 905-912.

Behrens Yamada, S., A. Kalin and C. Hunt. 2001b. Growth and longevity of the European green crab *Carcinus maenas* in the Pacific Northwest. Second International Conference on Bioinvasions, 2001, New Orleans, LA. Abstract Book, p. 165-166.

Berrill, M. 1982. The life cycle of the green crab *Carcinus maenas* at the northern end of its range. J. Crustacean Biol. 2: 31-39.

Boschma, H. 1972. On the occurrence of *Carcinus maenas* (Linnaeus) and its parasite *Sacculina carcini* Thompson in Burma, with notes on the transport of crabs to new localities. Zool. Meded. 47 (11): 145-155.

Brattey, J., R.W. Elner, L.S. Uhazy and A.E. Bagnall. 1985. Metazoan parasites and commensals of five crab (Brachyura) species from eastern Canada. Can. J. Zool. 63: 2224-2229.

Breves, J.P. and J.L. Specker. 2005. Cortisol stress response of juvenile winter flounder (*Pseudopleuronectes americanus* Walbaum) to predators. J. Exp. Mar. Biol. Ecol. 325: 1-7.

Brian, J.V. 2005. Inter-population variability in the reproductive morphology of the shore crab (*Carcinus maenas*): evidence of endocrine disruption in a marine crustacean? Mar. Poll. Bull. 50: 410-416.

Broekhuysen, G.L. 1936. On development, growth and distribution of *Carcinides maenas* (L.). Archs. Néer. Zool. 2: 257-399.

Buschbaum, C. 2002. Predation on barnacles of intertidal and subtidal mussel beds in the Wadden Sea. Helgol. Mar. Res. 56: 37-43.

Buttner, J.K., M. Fregeau, S. Weston, B. McAneney, J. Grundstrom, A. Murawski and E. Parker. 2004. Commercial culture of softshell clams has arrived and is growing on Massachusetts' North Shore. J. Shellfish Res. 23: 633.

Cameron, B. and A. Metaxas. 2005. Invasive green crab, *Carcinus maenas*, on the Atlantic coast and in the Bras d'Or Lakes, Nova Scotia, Canada: Larval supply and recruitment. J. Mar. Biol. Ass. U.K. 85: 847-855.

Campbell, A., D.J. Noakes and R.W. Elner. 1991. Temperature and lobster, *Homarus americanus*, yield relationships. Can. J. Fish. Aquat. Sci. 48: 2073-2082.

Camphuysen, C.J., C.M. Berrevoets, J.J.W.M. Cremers, A. Dekinga, R. Dekker, B.J. Ens, T.M. van der Have, R.K.H. Kats, T. Kuiken, M.F. Leopold, J. van der Meer and T. Piersma. 2002. Mass mortality of common eiders (*Somateria mollissima*) in the Dutch Wadden Sea, winter 1999/2000: starvation in a commercially exploited wetland of international importance. Biol. Cons. 106: 303-317.

Carlton, J.T. 2001. Introduced species in U.S. coastal waters: Environmental impacts and management priorities. Pew Oceans Commission, Arlington, VA.

Carlton, J.T. and A.N. Cohen. 2003. Episodic global dispersal in shallow water marine organisms: the case history of the European shore crabs *Carcinus maenas* and *C. aestuarii*. J. Biogeog. 30: 1809-1820.

Carr, E.M. and B.R. Dumbauld. 2000. Status of the European green crab invasion in Washington coastal estuaries: Can expansion be prevented? J. Shellfish Res. 19: 629-630.

Carver, C.E., A. Chisholm and A.L. Mallet. 2003. Strategies to mitigate the impact of *Ciona intestinalis* (L.) biofouling on shellfish production. J. Shellfish Res. 22: 621-631.

Catchpole, T.L., C.L.J. Frid and T.S. Gray. 2006. Importance of discards from the English *Nephrops norvegicus* fishery in the North Sea to marine scavengers. Mar. Ecol. Prog. Ser. 313: 215-226.

Cieluch, U., K. Anger, F. Aujoulat, F. Buchholz, M. Charmantier-Daures and G. Charmantier. 2004. Ontogeny of osmoregulatory structures and functions in the green crab *Carcinus maenas* (Crustacea, Decapoda). J. Exp. Biol. 207: 325-336.

Clark, A., S. Stiles, D. Jeffress and J. Choromanski. 2004. Observations on phenotypic plasticity and behavior in a genetic line of the bay scallop, *Argopecten irradians irradians*. J. Shellfish Res. 23: 634.

Clark, P.F., M. Neale and P.S. Rainbow. 2001. A morphometric analysis of regional variation in *Carcinus* Leach, 1814 (Brachyura: Portunidae: Carcininae) with particular reference to the status of the two species *C. maenas* (Linnaeus, 1758) and *C. aestuarii* Nardo, 1847. J. Crust. Biol. 21: 288-303.

Cohen, A.N. and J.T. Carlton. 1995. Nonindigenous aquatic species in a United States estuary: A case study of the biological invasions of the San Francisco Bay and Delta. Report to the US Fish and Wildlife Service, Washington, DC, and Connecticut Sea Grant.

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

Colautti, R.I., S.A. Bailey, C.D.A. van Overjijk, K. Amundsen and H.J. MacIsaac. 2006. Characterised and projected costs of nonindigenous species in Canada. Biol. Invas. 8: 45-59.

Congleton, W.R., T. Vassiliev, R.C. Bayer and B.R. Pearce. 2005. A survey of trends in Maine soft-shell clam landings. J. Shellfish Res. 24: 647.

Crooks, J.A. 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. Oikos 97: 153-166

Crothers, J.H. 1970. The distribution of crabs on rocky shores around the Dale Peninsula. Field Stud. (Lond.) 3: 263-274.

Currie, D.R., M.A. McArthur and B.F. Cohen. 1998. Exotic marine pests in the port of Geelong, Victoria. Marine and Freshwater Resources Institute, Victorian Dept. of Natural Resources and Environment, Australia. MAFRI Rep. 8: 65 p.

Darbyson, E.A. 2006. Local vectors of spread of the green crab (*Carcinus maenas*) and the clubbed tunicate (*Styela clava*) in the southern Gulf of St. Lawrence, Canada. M.Sc. Thesis, Dalhousie Univ., Biology Dept., Halifax, NS.

