GLOBAL INVADER: THE EUROPEAN GREEN CRAB

Sylvia Behrens Yamada

GLOBAL INVADER:
THE EUROPEAN GREEN CRAB

GLOBAL INVADER:
THE EUROPEAN GREEN CRAB

Sylvia Behrens Yamada

Oregon Sea Grant
Corvallis, Oregon

Washington Sea Grant
Seattle, Washington

ORESU-B-01-001

ISBN-1-881826-24-4

Oregon Sea Grant
Oregon State University
322 Kerr Administration Bldg.
Corvallis, OR 97331-2131
(541) 737-2716

Support

This publication was funded by the NOAA Office of Sea Grant and Extramural Programs, U.S. Department of Commerce, under grant number NA76RG0476 (Oregon Sea Grant project number M/A-1), and by appropriations made by the Oregon State legislature.

Sea Grant is a unique partnership with public and private sectors, combining research, education, and technology transfer for public service. This national network of universities meets the changing environmental and economic needs of people in our coastal, ocean, and great Lakes regions.

OREGON STATE UNIVERSITY

Credits

Editor: Sandy Ridlington, Oregon Sea Grant
Cover illustration: Laura L Hauck. *Carcinus maenas*, showing the typical green coloration pattern. Features that distinguish green crabs from other Pacific Northwest crabs include the five large triangular teeth behind the eyes and three lobes between the eyes.
Cover design: Monica Whipple
Illustration credits: See p. 118.

Dedication

This book is dedicated to the memory of Neil Richmond, who dedicated his life to the protection of our living marine resources.

Contents

Illustrations

Figures

Tables

Appendix A

Appendix B: Plates

Preface

Awareness of the presence of European green crabs, *Carcinus maenas*, on the U.S. Pacific coast dates from 1989 when a gill-net fisher found a single male crab in Estero Americano near San Francisco Bay. From that time on, scientists in the Pacific Northwest observed the northward progress of this invader. In 1995 green crabs were found in Bodega Bay, about 75 miles north of San Francisco, and in the same year they were found even farther north in Humboldt Bay. The size of the crabs found in both bays suggests that by 1995 they might have been present there for as long as two years. In late March of 1997, green crabs were found by an oyster grower in Coos Bay, Oregon, about 500 miles north of San Francisco. A year later more were found farther north in Yaquina Bay and Tillamook Bay, Oregon. Following the 1997/98 El Niño, a strong cohort of green crabs was discovered in seven Oregon estuaries, in two Washington Bays (Grays Harbor and Willapa), and on four sites on Vancouver Island, British Columbia. And now (2001) the green crab's range is known to extend as far north as Nootka Sound, British Columbia. Most scientists feel that the crabs have spread northward as larvae. If that is the case, then the size of the green crabs recovered in Oregon in fall 1997 (up to 85 mm carapace width) means that they had been there undiscovered for as long as two years. In any case, by 1998 it was very clear to all that the notorious global invader *Carcinus maenas* had reached the Pacific Northwest.

The green crab's reputation as an invader is well deserved. For example, *Carcinus maenas* was introduced from Europe to the Atlantic coast of the U.S. nearly 200 years ago and has since slowly spread to occupy habitat from as far south as New Jersey to the Maritime provinces of Canada. Sometime before 1900, green crabs were introduced into Australian coastal waters, and more recently they have somehow made their way to Tasmania, South Africa, and Japan.

Despite the fact that environments worldwide have experienced introductions of green crabs, and despite numerous studies of the course of their subsequent survival and spread, in 1997 no one knew what to expect from the invader in the waters of the Pacific Northwest. Informally coordinated at first, state agencies, oyster growers, the universities, and others in Oregon and Washington initially reacted by surveying and monitoring for the presence and spread of green crabs in bays and estuaries throughout the region. Later the efforts were more formally organized, but they were hampered by the fact that at the time few people in the Northwest had much experience with green crabs.

The Sea Grant programs of Oregon State University and the University of Washington responded to the need for information about *Carcinus maenas* by inviting all the parties involved regionally to meet together with experts from outside the region for a two-day workshop in February 1998. The workshop provided a forum for learning and discussion, and it helped to further organize and coordinate regional efforts to monitor the presence of green crabs and to attempt to limit their spread. Many of the forum's participants expressed frustration about the lack of a source of fundamental information about *Carcinus*, particularly a source that provided a Pacific Northwest perspective and a focus on the crab's history as a successful invader. Their clear articulation of the need led to our commitment to produce this publication and helped determine its content.

Soon after the workshop, the Oregon and Washington Sea Grant programs came together to create a partnership called the Marine Invasive Species Team (MIST). Since its inception, the MIST partners have held workshops and training programs, published and distributed educational pamphlets and brochures, written press releases, maintained a Web site, and produced a video on invasive species. This book is yet another product of the partnership.

The book is intended to serve as a reference and a source of basic scientific information on green crabs. Through its extensive list of citations, it will also provide users with access to the scientific literature on the biology and ecology of green crabs. Its citations will also lead readers to published accounts of the course of previous introductions of green crabs and to descriptions of efforts not only to monitor their spread, but also to reduce their impacts on marine ecosystems and resources. The book draws on worldwide field observations and scientific research, but by design it has a decidedly Pacific Northwest orientation. Among the book's intended audiences are university and agency-based researchers who are unfamiliar with *Carcinus* and need both some basic background information about it and access to the literature. Other intended audiences include resource managers and shellfish growers who are frequently very knowledgeable, but who need basic information about this newly arrived species. We are also confident that extension agents and specialists and other educators will find the book useful as a reference and as a source of the answers to clients' and students' questions about green crabs.

Green crabs were probably introduced into the mid-Atlantic area of the U.S. east coast sometime prior to 1820. In all but the most localized examples, they have resisted attempts to eradicate them, and most marine scientists now believe that they are there to stay. Despite their obvious adaptability and hardiness, it was not until about 1950 that they extended their range on the east coast of the U.S. from Cape Cod northward to Maine. Of course no one can predict the future with any certainty, but, given this species' history, one might expect a gradual but relentless spread throughout much of their potential range on the U.S. west coast. Since that range is thought to include all of the coast from Alaska to San Diego, this is an invasive species to be reckoned with. It certainly should not be ignored or neglected over the long term, even though its spread may be slow and episodic. It is our hope and expectation that this book will provide fundamental information that can help form the foundation for understanding and responding to the complex challenges created by the introduction of the green crab, *Carcinus maenas*, to waters of the Pacific Northwest.

Robert E. Malouf
Director, Oregon Sea Grant

Acknowledgments

I want to thank everyone who contributed to this book, especially my reviewers, John Crothers, Armand Kuris, Robert Malouf, Annette Olson, and Amy Schoener. All of them offered thoughtful comments for improving the book. Valuable input was also provided by Elizabeth Carr, Larry Daley, Brett Dumbauld, Toshio Furota, Charles Griffiths, Christopher Hunt, Greg Jensen, Todd Miller, Per-Olav Moksnes, and Russell Rogers. The keen observational and artistic skills of Laura Hauck are reflected in the cover drawing and in the scientific illustrations of the green crab. Cheryl Bright and her staff at the Smithsonian Museum of Natural History provided the specimens of *Carcinus maenas* and *C. aestuarii* for drawing figure 3 and Dave Reinert drew the maps for figures 1 and 7. Hilda Lei Ching, Armand Kuris, and Robert Olson provided information on parasites. Lynn and Paul Rudy, the Royal British Columbia Museum, Stanford University Press, and the Natural History Museum of London gave me permission to reproduce some of their crab figures and photos. William Walton kindly provided a preliminary copy of an annotated bibliography on the green crab. This document allowed me to include many of the latest references. The library staff of Oregon State University Valley Library, the Guinn Library at the Hatfield Marine Science Center, and the University of Washington Friday Harbor Laboratories provided me with many obscure references. Part of this book was written while in residence at the University of Washington Friday Harbor Laboratories. Finally, I thank my editor, Sandy Ridlington, who skillfully pulled the whole book together.

INTRODUCTION

In August 1991, a sportfisher in San Francisco Bay found an unusual crab inside his baited trap. With five triangular teeth, or spines, behind its eyes, this fan-shaped crab did not resemble any of the common native crabs that usually entered his trap. The fisher consulted a biologist and learned that the specimen was a European green crab, or *Carcinus maenas.* After this event, both biologists and fishers actively searched for further specimens of this crab, hoping that none would be found. The news, however, was not good. Green crabs were caught throughout San Francisco Bay: in lagoons, among rocks, in marsh vegetation, and in deep channels. The crabs ranged from 39 to 76 mm carapace width, and some of the females were carrying eggs. The presence of breeding adults suggested that *Carcinus maenas* had established a self-perpetuating population inside San Francisco Bay. Subsequently, some fishers reported that green crabs had been entering their traps, perhaps as early as 1989. It is now believed that green crabs had arrived in San Francisco Bay much earlier and that populations had built up for many generations inside warm lagoons and sloughs before spreading over the whole bay (Cohen et al. 1995).

Why did the discovery of the green crab in San Francisco Bay in 1991 cause so much alarm? After all, the green was not the first nonindigenous species to suddenly appear in San Francisco Bay. Over 230 nonnative species make up most of the biota in this heavily invaded bay (Cohen and Carlton 1998). The reason for concern stems from the fact that the green crab has a bad reputation as a major predator on clams, mussels, and other species, both in natural communities and in aquaculture operations. It was feared that this efficient predator could expand its range and permanently alter marine ecosystems along most of the west coast of North America.

The green crab has a long history as a global invader. Because it is tolerant of air exposure, starvation, and wide ranges in temperature and salinity, it is well equipped to survive ocean voyages and plane rides (table 1). During the nineteenth century, the green crab hitchhiked in sailing ships from its native range in Europe and North Africa to Australia and the east coast of North America and established populations there. Most likely, small crabs found refuge among the fouling community on the hull of ships or within their damp holds amongst the ballast rocks. In the 1980s, populations of green crabs were discovered in South Africa, Tasmania, Japan, and San Francisco Bay (fig. 1). We may never know how green crabs arrived at these destinations. They could have arrived as juveniles on the fouled hulls of ships or on the "feet" of semisubmersible, exploratory oil-drilling vessels or as larvae within the ballast tanks of ships. In Tasmania, the larvae could have traveled from the mainland of Australia on ocean currents. The practice of shipping live marine products, such as

Table 1. Summary of tolerance ranges for *Carcinus maenas*. Data based on Broekhuysen 1936, Ropes 1968, Crothers 1968, Rasmussen 1973, Wallace 1973, and Erikssen et al. 1975.

Air exposure	Field: 10 days in damp burrows in high tide zone Lab: 60 days if sheltered under seaweed
Temperature	
Range for short-term survival	0 to 33°C
Maximum	26°C
Minimum for growth	10°C
Minimum for feeding	7°C
Maximum to brood eggs	18°C
Salinity (sea water = 35‰)	
Range for short-term survival	4 to 54 ‰
Minimum for long-term survival	11‰
Minimum for larval development	17‰
Starvation (adults)	3 months

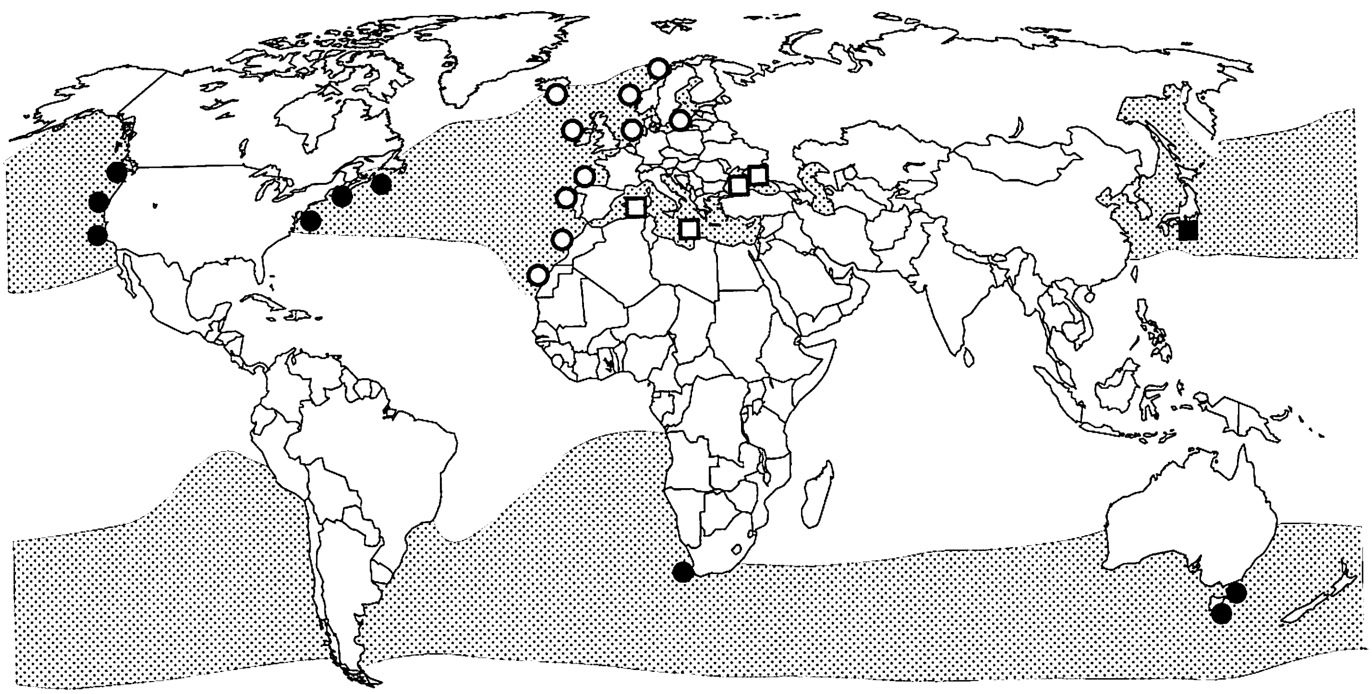


Fig. 1. World map showing the distribution of Atlantic and Mediterranean forms of the European green crab as of the year 2000. *Circles* = Atlantic *Carcinus maenas*; *squares* = Mediterranean *C. aestuarii*; *open symbols* = native range; *dark symbols* = locations of introduced populations. Because *C. maenas* need water temperatures of at least 10°C to molt and not more than 18°C to brood their eggs, the potential geographic range for *C. maenas* is defined by the 10°C summer and 18°C winter isotherms. Isotherms after Sverdrup et al. (1942).