Dare, P.J., G. Davies and D.B. Edwards. 1983. Predation on juvenile Pacific oysters (*Crassostrea gigas* Thunberg) and mussels (*Mytilus edulis* L.) by shore crabs (*Carcinus maenas* (L.)). MAFF Direct. Fish. Res., Lowestoft, England, Fish. Res. Tech. Rep. No. 73, 15 p.

Davies, G., P.J. Dare and D.B. Edwards. 1980. Fenced enclosures for the protection of seed mussels (*Mytilus edulis* L.) from predation by shore-crabs (*Carcinus maenas* (L.)). MAFF Direct. Fish. Res., Lowestoft, England, Fish. Res. Tech. Rep. No. 56, 18 p.

Davis, R.C. and F.T. Short. 1997. Restoring eelgrass, *Zostera marina* L., habitat using a new transplanting technique: the horizontal rhizome method. Aquat. Bot. 59: 1-15.

Davis, R.C., F.T. Short and D.M. Burdick. 1998. Quantifying the effects of green crab damage to eelgrass transplants. Restor. Ecol. 6: 297-302.

Dawirs, R.R. 1984. Influence of starvation on larval development of *Carcinus maenas* L. (Decapoda: Portunidae). J. Exp. Mar. Biol. Ecol. 80: 47-66.

Dawirs, R.R., C. Pueschel and F. Schorn. 1986. Temperature and growth in *Carcinus maenas* L. (Decapoda: Portunidae) larvae reared in the laboratory from hatching through metamorphosis. J. Exp. Mar. Biol. Ecol. 100: 47-74.

Day, L.R. and A.H. Leim. 1952. Unusual marine species on the Atlantic coast in 1952. In: Needler, A.W.H. Fisheries Research Board of Canada, Report of the Atlantic Biological Station for 1952. p. 151-154.

Depledge, M.H. 1984. Disruption of circulatory and respiratory activity in shore crabs (*Carcinus maenas* (L.)) exposed to heavy metal pollution. Comp. Biochem. Physiol. 78C: 445-459.

DeRivera, C.E., N. Gray Hitchcock, S.J. Teck, B.P. Steves, A.H. Hines and G.M. Ruiz. 2006. Larval development rate predicts range expansion of an introduced crab. Mar. Biol. (web published) DOI 10.1007/s00227-006-0451-9.

DeRivera, C.E., G.M. Ruiz, A.H. Hines and P. Jivoff. 2005. Biotic resistance to invasion: Native predator limits abundance and distribution of an introduced crab. Ecol. 86: 3364-3376.

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

D'Udekem d'Acoz, C. 1993. Activités reproductrices saisonnières des différentes classes de tailles d'une population de crabes verts *Carcinus maenas* (Linnaeus, 1758) dans le sud de la mer du Nord. Cah. Biol. Mar. 35: 1-13.

Dumas, J.V. and J.D. Witman. 1993. Predation by herring gulls (*Larus argentatus* Coues) on two rocky intertidal crab species (*Carcinus maenas* (L.) and *Cancer irroratus* Say). J. Exp. Mar. Biol. Ecol. 169: 89-101.

Dunstone, N. and J.D.S. Birks. 1987. The feeding ecology of mink (*Mustela vison*). J. Zool. 212: 69-83.

Ekendahl, A. 1998. Colour polymorphic prey (*Littorina saxatilis* Olivi) and predatory effects of a crab population (*Carcinus maenas* L.). J. Exp. Mar. Biol. Ecol. 222: 239-246.

Ellis, J.C., W. Chen, B. O'Keefe, M.J. Shulman and J.D. Witman. 2005. Predation by gulls on crabs in rocky intertidal and shallow subtidal zones of the Gulf of Maine. J. Exp. Mar. Biol. Ecol. 324: 31-43.

Elner, R.W. 1980. The influence of temperature, sex and chela size on the foraging strategy of the shore crab, *Carcinus maenas* (L.). Mar. Behav. Physiol. 7: 15-24.

Elner, R.W. 1981. Diet of green crab *Carcinus maenas* (L.) from Port Hebert, southwestern Nova Scotia. J. Shellfish Res. 1: 89-94.

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

El-Sabh, M.I. 1979. The lower St. Lawrence estuary as a physical oceanographic system. Le Nat. Can. 106: 55-73.

Enderlein, P. and M. Wahl. 2004. Dominance of blue mussels versus consumer-mediated enhancement of benthic diversity. J. Sea Res. 51: 145-155.

Enright, C.T., R.W. Elner, A. Griswold and E.M. Borgese. 1993. Evaluation of crabs as control agents for biofouling in suspended culture of European oysters. World Aquacult. 24(4): 49-51.

Eriksson, S. and A.-M. Edlund. 1977. On the ecological energetics of 0-group *Carcinus maenas* (L.) from a shallow sandy bottom in Gullmar Fjord, Sweden. J. Exp. Mar. Biol. Ecol. 30: 233-248.

Factor, J.R. and B.L. Dexter. 1993. Suspension feeding in larval crabs (*Carcinus maenas*). J. Mar. Biol. Ass. U.K. 73: 207-211.

Feller, R.J. 2006. Weak meiofaunal trophic linkages in *Crangon crangon* and *Carcinus maenas*. J. Exp. Mar. Biol. Ecol. 330: 274-283.

Floyd, T. and J. Williams. 2004. Impact of green crab (*Carcinus maenas* L.) predation on a population of soft-shell clams (*Mya arenaria* L.) in the southern Gulf of St. Lawrence. J. Shellfish Res. 23: 457-462.

Frandsen, R.P. and P. Dolmer. 2002. Effects of substrate type on growth and mortality of blue mussels (*Mytilus edulis*) exposed to the predator *Carcinus maenas*. Mar. Biol. 141: 253-262.

Freeman, A.S. 2007. Specificity of induced defenses in *Mytilus edulis* and asymmetrical predator deterrence. Mar. Ecol. Prog. Ser. 334: 145-153.

Freeman, A.S. and J.E. Byers. 2006. Divergent induced responses to an invasive predator in marine mussel populations. Science 313: 831-833.

Gardner, J.P.A. and M.L.H. Thomas. 1987. Growth, mortality and production of organic matter by a rocky intertidal population of *Mytilus edulis* in the Quoddy Region of the Bay of Fundy. Mar. Ecol. Prog. Ser. 39: 31-36.