Atlantic lobsters and bait worms, by air around the world has created a very effective new vector for species introductions. The seaweed wrapping used to keep the seafood and bait worms damp during shipment typically harbors small green crabs and snails. These hitchhikers can become potential colonists once the seaweed is discarded on a foreign shore (Carlton and Cohen 1998).

Whatever the mechanism of introduction into San Francisco Bay, green crabs flourished in this new habitat. They found a variety of food organisms, including mollusks, crustaceans, worms, marsh vegetation, and algae (Cohen et al. 1995). Under the mild California winters, green crabs grew and matured more rapidly than in Europe, reaching sexual maturity within one year. Green crab numbers built up within the bay, and by 1993 the larvae produced by these colonists traveled on ocean currents and "seeded" new breeding populations in other estuaries along the coast (Grosholz and Ruiz 1995).

When green crabs are abundant, young bivalves, urchins, and barnacles cannot establish themselves. In New England, soft-shelled clam *(Mya arenaria)* landings declined from a record high of 14.5 million pounds in 1938 to a low of 2.3 million pounds in 1959. This decrease has, in part, been attributed to the range expansion of the green crab (Welch 1968). The addition of a new, efficient crab predator to the Pacific coast of North America could change the food web dynamics of these marine ecosystems. In Bodega Harbor, densities of green crabs averaging 0.2 crabs/m^2 have already been linked to a decrease in the abundance of a native crab and two small clam species (Grosholz et al. 2000). Preliminary observations indicate that green crabs could interfere with Manila clam culture and with efforts to restore the native oyster *(Ostrea conchaphila)* (Palacios and Ferraro 2001). It is predicted that the areas most altered by green crabs will be mudflats in estuaries and bays. Green crab predation and competition could adversely affect species, such as the Dungeness crab and flatfish, that use these mudflats as nursery habitat. If green crabs were to expand their range on the Pacific coast of North America, they could exert a considerable ecological and economic effect (Lafferty and Kuris 1996; Jamieson et al. 1998).

The arrival of the green crab on the Pacific coast of North America triggered a string of questions. How did green crabs get into San Francisco Bay? How fast will they spread along our coast? What is their potential range? What will their impact be on our natural communities and on the seafood industry? Do green crabs have natural enemies? Can we control them? These questions cannot be answered in a vacuum. To answer them, one needs to know the life history of the green crab and its ecological role in both its native and adopted communities. Because green crabs are physiologically tolerant and efficient predators, they are frequently used as model experimental animals in lab experiments and field studies. Thus, we know a lot about their biology and ecology. The goal of this book is to summarize what is known about the green crab and to use this information in predicting its potential role on the Pacific coast of North America and in other parts of the world where it might yet appear. With this knowledge, scientists, shellfish growers, and resource managers will be better equipped to understand the invasion process, to assess the impact of this new invader on the marine ecosystem and shellfish operations, and to make informed decisions on whether and when to implement control measures.

This book is divided into two major sections. Chapter 1, "Biology and Life History of *Carcinus maenas*," is intended as a reference text. The detail devoted to each topic is a reflection of the research interest in this topic and its relevance to understanding the invasion process on the Pacific coast of North America. Chapter 2, "Global Invasions," includes a comparison of five case studies of green crab invasions, predictions on the spread of green crabs, the crabs' possible ecological and economic impact on ecosystems of the Pacific coast of North America, and an evaluation of control measures.

CHAPTER ONE

Biology and Life History of *Carcinus maenas*

Taxonomy

Before we can study green crabs, it is important to know how to distinguish them from other crabs. Furthermore, two very similar species of the European green crab have found new homes around the world: the Atlantic form, *Carcinus maenas*, and the Mediterranean form, *Carcinus aestuarii*. The following section will allow the reader to focus on the diagnostic features used in species identification.

Taxonomy of Green Crabs

The European green crab, *C. maenas*, is an arthropod in the subphylum Crustacea (table 2). Crustaceans, like all arthropods, possess segmented bodies with jointed appendages and shed their exoskeleton in the growth process. Crustaceans are distinguished from other arthropods, such as insects and spiders, by possessing two pairs of antennae and one pair of branched appendages per segment. Both branches are present in the mouth parts and abdominal segments of crabs, but the claws and walking legs lost their external branches. Other crustacean features include one pair of mandibles, or jaws, and two pairs of maxillae used for feeding, sensory reception, and ventilation of the gill chamber.

Members of the class Malacostraca possess three body regions and a tail: head (composed of five segments), thorax (eight segments), abdomen, and telson, or tail. Representatives include the isopods (pill bugs), amphipods (sand fleas), shrimps, crabs, and crayfishes. Order Decapoda, characterized by the presence of five pairs of legs (deca = 10, poda = feet), is divided by life style into the swimmers, or Natantia, and the crawlers, or Reptantia. In Brachyura, or true crabs, the head and thorax are fused and the flattened abdomen is tucked under the body. Crabs have one pair of claws and four pairs of walking legs (fig. 2).

Table 2. Hierarchical classification system for the European green crab.

Kingdom	Animal
Phylum	Arthropoda
Subphylum	Crustacea
Class	Malacostraca
Order	Decapoda
Suborder	Repantia
Section	Brachyura
Family	Portunidae
Genus	*Carcinus*
Species	*maenas*

Most crabs in the family Portunidae possess paddlelike legs for swimming. *Carcinus maenas* is unusual among the portunids in that its legs are clearly adapted for walking rather than swimming. *C. maenas* typically has a mottled, olive green coloration, but other colors, such as yellow, orange, and red, are also observed (Appendix B, plates 1 and 4). Five evenly spaced sharp spines, or teeth, on each side adorn the anterior-lateral margin of the shell, or carapace (fig. 2). In its native habitat, *C. maenas* ranges from up to 70 mm carapace width for females and over 90 mm for males (Crothers 1968; Rasmussen 1973).

Two closely related species of *Carcinus* have been moved around the world with maritime commerce: *Carcinus maenas* from the Atlantic and

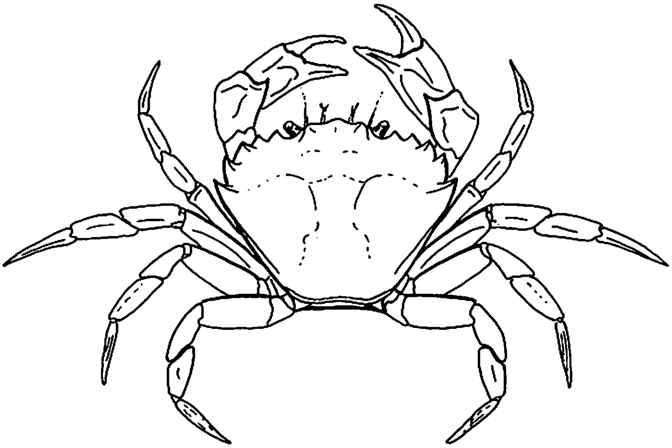


Fig. 2. *Carcinus maenas*, showing some of the crustacean and brachyuran features. Note the two pairs of antennae and paired jointed appendages, characteristic of all crustaceans, and the fused head and thorax, one pair of claws, and four pairs of walking legs, characteristic of Brachyuran crabs.

Carcinus aestuarii (formerly known as *C. mediterraneus*) from the Mediterranean. These two species are very similar in appearance but can be distinguished by their morphological features and by molecular genetic analysis.

The paired copulatory appendages of adult male *C. maenas* are crescent shaped and curve outward, with the center of the crescents touching, whereas those of *C. aestuarii* are straight and parallel (fig. 3). The carapace of *C. maenas* is slightly wider than that of *C. aestuarii*. For crabs larger than 20 mm carapace width, the width-to-length ratio is typically greater than 1.29 for *C. maenas* and less than 1.27 for *C. aestuarii* (Rice and Ingle 1975; Zariquiey Alvarez 1968; Behrens Yamada and Hauck, in press; Clark et al. 2001). In *C. maenas*, the three lobes between the eyes are scalloped whereas

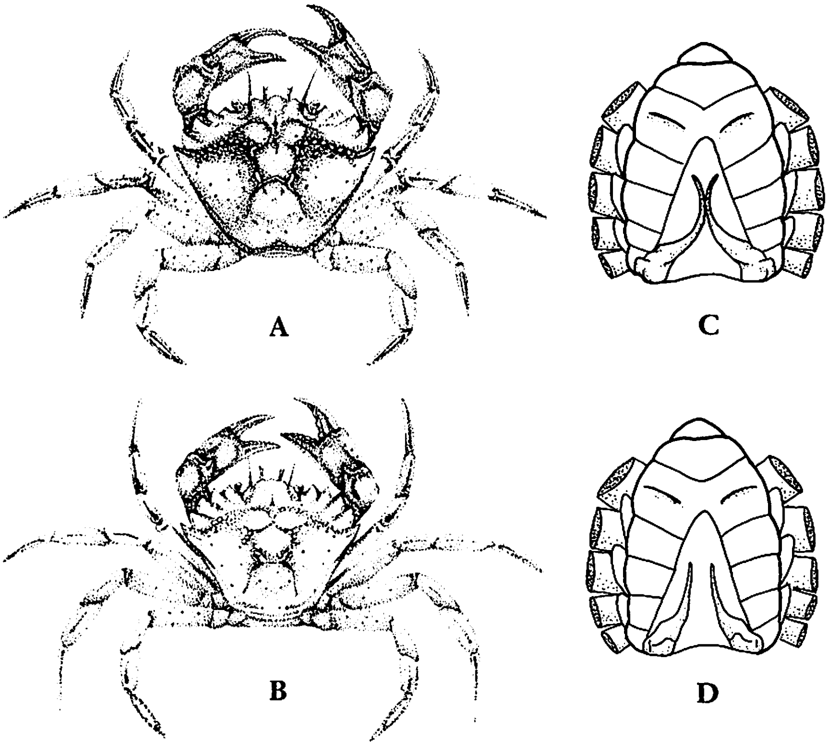


Fig. 3. Two forms of the green crab inhabit European and African shores: *(A)* the Atlantic *Carcinus maenas* and *(B)* the Mediterranean *Carcinus aestuarii (C. mediterraneus)*. Males of these two species are easily distinguished by lifting their triangular abdomen and examining the shape of their copulatory organs, or pleopods. In *C. maenas*, the pleopods curve outward in a crescent shape, with the backs of the crescents touching *(C)*. In *C. aestuarii*, the pleopods are parallel and straight *(D)*. For similar-sized individuals, *C. maenas* has a wider carapace than *C. aestuarii*.

in *C. aestuarii*, the central lobe protrudes. The fifth anterior-lateral spines of *C. maenas* appear to point forward, while those of *C. aestuarii* often are more raised and appear to point outward.

The origin of introduced *Carcinus* populations can be determined by comparing the base sequences of their DNA to those of possible source populations. The DNA sequences in a founder population will be a subsample of those found in the source population. Both mitochondrial and nuclear DNA analyses on California *Carcinus* suggest that, at present, only *C. maenas* has been introduced to the west coast of North America and that the founders originated from the east coast of North America. The loss of genetic diversity in the California population indicates that this population was derived from about eight founding individuals (Geller et al. 1997; Geller and Bagley 1997; Bagley and Geller 2000).

Key Morphological Features for Distinguishing Green Crabs from Other Crabs of the Pacific Coast of North America

Color is not a good feature for distinguishing *Carcinus maenas* from native crabs in the Pacific Northwest because many native crabs can be green, including the Dungeness crab, the hairy Oregon shore crab, the kelp crab, the helmet crab, and some individuals of the purple shore crab (Appendix A; Appendix B, plates 4–17). Furthermore, *C. maenas* can also display yellow, orange, and red coloration on its underside (plate 1). The features that do set green crabs apart from native crabs are the *five evenly spaced triangular teeth, or spines, on each side of the carapace and the three rounded lobes between the eyes* (fig. 2). While *C. maenas* may resemble juvenile Dungeness crabs *(Cancer magister)* in shape, one can always distinguish the two by simply counting the spines behind the eyes: *Cancer magister* has 10 small ones, whereas *C. maenas* has 5 larger ones. The five large spines also set *Carcinus maenas* apart from other common native crabs. The hairy Oregon shore crab *(Hemigrapsus oregonensis)* and the purple shore crab *(H. nudus)* possess 3 spines while the red rock crab *(Cancer productus)* possesses 10 (Appendix A; Appendix B, plates 4–17).