Gee, J.M., R.M. Warwick, J.T. Davey and C.L. George. 1985. Field experiments on the role of epibenthic predators in determining prey densities in an estuarine mudflat. Est. Coast. Shelf Sci. 21: 429-448.

Geller, J.B., E.D. Walton, E.D. Grosholz and G.M. Ruiz. 1997. Cryptic invasions of the crab *Carcinus* detected by molecular phylogeography. Mol. Ecol. 6: 901-906.

Gillespie, G.E., A.C. Phillips, D.L. Paltzat and T.W. Therriault. 2007. Status of the European green crab, *Carcinus maenas*, in British Columbia – 2006. Can. Tech. Rep. Fish. Aquat. Sci. 2700: 38 p.

Gillis, D.J., J.N. MacPherson and T.T. Rattray. 2000. The status of green crab (*Carcinus maenas*) in Prince Edward Island in 1999. PEI Department of Fisheries and Tourism, Fisheries and Aquaculture Division, Charlottetown, PEI.

Gimenez, L. and K. Anger. 2005. Effects of temporary food limitation on survival and development of brachyuran crab larvae. J. Plankton Res. 27: 485-494.

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.

Goddard, J.H.R. 2001. Experimental infection of native California crabs by *Sacculina carcini*, a potential biocontrol agent of introduced European crabs. Second International Conference on Marine Bioinvasions, April 9-11 2001, New Orleans, LA. Abstract Book, p. 59-60.

Goddard, J.H.R., M.E. Torchin, A.M. Kuris and K.D. Lafferty. 2005. Host specificity of *Sacculina carcini*, a potential biological control agent of the introduced European green crab *Carcinus maenas* in California. Biol. Invas. 7: 895-912.

Goggin, L. 1997. Parasites (excluding *Sacculina*) which could regulate populations of the European green crab *Carcinus maenas*. In: Thresher, R.E. (ed.) Proceedings the first international workshop on the demography, impacts and management of introduced populations of the European crab, *Carcinus maenas*. CRIMP Tech. Rep. 11. Centre for Research on Introduced Marine Pests, CSIRO Marine Laboratories, Hobart, Australia. p. 87-91.

Gomes, V. 1991. First results of tagging experiments on crab *Carcinus maenas* (L.) in the Ria de Aveiro Lagoon, Portugal. Ciênc. Biol. Ecol. Syst. (Portugal) 11: 21-29.

Gray Hitchcock, N., S. Teck, D. Lipski, B. Steves, C. de Rivera and G. Ruiz. 2003. Predicting European green crab, *Carcinus maenas*, invasion in Alaska. Third International Conference on Bioinvasions, March 16-19 2003, Abstract Book, p. 46.

Griffiths, C.L., P.A.R. Hockey, C. Erkom Schurink and P.J. Le Roux. 1992. Marine invasive aliens on South African shores: Implications for community structure and trophic functioning. S. Afr. J. Mar. Sci. 12: 713-722.

Griffiths, C.L. and C.A. Richardson. 2006. Chemically induced predator avoidance behaviour in the burrowing bivalve *Macoma balthica*. J. Exp. Mar. Biol. Ecol. 331: 91-98.

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

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

Grosholz, E. and G. Ruiz (editors) 2002. Management plan for the European green crab. Submitted to the Aquatic Nuisance Species Task Force. Green Crab Control Committee, US-ANS Task Force. Nov 2002.

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

Harris, L.G. and A.C. Jones. 2005. Temperature, herbivory and epibiont acquisition as factors controlling the distribution and ecological role of an invasive seaweed. Biol. Invas. 7: 913-924.

Hart, J.F.L. 1982. Crabs and their relatives of British Columbia. British Columbia Provincial Museum Handbook 40. Victoria, BC. 266 p.

Hart, J.L. 1955. The green crab – a shellfish enemy. Fisheries Research Board of Canada, Report of the Atlantic Biological Station, St. Andrews, N.B. for 1955: p.11.

Henry, R.P., S. Gehnrich, D. Weihrauch and D.W. Towle. 2003. Salinity-mediated carbonic anhydrase induction iin the gills of the euryhaline green crab, *Carcinus maenas*. Comp. Biochem. Physiol. A 136: 243-258.

Hidalgo, F.J., P.J. Barón and J.M. (Lobo) Orensanz. 2005. A prediction comes true: the green crab invades the Patagonian coast. Biol. Invas. 7: 547-552.

Hiddink, J.G., R.P. Kock and W.J. Wolff. 2002a. Active pelagic migrations of the bivalve *Macoma balthica* are dangerous. Mar. Biol. 140: 1149-1156.

Hiddink, J.G., S.A.E. Marijnissen, K. Troost and W.J. Wolff. 2002b. Predation on 0-group and older year classes of the bivalve *Macoma balthica*: interaction of size selection and intertial distribution of epibenthic predators. J. Exp. Mar. Biol. Ecol. 269: 223-248.

Hines, A.H., G.M. Ruiz, N. Gray Hitchcock and C. deRivera. 2004. Projecting range expansion of invasive European green crabs (*Carcinus maenas*) to Alaska: Temperature and salinity tolerance of larvae. Research report by Smithsonian Environmental Research Center, Edgewater, MD. Prepared for Prince William Sound Regional Citizen's Advisory Council, Anchorage, AK. 22 p.

Hoagland, P. and D. Jin. 2006. Science and economics in the management of an invasive species. BioSci. 56: 931-935.

Hoeg, J.T., H. Glenner, and M. Werner. 1997. The epicaridean parasite *Portunion moenadis* as a biological control agent on *Carcinus maenas*. In: Thresher, R.E. (ed.) Proceedings the first international workshop on the demography, impacts and management of introduced populations of the European crab, *Carcinus maenas*. CRIMP Tech. Rep. 11. Centre for Research on Introduced Marine Pests, CSIRO Marine Laboratories, Hobart, Australia. p. 85-86.

Hogarth, P. 1975. Pattern polymorphism and predation in the shore crab, *Carcinus maenas* (L.). Crustaceana 28: 316-319.

Hughes, R.N. and R.W. Elner. 1979. Tactics of a predator, *Carcinus maenas* and morphological responses of the prey, *Nucella lapillus*. J. Anim. Ecol. 48: 65-78.