Life Cycle

Reproduction

Distinguishing the Sexes

The sexes in *C. maenas* can be distinguished by examining their abdomen and by observing their behavior. The abdomen of males is triangular, whereas that of females is broader and rounder (fig. 4). Immature

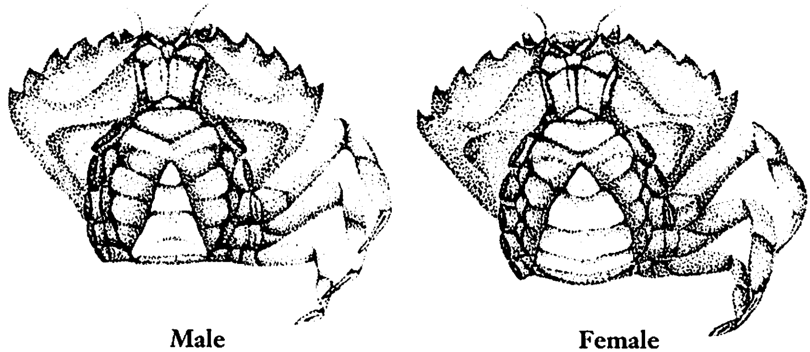


Fig. 4. Older juvenile and adult *C. maenas* can be sexed by examining the shape of their abdomen. Males have a triangular-shaped abdomen whereas that of females is more rounded. In males, the first two pleopods make up the copulatory organs (fig. 3C) while the four pairs of featherlike pleopods of females are adapted for holding the eggs.

crabs smaller than 15 mm cannot be sexed this way, as their abdomen has not differentiated. One has to unfold their abdomen and count the appendages, or pleopods. Males have two pairs of pleopods on abdominal segments 1 and 2, while females have four pairs on abdominal segments 2 to 5. The pleopods of the males are modified into syringelike copulatory organs: the first pleopods form hollow tubes while the second pair act as pistons. The long, feathery pleopods of the female are adapted for carrying the eggs.

Males and females larger than 30 mm carapace width differ in behavior. Males typically stretch out their claws and legs when picked up, whereas females usually fold their appendages close to their body. This behavior has been called the egg-protection reflex *(Eierschutzreflex)*. Subtler sex differences include longer legs and larger claws in the male and a deeper, more dome-shaped body in the female (Crothers 1967).

Mating Behavior

Female *C. maenas* mate immediately after molting when they are soft-shelled. Females typically mate with males that are larger than themselves. A male will guard a female in a precopulatory embrace, copulate with her right after molting, and then guard her again until her shell is hardened. Females approaching molting release a pheromone, or chemical messenger, that attracts males (Bamber and Naylor 1997). Anonymous (1998) describes an incident in which a male green crab was dropped into a bucket of receptive female crabs. When that male was returned to a tank of males, the males attempted to mate with this "pseudo male" and with each other, resulting in a "writhing ball of crabs." Male crabs will also attempt to mate with tennis balls or rocks as long as they have been in contact with receptive females. It thus appears that the olfactory signal from the female pheromone is so strong that it overrides other sensory cues. If this pheromone could ever be isolated and produced chemically, it could be used in traps to attract male green crabs for monitoring and population control.

Broekhuysen (1936) states that a male crab attempts to mate with any crab that responds passively to his touch. The male walks over the female on his tiptoes and uses his legs to form a "cage" around her. A receptive female folds her legs inward and allows the male to clasp her in the precopulatory embrace with her dorsal side against his ventral side. This precopulatory embrace can last from 2 to 16 days. The male carries the female with his posterior walking legs, leaving the claws free for feeding and mate defense. If more than one male is attracted to a receptive female, competition for mates can be intense. Disputes are invariably settled by size. Larger males are more successful than their smaller counterparts in acquiring, defending, and mating with receptive females. The distance between the tips of the extended claw is the clearest predictor of winning a conflict (Berrill and Arsenault 1982). Males with only one claw are less likely to mate with females when other male crabs are present. Abello et al. (1994) evaluated this handicap in mate defense to be equivalent to a reduction in size of 8 mm carapace width.

When the female molts, the male turns her over and copulates with her. During the copulatory embrace, the ventral side of the female makes contact with the ventral side of the male. The female holds onto the male with the tips of her walking legs while both animals unfold their abdomens and align the pleopods of the male with the paired sex openings, or gonopores, of the female. The male injects sperm packets into the female openings, using the pumping action of the second pleopods, and deposits them in the spermathecae, or sperm storage pouches, inside the female reproductive tract. Stored sperm remains viable for a year (Klein Breteler 1981). The copulatory embrace can last as long as 2.7 days. During this time, the pair shelters in crevices, under rocks, or in vegetation.

Following mating, the male crab continues to embrace the female, but positions her again right side up as in the precopulatory embrace. In many cases, this phase is very short and lasts much less than a day. However, when other males are present, the postcopulatory embrace can last over two days (Berrill and Arsenault 1982). It thus appears that a male embraces a female after copulation not only to protect her from predators during this vulnerable period, but also to prevent other males from mating with her.

Brooding of Eggs

Once a female has mated, she can produce one or more broods (d'Udekem d'Acoz 1993). Eggs are fertilized as they descend the reproductive tract. Some of the sperm may be retained in the spermathecae for subsequent broods. As the eggs are exuded out the gonopore, they are encased in a sticky, translucent membrane and are attached to the hairs of the pleopods (plates 2a and 2b). Broekhuysen (1936) observed that in order for the eggs to attach successfully to the pleopods, the female must bury herself in sand and form a large, enclosed cavity beneath her body. Each egg must be forced against the pleopods with sufficient pressure to rupture the outer egg membrane before the egg will adhere. Eggs measure about 0.37 mm in diameter. The number of eggs per brood increases with the size of the female. Broekhuysen (1936) reports that a 46 mm female brooded 185,000 eggs. Brooding, or ovigerous, females seek stable temperature and salinity conditions by migrating into deeper waters during the cold season. They hide under rocks or inside crevices or bury themselves in soft sediments (Dries and Adelung 1982; van der Meeren 1992; Neil Richmond, unpublished observation). Most of the mature females brood eggs. Ropes (1968) found that 94% of the females that were excavated from a tidal channel were ovigerous. By providing artificial shelters, it might be possible to trap ovigerous females before they release their larvae.

Females carry their brood for several months, depending on the water temperature. Captive female green crabs kept in a closed seawater tank at 12°C at Oregon State University were ovigerous for about two months, from the beginning of December to mid-February. Females care for their eggs by removing foreign objects with their walking legs and aerating them by fanning their pleopods. The color of the eggs changes from bright orange to grayish black during development, reflecting the consumption of the yolk by the embryos. The increase in dark pigmentation is due to the formation of the large compound eyes (Strathmann 1987). Once the embryos are fully developed, the female agitates the eggs and initiates the hatching process. Hatching within a brood is simultaneous and usually occurs soon after a nighttime high tide (Queiroga et al. 1994; Zeng and Naylor 1996c).

Early Development and Larval Stages

Description of Larval Stages

C. maenas has six larval stages, separated by molting events: 1 protozoea, 4 zoea, and 1 megalopa (table 3, fig. 5). The hatching stage, or protozoea, emerges from the egg encased in a thin, transparent membrane. Superficially the protozoea resembles a mosquito larva in that it possesses a big head and flexes its tubular, segmented abdomen in a jerky swimming movement (Hart 1982). The spines and appendages are folded up and held flat against the body. This compact shape allows the larvae to easily escape from the egg case (Jensen 1995). Because the protozoea stage lasts only a few hours, it is often missed.

The next four stages are the feeding zoea stages, ranging from 1.3 to 2.5 mm in body length (table 3). The characteristic features of a zoea include a pair of large, black compound eyes, a helmet-shaped carapace with a prominent dorsal spine, an anterior spine, two pairs of well-developed maxillipeds with projecting bristles, or swimming setae, and a tube-like, segmented abdomen terminating in a pair of sharp points. Zoea are transparent, with the exception of few branching chromatophores, or pigment cells, on the sides of the carapace. The beating heart is clearly visible below the dorsal spine.

Zoea swim through the water by beating their feathered setae and flexing their abdomen. It has been suggested that the spines maintain direction and balance during swimming and that their increased surface area helps with buoyancy and as a predator deterrent (Jensen 1995).

Zoea feed by scooping up plankton with the flattened spiny end of the abdomen and pressing them to the mouth (Strathmann 1987). Dawirs (1985) was able to rear *C. maenas* zoea to megalopae by feeding them a diet of brine shrimp larvae. In the lab, zoea will also feed on algal cells such as *Isochrysis* sp. and *Dunaliella* sp. (Nagaraj 1993; Christopher Hunt, unpublished observation). Recent studies suggest that the natural diet of green crab zoea includes zooplankton, bacteria, small algal cells, and organically enriched detrital particles (Factor and Dexter 1993; Kumlu and Jones 1997).

During succeeding molts, the zoea add more setae to their maxillipeds and develop limb buds on the carapace and abdomen (table 3). These precursors to claws, walking legs, and pleopods do not become functional until metamorphosis into the megalopa stage. Under favorable salinity and food conditions, each zoea stage lasts from 8 to 11 days at 12°C and 4 to 6 days at 18°C (Dawirs 1985).

The 4th zoea molts into the megalopa, the transitional stage between the planktonic larval and the sedentary adult form. Megalopae are equipped

Table 3. Characteristics of the zoea and megalopae larvae of *Carcinus maenas*. Measurements for megalopae are CL, carapace length (Rice and Ingle 1975), and CW, carapace width (Berrill 1982).

Larval stage	**Total length (mm)**	**# setae on maxil-lipeds**	**Claw and walking legs**	**Number of abdominal segments**	**Pleopods (abdominal appendages)**
Zoea 1	1.3–1.4	4	absent	5	absent
Zoea 2	1.6–1.9	6	absent	5	absent
Zoea 3	2.1–2.2	8	buds	6	buds present
Zoea 4	2.2–2.5	10	differentiating	6	long, slender
Megalopa	1.3–1.4 CL 1.1 CW	–	adultlike	6	featherlike

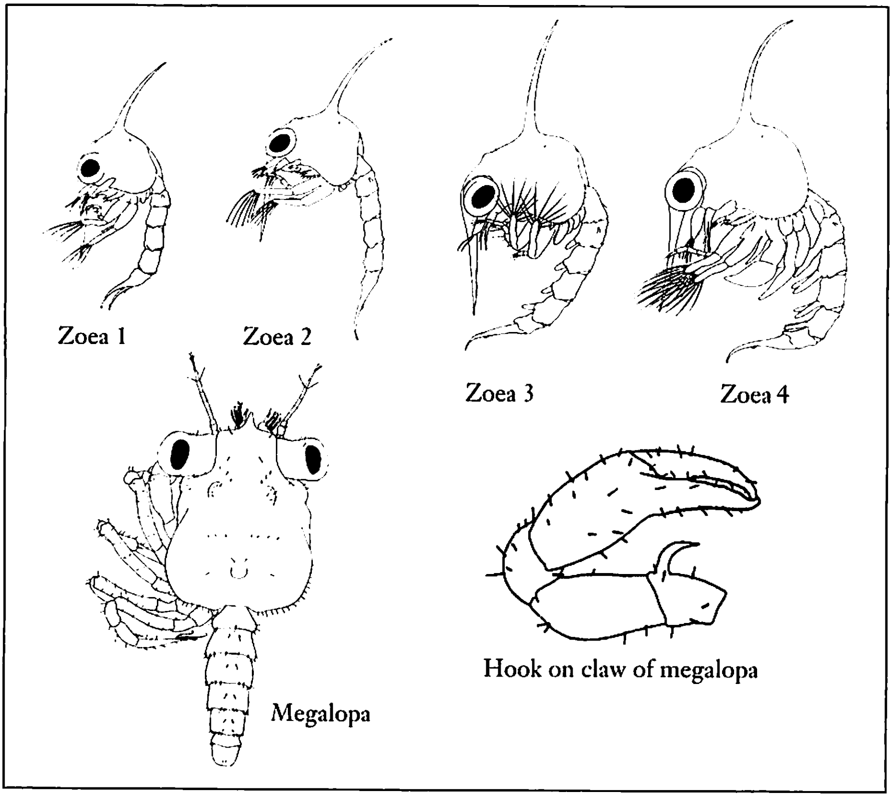


Fig. 5. The larval stages of *Carcinus maenas* include four free-swimming zoea stages and a transitional megalopa stage. The megalopae of *Carcinus maenas* can be distinguished from other crab species by the prominent hook on the base of the claw. Figures copied with permission from Rice and Ingle 1975.

to live in both worlds in that they possess plumose pleopods on their abdomen and a tail for rapid propulsion through the water as well as claws and walking legs for crawling and clinging to substrates. The abdomen is still tubular and extended, as in the zoea, rather than flat and flexed beneath the body, as in the adult. The gills are formed and function in gas exchange. Megalopae are 1.3 to 1.4 mm long and 0.9 to 1.1 mm carapace width. The megalopae of *C. maenas* can be distinguished from those of other species by a prominent hook at the base of the claw (fig. 5). The duration of the megalopal stage is around 23 days at 12°C and 13 days at 18°C. The total developmental time in the plankton is estimated to be around 62 days at 12°C and 32 days at 18°C (Dawirs 1985).

Vertical Migration and Dispersal

Zoeae and megalopae of many crab species make up an important part of the coastal plankton. Both the zoeae 1 and the later megalopae undergo vertical migrations whereby the larvae move up and down in the water column in phase with the tidal cycle. The circatidal migrations are endogenous in that they occur even in zoeae 1 that have never experienced a tidal cycle throughout their development. The suggestion is that the 12.4-hour activity rhythm is inherited and that the mechanical agitation of the hatching process sets the phase of the larval swimming rhythm (Zeng and Naylor 1996c, 1996d).

Zoeae 1 migrate to the surface soon after a high tide and thus can be transported out to sea with the ebbing tide (Zeng and Naylor 1966a; Queiroga et al. 1997). Conversely, the late megalopae migrate to the surface after low tide and thus are carried back to shore and into estuaries with the flood tide (Zeng and Naylor 1996b). These adaptations allow the intermediate larval stages to live offshore where they can feed on plankton and be dispersed by ocean currents. The returning late megalopae can thus colonize new habitats.