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

Hunt, H.L. and L.S. Mullineaux. 2002. The roles of predation and postlarval transport in recruitment of the soft shell clam (*Mya arenaria*). Limnol. Oceanogr. 47: 151-164.

Hunter, E. and E. Naylor. 1993. Intertidal migration by the shore crab *Carcinus* maenas. Mar. Ecol. Prog. Ser. 101: 131-138.

Jacobsen, H.P. and O.B. Stabell. 1999. Predator-induced alarm responses in the common periwinkle, *Littorina littorea*: dependence on season, light conditions, and chemical labeling of predators. Mar. Biol. 134: 551-557.

Jamieson, G.S. 2000. European green crab, *Carcinus maenas*, introductions in 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.

Jamieson, G.S., M.G.G. Foreman, J.Y. Cherniawsky and C.D. Levings. 2002. European green crab (*Carcinus maenas*) dispersal: The Pacific experience. In: Paul, A.J., E.G. Dawe, R. Elner, G.S. Jamieson, G.H. Kruse, R.S. Otto, B. Sainte-Marie, T.C. Shirley and D. Woodby (eds.). Crabs in cold water regions: Biology, management and economics. University of Alaska Sea Grant College Progam AK-SG-02-01. pp. 561-576.

Jamieson, G.S., E.D. Grosholz, D.A. Armstrong and R.W. Elner. 1998. Potential ecological implications from the introduction of the European green crab, *Carcinus maenas* (Linnaeus), to British Columbia, Canada, and Washington, USA. J. Nat. Hist. 32: 1587-1598.

JCG Resource Consultants. 2002. Green crab fishery resource development study for Prince Edward Island, Phase I. JCG Resource Consultants, Charlottetown, PEI. Prepared for PEI Minister of Development and Technology. October, 2002. 24 p.

Jensen, G.C., P.S. McDonald and D.A. Armstrong. 2002. East meets west: competitive interactions between green crab *Carcinus maenas*, and native and introduced shore crab *Hemigrapsu*s spp. Mar. Ecol. Prog. Ser. 225: 251-262.

Johannesson, B. 1986. Shell morphology of *Littorina saxatilis* Olivi: The relative importance of physical factors and predation. J. Exp. Mar. Biol. Ecol. 102: 183-195.

Jones, J.C. and J.D. Reynolds. 1999. The influence of oxygen stress on female choice for male nest structure in the common goby. Anim. Behav. 57: 189-196.

Jubb, C.A., R.N. Hughes and T. Rheinallt. 1983. Behavioural mechanisms of size-selection by crabs, *Carcinus maenas* (L.) feeding on mussels, *Mytilus edulis* L. J. Exp. Mar. Biol. Ecol. 66: 81-87.

Kelley, D.F. 1987. Food of bass in U.K. waters. J. Mar. Biol. Ass. U.K. 67: 275-286.

Kerkut, G.A. and K.A. Munday. 1962. The effect of copper on the tissue respiration of the crab *Carcinus maenas*. Cah. Biol. Mar. 3: 27-35.

Kuris, A. 1997. Nemertean egg predators as potential biocontrol agents for *Carcinus maenas*. In: Thresher, R.E. (ed.) Proceedings the first international workshop on the demography, impacts and management of introduced populations of the European crab, *Carcinus maenas*. CRIMP Tech. Rep. 11. Centre for Research on Introduced Marine Pests, CSIRO Marine Laboratories, Hobart, Australia. p. 88-90.

Lafferty, K.D. and A.M. Kuris. 1996. Biological control of marine pests. Ecol. 77: 1989-2000.

Le Calvez, J.C. 1987. Location of the shore crab *Carcinus maenas* L., in the food web of a managed estuary ecosystem: The Rance Basin (Brittany, France). Inv. Pesq. 51 (Suppl. 1): 431-442.

Legeay, A. and J.-C. Massabuau. 2000a. Effect of salinity on hypoxia tolerance of resting green crabs, *Carcinus maenas*, after feeding. Mar. Biol. 136: 387-396.

Legeay, A. and J.-C. Massabuau. 2000b. The ability to feed in hypoxia follows a seasonally dependent pattern in shore crab *Carcinus maenas*. J. Exp. Mar. Biol. Ecol. 247: 113-129.

Leim, A.H. 1951. Unusual marine species on the Atlantic coast in 1951. In: Needler, A.W.H. Fisheries Research Board of Canada, Report of the Atlantic Biological Station for 1951, p. 138-140.

Le Roux, P. J., G. M. Branch, and M. A. P. Joska. 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. 9:85-92.

Lindsay, J.A. and N.B. Savage. 1978. Northern New England's threatened soft-shell clam populations. Environ. Manage. 2: 443-452.

Locke, A., G.J. Klassen, K. Ellis, J.M. Hanson, D. Garbary and N. MacNair. 2003. Effects of recent invasions in the southern Gulf of St. Lawrence: Predictions and early observations. *In* Proceedings of the 11th International Aquatic Invasive Species Conference, 25-28 February 2002, Alexandria VA. p. 143-153.

Locke, A., J.M. Hanson, K.M. Ellis, J. Thompson and R. Rochette. 2007. Invasion of the southern Gulf of St. Lawrence by the clubbed tunicate (*Styela clava* Herdman): Potential mechanisms for invasion of southern Gulf of St. Lawrence estuaries. J. Exp. Mar. Biol. Ecol. 342: 69-77.

Lohrer, A.N. and R.B. Whitlatch. 1997. Ecological studies on the recently introduced Japanese shore crab (*Hemigrapsus sanguineus*), in Eastern Long Island Sound. In: Balcom, N.C. (ed.) Proc 2nd Northeast Conference on Nonindigenous Aquatic Nuisance Species. Connecticut Sea Grant College, University of Connecticut, Groton, CT. pp. 49-60.

Lowe, S., M. Browne and S. Boudjelas. 2000. 100 of the world's worst invasive alien species: A selection from the GlobalInvasive Species database. The World Conservation Union (IUCN).

Lützen, J. 1984. Growth, reproduction and life span in *Sacculina carcini* Thomspon (Cirripedia: Rhizocephala) in the Isefjord, Denmark. Sarsia 69: 91-106.

Mackinnon, C. 1997. Preliminary evaluation of impacts of *Carcinus maenas* on bivalve populations in Tasmania. In: Thresher, R.E. (ed.) Proceedings the first international workshop on the demography, impacts and management of introduced populations of the European crab, *Carcinus maenas*. CRIMP Tech. Rep. 11. Centre for Research on Introduced Marine Pests, CSIRO Marine Laboratories, Hobart, Australia. p. 53-54.

MacPhail, J.S. 1953. Abundance and distribution of the green crab – a clam predator. . In: Needler, A.W.H. Fisheries Research Board of Canada, Report of the Atlantic Biological Station for 1953. p. 33-34.

MacPhail, J.S. and E.I. Lord. 1954. Abundance and distribution of the green crab. In: Hart, J.L. Fisheries Research Board of Canada, Report of the Atlantic Biological Station. p. 28.

MacPhail, J.S., E.I. Lord and L.M. Dickie. 1953. Preliminary experiments on the food of the green crab. In: Needler, A.W.H. Fisheries Research Board of Canada, Report of the Atlantic Biological Station for 1953. p. 32-33.

Martin-Diaz, M.L., D. Sales and T.A. Del Valls Casillas. 2004. Influence of salinity in hemolymph vitellogenin of the shore crab *Carcinus maenas*, to be used as a biomarker of contamination. Bull. Environ. Contam. Toxicol. 73: 870-877.

Martin-Diaz, M.L., A. Villena-Lincoln, S. Bamber, J. Blasco and T.A. DelValls. 2005. An integrated approach using bioaccumulation and biomarker measurements in female shore crab, *Carcinus maenas*. Chemosphere 58: 615-626.

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

Mason, C.F. and S.M. MacDonald. 1980. The winter diet of otters (*Lutra lutra*) on a Scottish sea loch. J. Zool. 192: 558-561.

Mathews, L.M., A.E. McKnight, R. Avery and K.T. Lee. 1999. Incidence of autotomy in New England populations of green crabs, *Carcinus maenas*, and an examination of the effect of claw autotomy on diet. J. Crust. Biol. 19: 713-719.

McDermott, J.J. 1999. The western Pacific brachyuran (*Hemigrapsus sanguineus*: Grapsidae) in its new habitat along the Atlantic coast of the United States: geographic distribution and ecology. ICES J Mar. Sci. 55: 289-298.

McDonald, P.S., G.C. Jensen and D.A. Armstrong. 1998. Green crabs and native predators: Possible limitations on the west coast invasion. J. Shellfish Res. 17: 1283.

McDonald, P.S., G.C. Jensen and D.A. Armstrong. 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.

McDonald, P.S., G.C. Jensen and D.A. Armstrong. 2004. Between a rock and a hard place: The ecology of ovigerous green crab, *Carcinus maenas* (L.), with emphasis on implications for monitoring and control efforts. J. Shellfish Res. 23: 657.

McEnnulty, F.R., T.E. Jones and N.J. Bax. 2001. The web-based Rapid Response Toolbox. (crimp.marine.csiro.au/nimpis/controls.htm, accessed June 13 2002)

McGaw, I.J., C.L. Reiber and J.A. Guadagnoli. 1999. Behavioral physiology of four crab species in low salinity. Biol. Bull. 196: 163-176.

McKnight, A., L.M. Mathews, R. Avery and K.T. Lee. 2000. Distribution is correlated with color phase in green crabs, *Carcinus maenas* (Linnaeus, 1758) in southern New England. Crustaceana 73: 763-768.

Medcof, J.C. and L.M. Dickie. 1955. Watch for the green crab – a new clam enemy. Fisheries Research Board of Canada, Gen. Ser. Circ. 26. Atlantic Biological Station, St. Andrews, N.B.

Menge, B.A. 1976. Organization of the New England rocky intertidal community: Role of predation, competition, and environmental heterogeneity. Ecol. Monog. 46: 355-393.

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

Menge, B.A. 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. Ecol. Monogr. 65: 12-74.

Miller, R.J. and J.T. Addison. 1995. Trapping interactions of crabs and American lobster in laboratory tanks. Can. J. Fish. Aquat. Sci. 52: 315-324.

Minchin, D. 1997. The influence of the parasitic cirripede *Sacculina carcini* on its brachyuran host *Carcinus maenas* within its home range. In: Thresher, R.E. (ed.) Proceedings the first international workshop on the demography, impacts and management of introduced populations of the European crab, *Carcinus maenas*. CRIMP Tech. Rep. 11. Centre for Research on Introduced Marine Pests, CSIRO Marine Laboratories, Hobart, Australia. p. 81-86.

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

Miron, G., T. Landry and N.G. MacNair. 2002. Predation potential by various epibenthic organisms on commercial bivalve species in Prince Edward Island: Preliminary results. Can. Tech. Rep. Fish. Aquat. Sci. 2392.

Moksnes, P.-O. 2002. The relative importance of habitat-specific settlement, predation, and juvenile dispersal for distribution and abundance of young juvenile shore crabs *Carcinus maenas* L. J. Exp. Mar. Biol. Ecol. 271: 41-73.

Montanie, H., J.-P. Bossy and J.-R. Bonami. 1993. Morphological and genomic characterization of two reoviruses (P and W2) pathogenic for marine crustaceans: do they constitute a novel genus of the Reoviridae family? J. Gen. Virol. 74: 1555-1561.

Moore, P.G. and J. Howarth. 1996. Foraging by marine scavengers: Effects of relatedness, bait damage and hunger. J. Sea Res. 36: 267-273.

Moreira, F. 1999. On the use by birds of intertidal areas of the Tagus estuary: implications for management. Aquat. Ecol. 33: 301-309.

Moreira, S.M., M. Moreira-Santos, L. Guilhermino and R. Ribeiro. 2006. An *in situ* postexposure feeding assay with *Carcinus maenas* for estuarine sediment-overlying water toxicity evaluations. Environ. Poll. 139: 318-329.

Morgan, D.E., J. Goodsell, G.C. Mathiessen, J. Garey and P. Jacobson. 1980. Release of hatchery-reared bay scallops (*Argopecten irradians*) onto a shallow coastal bottom in Waterfor, Connecticut. Proc. World Mariculture Soc. 11: 247-261.

Munch-Petersen, S., P. Sparre and E. Hoffman. 1982. Abundance of the shore crab, *Carcinus maenas* (L.), estimated from mark-recapture experiments. Dana, Charlottenlund 2: 97-121.