Late megalopae that are brought to shore with a flood tide have the ability to test the suitability of a substrate before settling permanently (Hedvall et al. 1998). If they land in an unfavorable habitat, they can reenter the plankton on the following tide and try for another chance of finding a suitable substrate by riding another flood tide to shore. If, however, the megalopae find themselves on a preferred substrate, such as fine mud high in organic matter, mussel beds, filamentous algae, sea grass, or cord grass, they settle and metamorphose into the first crab stage (Crothers 1967; Klein Breteler 1976; Pihl and Rosenberg 1982; Hedvall et al. 1998). Zeng et al. (1997, 1999) observed that megalopae settle directly into the preferred upper tidal zone and metamorphose around the times of a high tide. This behavior is adaptive because it ensures that the new recruits are deposited in the upper intertidal zone, above the foraging range of most marine predators. Knowing that megalopae settle high on the shore would be helpful in designing any monitoring or control program for young-of-the-year green crabs.

Postlarval Development and Growth

Early Crab Stages

It is estimated that *Carcinus maenas* has about 17 crab stages (Crothers 1968). In the first crab stage, the carapace length and width are almost equal and the abdomen is folded under the thorax. The characteristic five spines behind the eyes are present but are unequal in size. During subsequent molts, the carapace increases more in width than in length, and by the fifth crab stage, the characteristic adult shape, with the five sharp, triangular teeth, appears (Shen 1935; Crothers 1967). Crabs in stage 5 are between 5 and 6 mm carapace width (Klein Breteler 1975a).

Sexual differentiation occurs in the pleopods and in the shape of the abdomen. The presence and shape of pleopods can be used to determine the developmental stage of young crabs. The pleopods on the sixth segment are lost by crab 1 stage in both sexes. By stage 3, a new pair of pleopods develops on the first abdominal segment in males, but not in females. In later stages, the posterior pleopods degenerate in the male while the first two differentiate into a pair of copulatory appendages (see section on distinguishing the sexes above). The four remaining pleopods in the female elongate and the setae form featherlike fringes for holding the eggs.

During the first four molts, the abdominal segments in both sexes become progressively more flattened. By stage 5, the male abdomen takes on its distinctive form with the three mid segments fusing, and by stage 9, the shape of the male abdomen is noticeably narrower than that of the female (fig. 4). The size and age of sexual maturity is likely to vary in time and place. Puberty can be determined in the female by examining the locking mechanism of the abdomen (Mohamedeen and Hartnoll 1989). The abdomen is firmly locked in place in stage 10, but by stages 12 or 13 (postpuberty stage), the locking mechanism is absent and the abdomen can be lifted.

Puberty in *C. maenas* from the Isle of Man occurs when the female is around 34 mm carapace width (Mohamedeen and Hartnall 1989). The abdomen of a 25 mm female crab from Oregon was locked, but that of a 38 mm female could be lifted. In Bodega Harbor, California, and in the southern North Sea, females around 25 mm have been observed in precopulatory embraces. After molting and mating, those females would also be around 34 mm, as on the Isle of Man.

Green crabs change color during their development. The larval stages and early crab stages appear transparent because the exoskeleton is very thin. The color in these early stages is a function of the coloration of the blood and ingested food and the presence of chromatophores beneath the epidermis. *C. maenas* possess three monochromatic chromatophores: red, white, and black (Powell 1962). The coloring pattern of young crabs depends on the degree of activity of the various chromatophores. For example, when the black granulated pigment is dispersed throughout the chromatophores, the crab appears dark, but when it is concentrated in the center, the crab appears pale. Antagonistic pairs of hormones are involved in pigment dispersion and concentration (Lutz 1985). Young crabs display a characteristic juvenile pattern with light- and dark-striped legs. They also have the ability to adapt their coloration to that of their background. However, as crabs age, their exoskeleton thickens and masks the action of the chromatophores (Crothers 1968). The green, yellow, and orange coloration of older crabs is due to calcified salts and pigments in the outer layer of their exoskeleton. Older crabs that have not molted for a long time often appear white because of the erosion of the outer pigmented layer and the exposure of the white calcified layer (Crothers 1968).

The Molting Process

The molting process in *C. maenas* is described by Bückmann and Adelung (1964) and Adelung (1971). Under constant laboratory conditions with adequate food, *C. maenas* molts at predictable intervals. Once a crab has experienced a critical minimum amount of tissue growth and the water temperature is above 10°C, the molting process can start. As calcium is being absorbed from the old exoskeleton, sutures, or seams, between the skeletal plates become visibly thinner and the carapace changes from a shiny, olive green to a dull, light gray. At this point, the crab stops feeding. About 12 hours later, the sutures on the lateral side of the body start to split and the new cuticle becomes visible beneath. Soon after, the crab stops moving and begins to ingest large volumes of seawater. As the water diffuses into the tissues, the whole body swells. When the internal pressure becomes great enough, the old exoskeleton splits along suture lines, from the sides to the back. The sutures in the mouth region do not split, but act like a hinge between the upper and lower plates of the carapace. The crab now backs out of its old skin using rhythmic muscle contractions of its appendages. This process typically last only 5 to 30 minutes.

After molting, the skeleton is totally soft and the crab can move only in water. During this time the crab ingests more water to increase its volume. After about one to two hours, the water uptake stops and the cuticle starts to harden. The initial hardening process lasts one to two days and progresses at different rates in the different body regions. Only after the skeleton has begun to harden does the crab start feeding. During the following days, the cuticle is strengthened through the addition of calcium salts and chitin. The hardening process depends on temperature and crab size and takes from four days to a few weeks to complete.

Variation in Growth

The growth rate in *C. maenas* is extremely variable (table 4). Many factors, including temperature, salinity, food availability, age, and intraspecific interactions, play a role in determining how often a crab molts and what the molt increment will be. Water temperature sets the length of the growing season. When water temperatures drop below 10°C in winter, crabs stop molting. When they drop below 7°C, crabs stop feeding and start looking for shelter in deep crevices or in the sediment (Ropes 1968). Thus, in Maine, western Sweden, eastern Denmark, and the German Baltic, where water temperatures drop below 10°C for at least half the year, crabs grow more slowly than in southern Britain, the southern North Sea, and Oregon (table 4).

Mohamedeen and Hartnoll (1989) present the most complete data set on the effect of temperature on growth. They reared *C. maenas* from postlarvae to sexual maturity at 15°C and 20°C on the Isle of Man. Crabs were kept in full-strength seawater and fed scallop adductor muscle. Growth is very rapid during the first 10 crab stages. Crabs grow faster at 20°C but attain a larger body size at 15°C. At 20°C, crabs molt every 6 to 15 days and attain a carapace width of 19 mm by stage 10. At 15°C, the intermolt period lasts from 9 to 27 days and crabs attain 25 mm by stage 10. Crabs from the Wadden Sea in the Netherlands, reared at constant 20°C, exhibited similar molt intervals but were larger than those from the Isle of Man reared at 20°C (Klein Breteler 1975a). Young crabs reared in central Maine (10–15°C), the Netherlands (20°C), Plymouth (ambient temperature), and the Isle of Man (15°C) are similar in size to those growing under natural conditions in the Dutch Wadden Sea (Berrill 1982; Klein Breteler 1975a, b; Shen 1935).