Naczk, M., J. Williams, K. Brennan, C. Liyanapathirana, and F. Shahidi. 2004. Compositional characteristics of green crab (*Carcinus maenas*). Food Chem. 88: 429-434.

Nagaraj, M. 1993. Combined effects of temperature and salinity on the zoeal development of the green crab, *Carcinus maenas* (Linnaeus, 1758) (Decapoda: Portunidae). Scient. Mar. 57: 1-8.

Napier, I.R. 2002. Development and management of crab fisheries in Shetland, Scotland. In: Paul, A.J., E.G. Dawe, R. Elner, G.S. Jamieson, G.H. Kruse, R.S. Otto, B. Sainte-Marie, T.C. Shirley and D. Woodby (eds.). Crabs in cold water regions: Biology, management and economics. University of Alaska Sea Grant College Progam AK-SG-02-01. pp. 705-716.

Naylor, E. 1962. Seasonal changes in a population of *Carcinus maenas* (L.) in the littoral zone. J. Anim. Ecol. 31: 601-609.

Nelson, G.A., B.C. Chase and J. Stockwell. 2003. Food habits of striped bass (*Morone saxatilis*) in coastal waters of Massachusetts. J. Northw. Atl. Fish. Sci. 32: 1-25.

Newman, M.W. and C.A. Johnson. 1975. A disease of blue crabs (*Callinectes sapidus*) caused by a parasitic dinoflagellate, *Hematodinium* sp. J. Parasitol. 61: 554-557.

Ostlund-Nilsson, S. 2000. Are nest characters of importance when choosing a male in the fifteen-spined stickleback (*Spinachia spinachia*)? Behav. Ecol. Sociobiol. 48: 229-235.

Owens, L. 1993. Description of the first haemocytic rod-shaped virus from a penaeid prawn. Dis. Aquat. Org. 16: 217-221.

Paille, N., J. Lambert, N. Simard and S. Pereira. 2006. Le crabe vert (*Carcinus maenas*) : Revue de littérature et situation aux Iles-de-la-Madeleine. Can. Fish. Aquat. Sci. Indus. Rep. 276.

Palacios, K.C. and S.P. Ferraro. 2003. Green crab (*Carcinus maenas* Linnaeus) consumption rates on and prey preferences among four bivalve prey 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.

Pihl, L. and R. Rosenberg. 1984. Food selection and consumption of the shrimp *Crangon crangon* in some shallow marine areas in western Sweden. Mar. Ecol. Prog. Ser. 15: 159-168.

Pimentel, D., L. Lach, R. Zuniga and D. Morrison. 2000. Environmental and economic costs of nonindigenous species in the United States. BioSci. 50: 53-65.

Polte, P., A. Schanz and H. Asmus. 2005. The contribution of seagrass beds (*Zostera noltii)* to the function of tidal flats as a juvenile habitat for dominant, mobile epibenthos in the Wadden Sea. Mar. Biol. 147: 813-822.

Proctor, C. 1997. Possible impacts of *C. maenas* on Tasmanian mariculture and fisheries. In: Thresher, R.E. (ed.) Proceedings the first international workshop on the demography, impacts and management of introduced populations of the European crab, *Carcinus maenas*. CRIMP Tech. Rep. 11. Centre for Research on Introduced Marine Pests, CSIRO Marine Laboratories, Hobart, Australia. p. 63-64..

Quieroga, H. 1996. Distribution and drift of the crab *Carcinus maenas* (L.) (Decapoda, Portunidae) larvae over the continental shelf off northern Portugal in April 1991. J. Plankton Res. 18: 1981-2000.

Quieroga, H. 1998. Vertical migration and selective tidal stream transport in the megalopa of the crab *Carcinus maenas*. Hydrobiol. 375/376: 137-149.

Quieroga, H., J.D. Costlow and M.H. Moreira. 1997. Vertical migration of the crab *Carcinus maenas* first zoea in an estuary: Implications for tidal stream transport. Mar. Ecol. Prog. Ser. 149: 121-132.

Rainbow, P.S. and W.H. Black. 2001. Effects of changes in salinity on the apparent water permeability of three crab species: *Carcinus maenas*, *Eriocheir sinensis* and *Necora puber*. J. Exp. Mar. Biol. Ecol. 264: 1-13.

Rangeley, R.W. and M.L.H. Thomas. 1987. Predatory behaviour of juvenile shore crab *Carcinus maenas* (L.). J. Exp. Mar. Biol. Ecol. 108: 191-197.

Ray, G.L. 2005. Invasive animal species in marine and estuarine environments: biology and ecology. Aquatic Nuisance Species Research Program, U.S. Army Corps of Engineers. ERDC/EL TR-05-2. January 2005.

Rheinallt, T. 1986. Size selection by the crab *Liocarcinus puber* feeding on mussels *Mytilus edulis* and on shore crabs *Carcinus maenas*: The importance of mechanical factors. Mar. Ecol. Prog. Ser. 29: 45-53.

Rice, M.A. 2001. Environmental impacts of shellfish aquaculture: Filter feeding to control eutrophication. In: Tlusty, M., D. Bengtson, H.O. Halvorson, S. Oktay, J. Pearce and R.B. Rheault Jr. (eds.) Marine aquaculture and the environment: a meeting for stakeholders in the Northeast. Cape Cod Press, Falmouth, MA. p. 77-84.

Rice, A.D. and R.W. Ingle. 1975. The larval development of *Carcinus maenas* (L.) and *C. mediterraneus* Czerniavsky (Crustacea, Brachyura, Portunidae) reared in the laboratory. Bull. Br. Museum (Nat. Hist.) 28: 103-119.

Richards, M., F. Edwards and M. Huxham. 2002. The effects of the adult density of *Macoma balthica* on the recruitment of juvenile bivalves: a field experiment. J. Sea Res. 47: 41-54.

Roff, J.C., L.P. Fanning and A.B. Stasko. 1984. Larval crab (Decapoda: Brachyura) zoeas and megaloas of the Scotian Shelf. Can. Tech. Rep. Fish. Aquat. Sci. 1264: 22 p.

Rogers, R. 2001. The Green Menace: The European green crab. Environ. Practice 3: 93-95.

Roman, J. 2006. Diluting the founder effect: cryptic invasions expand a marine invader's range. Proc. R. Soc. B. 273: 2453-2459.

Roman, J. and S.R. Palumbi. 2004. A global invader at home: population structure of the green crab, *Carcinus maenas*, in Europe. Molec. Ecol. 13: 2891-2898.

Ropes, J.W. 1968. The feeding habits of green crab, *Carcinus maenas* (L.). Fish. Bull. 67(2): 183-203.

Ropes, J.W. 1989. The food habits of five crab species at Pettaquamscutt River, Rhode Island. Fish. Bull. 87: 197-204.

Rossong, M.A., P.J. Williams, M. Comeau, S.C. Mitchell and J. Apaloo. 2006. Agonistic interactions between the invasive green crab, *Carcinus maenas* (Linnaeus) and juvenile American lobster, *Homarus americanus* (Milne Edwards). J. Exp. Mar. Biol. Ecol. 329: 281-288.

Rotjan, R.D., J. Blum and S.M. Lewis. 2004. Shell choice in *Pagurus longicarpus* hermit crabs: Does predation threat influence shell selection behavior? Behav. Ecol. Sociobiol. 56: 171-176.

Ruiz, G.M., A.W. Miller and W.C. Walton. 1998. The bi-coastal invasion of North America by the European green crab: Impacts and management strategies. Submitted to the Aquatic Nuisance Species Task Force, U.S.A.. March 1998.

Say, T. 1817. An account of the Crustacea of the United States. Reprinted in 1969 by Verlag Von J. Cramer. New York.

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

Schratzberger, M. and R.M. Warwick. 1999. Impact of predation and sediment disturbance by *Carcinus maenas* (L.) on free-living nematode community structure. J. Exp. Mar. Biol. Ecol. 235: 255-271.

Secord, D. 2003. Biological control of marine invasive species: cautionary tales and land-based lessons. Biol. Invas. 5: 117-131.

Sharp, G., R. Semple, K. Connolly, R. Blok, D. Audet, D. Cairns and S. Courtenay. 2003. Ecological assessment of the Basin Head Lagoon: A proposed Marine Protected Area. Can. Manuscr. Rep. Fish. Aquat. Sci. 2641.

Sibly, R.M. and R.H. MacCleery. 1982. The distribution between feeding of herring gulls breeding at Walney Island, UK. J. Anim. Ecol. 52: 51-68.

Skonberg, D.I. and B.L. Perkins. 2002. Nutrient composition of green crab (*Carcinus maenas*) leg meat and claw meat. Food Chem. 77: 401-404.

Smith, L.D. 2004. Biogeographic differences in claw size and performance in an introduced crab predator *Carcinus maenas*. Mar. Ecol. Prog. Ser. 276: 209-222.

Smith, O.R., J.P. Baptist and E. Chin. 1955. Experimental farming of the soft-shell clam Mya arenaria, in Massachusetts, 1949-1953. Comm. Fish. Rev. 17: 1-16.

Smith, P., G. Edwards, B. O'Connor, M. Costello and J. Costello. 1997. Photographic evidence of the importance of macrofauna in the removal of feed pellets from the sediment under marine salmon farms. Bull. Eur. Assoc. Fish Pathol. 17: 23-26.

Snedden, L.U., A.C. Taylor and F.A. Huntingford. 1999. Metabolic consequences of agonistic behaviour: Crab fights in declining oxygen tensions. Anim. Behav. 57: 353-363.

Spaargaren, D.H. 1984. On ice formation in sea water and marine animals at subzero temperatures. Mar. Biol. Lett. 5: 203-216.

Squires, H.J. 1990. Decapod Crustacea of the Atlantic Coast of Canada. Can. Bull. Fish. Aquat. Sci. 221.

Stentiford, G.D. and S.W. Feist. 2005. A histopathological survey of shore crab (*Carcinus maenas*) and brown shrimp (*Crangon crangon*) from six estuaries in the United Kingdom. J. Invert. Pathol. 88: 136-146.

Styrishave, B., K. Rewitz and O. Andersen. 2004. Frequency of moulting by shore crabs *Carcinus maenas* (L.) changes their colour and their success in mating and physiological performance. J. Exp. Mar. Biol. Ecol. 313: 317-336.

Svane, I. 1997. On the ecology of *Carcinus maenas* in European waters. In: Thresher, R.E. (ed.) Proceedings the first international workshop on the demography, impacts and management of introduced populations of the European crab, *Carcinus maenas*. CRIMP Tech. Rep. 11. Centre for Research on Introduced Marine Pests, CSIRO Marine Laboratories, Hobart, Australia. p. 4-18.

Taylor, D.L. 2005. Predatory impact of the green crab (*Carcinus maenas* Linnaeus) on post-settlement winter flounder (*Pseudopleuronectes americanus* Walbaum) as revealed by immunological dietary analysis. J. Exp. Mar. Biol. Ecol. 324: 112-126.

Taylor, A.C. and E. Naylor. 1977. Entrainment of the locomotor rhythm of *Carcinus maenas* by cycles of salinity change. J. Mar. Biol. Ass. U.K. 57: 273-277.

Teo, S.L.-M. and J.S. Ryland. 1994. Toxicity and palatability of some British ascidians. Mar. Biol. 120: 297-303.

Thiel, M. and T. Dernedde. 1994. Recruitment of shore crabs *Carcinus maenas* on tidal flats: mussel clumps as an important refuge for juveniles. Helgol. Meeresunters 48: 321-332.

Thompson, W.J. 2007. Population-level effects of the European green crab (*Carcinus maenas*, L.) in an eelgrass community of the southern Gulf of St. Lawrence. M.Sc. Thesis, University of New Brunswick, 95 p.

Thresher, R., C. Proctor, G. Ruiz, R. Gurney, C. MacKinnon, W. Walton, L. Rodriguez and N. Bax. 2003. Invasion dynamics of the European shore crab, *Carcinus maenas*, in Australia. Mar. Biol. 142: 867-876.

Thresher, R.E., M. Werner, .T. Høeg, I. Svane, H. Glenner, N.E. Murphy and C. Wittwer. 2000. Developing the options for managing marine pests: specificity trials on the parasitic castrator, *Sacculina carcini*, against the European crab, *Carcinus maenas*, and related species. J. Exp. Mar. Biol. Ecol. 254: 37-51.

Todd, P.A., R.J. Ladle, R.A. Briers and A. Brunton. 2005. Quantifying two-dimensional dichromatic patterns using a photographic technique: case study on the shore crab (*Carcinus maenas* L.). Ecol. Res. 20: 497-501.

Torchin, M.E., K.D. Lafferty and A.M. Kuris. 2001. Release from parasites as natural enemies: increased performance of a globally introduced marine crab. Biol. Invas. 3: 333-345.

Torres, G., L. Giménez and K. Anger. 2002. Effects of reduced salinity on the biochemical composition (lipid, protein) of zoea 1 decapod crustacean larvae. J. Exp. Mar. Biol. Ecol. 277: 43-60.

Tremblay, M.J., K. Paul and P. Lawton. 2005. Lobsters and other invertebrates in relation to bottom habitat in the Bras d'Or Lakes: Application of video and SCUBA transects. Can. Tech. Rep. Fish. Aquat. Sci. 2645: 47 p.

Tremblay, M.J., A. Thompson and T. Paul. 2006. Recent trends in the abundance of the invasive green crab (*Carcinus maenas*) in Bras d'Or Lakes and eastern Nova Scotia based on trap surveys. Can. Tech. Rep. Fish. Aquat. Sci. Tech. Rep. 2673: 32 p.

Trussell, G.C. 2000. Predator-induced plasticity and morphological trade-offs in latitudinally separated populations of *Littorina obtusata*. Evol. Ecol. Res. 2: 803-822.

Trussell, G.C., P.J. Ewanchuk, M.D. Bertness and B.R. Silliman. 2004. Trophic cascades in rocky shore tide pools: Distinguishing lethal and nonlethal effects. Oecologia 139: 427-432.

Turner, W.H., K.A. Tammi and B.A. Starr. 1996. What a year to be a mud crab! Three years on the Bay Scallop Restoration Project, Westport River estuary, Massachussetts. J. Shellfish Res. 15: 511.

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

Vale, P. and M.A. de M. Sampayo. 2002. First confirmation of human diarrhoeic poisonings by okadaic acid esters after ingestion of razor clams (*Solen marginatus*) and green crabs (*Carcinus maenas*) in Aveiro lagoon, Portugal, and detection of okadaic acid esters in phytoplankton. Toxicon 40: 989-996.

Walton, W.C. 1997. Invasive history of *Carcinus maenas* on the North American east coast and potential impacts upon a commercial shellfish, the hardshell clam *Mercenaria*

mercenaria. In: Thresher, R.E. (ed.) Proceedings the first international workshop on the demography, impacts and management of introduced populations of the European crab, *Carcinus maenas*. CRIMP Tech. Rep. 11. Centre for Research on Introduced Marine Pests, CSIRO Marine Laboratories, Hobart, Australia. p. 21-24.

Walton, W.C. 2000. Mitigating effects of nonindigenous marine species: evaluation of selective harvest of the European green crab, *Carcinus maenas*. J. Shellfish Res. 19: 634.

Walton, W.C., C. MacKinnon, L.F. Rodriguez, C. Proctor and G.M. Ruiz. 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.

Walton, W.C., G.M. Ruiz and B.A. Starr. 1999. Mitigating predation by the European green crab, *Carcinus maenas*, upon publicly maricultured quahogs, *Mercenaria mercenaria*. J. Shellfish Res. 18: 305.

Walton, W.C. and W.C. Walton. 2001. Problems, predators, and perception: management of quahog (hardclam), *Mercenaria mercenaria*, stock enhancement programs in southern New England. J. Shellfish Res. 20: 127-134.

Wasson, K, K. Fenn and J.S. Pearse. 2005. Habitat differences in marine invasions of central California. Biol. Invas. 7: 935-948.

Welch, W.R. 1968. Changes in abundance of the green crab, *Carcinus maenas* (L.) in relation to the recent temperature changes. Fish. Bull 67: 337-345.

Wennhage, H. 2002. Vulnerability of newly settled plaice (*Pleuronectes platessa* L.) to predation: effects of habitat structure and predator functional response. J. Exp. Mar. Biol. Ecol. 269: 129-145.

Wheatly, M.G. 1981. The provision of oxygen to developing eggs by female shore crabs (*Carcinus maenas*). J. Mar. Biol. Ass. U.K. 61: 117-128.

Williams, A.B. 1984. Shrimps, lobsters and crabs of the Atlantic coast of the eastern United States, Maine to Florida. Smithsonian Institution, Washington, DC.

Williams, B.G. 1967. Laboratory rearing of the larval stages of *Carcinus maenas* (L.) [Crustacea: Decapoda]. J. Nat. Hist. 2: 121-126.

Williams, P.J., T.A. Floyd and M.A. Rossong. 2006. Agonistic interactions between invasive green crabs, *Carcinus maenas* (Linnaeus) and sub-adult American lobsters, *Homarus americanus* (Milne Edwards). J. Exp. Mar. Biol. Ecol. 329: 66-74.

Wong, M.C., M.A. Barbeau, A.W. Hennigar and S.M.C. Robinson. 2005. Protective refuges for seeded juvenile scallops (*Placopecten magellanicus*) from sea star (*Asterias* spp.) and crab (*Cancer irroratus* and *Carcinus maenas*) predation. Can. J. Fish. Aquat. Sci. 62: 1766-1781.

Young, T., S. Komarow, L. Deegan and R. Garritt. 1999. Population size and summer home range of the green crab, *Carcinus maenas*, in salt marsh tidal creeks. Biol. Bull. 197: 297-299.

Zeidler, W. 1997. The European shore crab (*Carcinus maenas*) in South Australian waters. In: Thresher, R.E. (ed.) Proceedings the first international workshop on the demography, impacts and management of introduced populations of the European crab, *Carcinus maenas*. CRIMP Tech. Rep. 11. Centre for Research on Introduced Marine Pests, CSIRO Marine Laboratories, Hobart, Australia. p. 34.

Zeng, C., P. Abello and E. Naylor. 1999. Endogenous tidal and semilunar moulting rhythms in early juvenile shore crabs *Carcinus maenas*: Implications for adaptation to a high intertidal habitat. Mar. Ecol. Prog. Ser. 191: 257-266.

Zeng, C. and E. Naylor. 1996. Endogenous tidal rhythms of vertical migration in field collected zoea-1 larvae of the shore crab *Carcinus maenas*: Implications for ebb tide offshore dispersal. Mar. Ecol. Prog. Ser. 132: 71-82.