Klein Breteler (1975b) set up a laboratory experiment to determine the role of temperature and food on the molt frequency and molt increment in young *C. maenas*. The two temperatures, 15°C and 20°C, are

Table 4. Comparison of the length of the growing season and life history features of *Carcinus maenas* in Europe and North America. References: *1* = Berrill 1982; *2* = Dries and Adelung 1982; *3* = Rasmussen 1973, Munch-Petersen et al. 1982; *4* = Eriksson and Edlund 1977, Pihl and Rosenberg 1982, Moksnes 1999, Per-Olaf Moksnes, unpublished observation; *5* = Broekhuysen 1936, Crothers 1967, Klein Breteler 1975a, d'Udekem d'Acoz 1993; *6* = Gilbert and Wyatt 1969, Behrens Yamada et al. 2000 and unpublished observations.

Location	# of months water temp. is above 10°C	Peak of larval settlement	CW by first winter (mm)	CW by second winter (mm)	CW of females at first mating (mm)	Age at first mating (mm)	Maximum carapace width (mm)	Generation time (years)	Maximum life span (years)	Ref.
Central Maine	5	September	3–10	13–28	34	2–3	82 males 70 females	3–4	5–6	1
Baltic/Germany	6	September	7.5	25–45	30	2	75 males 60 females	3	4+	3
Kattegat/ Denmark	6	August–September	7–13	30–45	30	2	92 males	3	4+	4
Western Sweden	6	July–August	5–20	25–35	30 estimate	2	100 males	2–3	4+ estimate	2
Southern Britain and southern North Sea	7	July	5–30	25–50	30	1–2	86 males 70 females	1–2	3–4	5
Oregon, 1997/98 El Niño cohort	8–9	Winter–Spring	32–60	52–80	<35	<1	96 males 79 females	1	3–4	6

typical for the Dutch Wadden Sea in the summer. Crabs were fed fresh mussel mantle tissue. Half the crabs were fed to excess every day, while the other half were fed only twice a week. Both temperature and food had a significant effect on the time it took the crabs to reach stage 7. At the higher temperature and higher food level, crabs attained stage 7 in only 50 days, whereas at the lower temperature and lower food level it took 130 days. Food level was important in determining the carapace width attained at a certain stage. Young crabs reared at the high food level attained 10 mm by stage 7, but those raised at the low level grew to less than 8 mm. The sizes of stage 7 crabs growing under natural conditions in Maine and the Dutch Wadden Sea indicate that *C. maenas* are not food limited (Berril 1982; Klein Breteler 1975c).

For crabs growing under constant conditions, the growth increments between molts are a constant proportion of the premolt carapace width (Adelung 1971). For example, under ideal conditions growth increments for adult crabs range between 30% and 31% and under marginal conditions between 20% and 23% (Adelung 1971). The growing conditions must have been ideal for green crabs in Oregon during the spring and summer of 1998 because their molt increments averaged 31%, with a range between 27% and 36% (Behrens Yamada et al. 2000). The rate of molting in *C. maenas* decreases with age. Whereas the frequency of molting in the early crab stages can be as rapid as once a week, later stages may molt less than once a year. An 86 mm male crab trapped in October 1997 was kept in a display tank until July 1999, when it died. It did not molt once during its 21 months in captivity. Crabs that have not molted in a long time develop a thick carapace and tend to accumulate encrusting organisms such as barnacles, bryozoans, sponges, hydroids, and algae.

Intraspecific interactions can also affect the growth rate of *C. maenas*. Bückmann and Adelung (1964) found that when a large and a small crab were kept in the same container, the smaller crab delayed its molting cycle but the larger crab did not. Because larger crabs are known to cannibalize soft, defenseless, smaller, molting crabs, molting in the presence of a larger crab would be suicidal. The mere sight of a larger crab, viewed through the glass wall of an aquarium, was enough of a signal to delay molting in 25% of small crabs. Klein Breteler (1975a) noted that newly recruited crabs in the first settlement wave in the Dutch Wadden Sea grew significantly larger than those in subsequent waves. Molt increments for the first five crab stages averaged 42% per molt in July and August but only 32% in October and November. He suggests that this decrease in growth increment over the settlement season could be due to intraspecific interactions with larger recruits.

Comparison of Life History Features around the World

When life history features of *C. maenas* from various studies are compared, water temperature stands out as a dominant factor in determining growth, age at sexual maturity, and generation time (table 4). Crabs stop molting and drastically reduce their activity below 10°C, and below 7°C, they stop feeding (Ropes 1968; Eriksson and Edlund 1977). In central Maine, western Sweden, eastern Denmark, and the German Baltic, where surface water temperatures drop below 10°C for about half the year, the growing season is very short (Rasmussen 1973; Berrill 1982; Dries and Adelung 1982; Phil and Rosenberg 1982). The mating, brooding of eggs, and settlement of megalopae all occur within a narrow time frame. Since megalopae don't settle until late summer, young crabs experience only one to two months of favorable growing conditions before winter arrives. They typically enter their first winter with a carapace width of only 3–15 mm (table 4). Sexual maturity is not reached until the second or third year, when they reach a size of 34–45 mm. Generation time under these conditions is three to four years (Eriksson and Edlund 1977; Berrill 1982; Pihl and Rosenberg 1982).

In southern Britain and the southern North Sea, winters are milder and the growing season is longer. The reproductive season is not as well-defined in that the mating season can extend from April to November and brooding females have been observed in almost every month of the year (Broekhuysen 1936; Crothers 1967; d'Udekem d'Acoz 1993). Some older females can produce two broods per year: one in the winter and one in spring (d'Udekem d'Acoz 1993). In the Dutch Wadden Sea, the settlement of megalopae from the plankton can start as early as June, peaks in July, and, in some years, continues into November. Recruits in the earliest settlement wave tend to survive better and grow faster than those in subsequent waves (Klein Breteler 1975a). These young crabs typically experience three to four months of good growing conditions before the arrival of winter. By then they attain a carapace width of 16–30 mm. Sexual maturity typically occurs in the following spring or summer. Generation time is one to two years.

The life history patterns of *C. maenas* on the west coast of North America have been studied for only a few years. When green crabs were first discovered in San Francisco Bay in 1989, the population was already well established and it was thus not possible to distinguish separate year classes. When the crabs colonized new estuaries in California in 1993 and in Oregon and Washington in 1998, scientists were able to follow the growth of these strong year classes. These two colonizations followed a similar pattern. In both cases, young crabs simultaneously appeared in a number of adjacent estuaries in late spring and summer, and in both cases it appears that strong coastal currents carried the larvae north from well-established populations in the south (Grosholz and Ruiz 1995; Behrens Yamada and Hunt 2000). Growth rate of the new year class during the two colonization events was also similar. The crabs averaged 14–18 mm carapace width in June, 21–27 mm in July, 35–42 mm in August, and around 47 mm in the fall and winter (fig. 6a; Grosholz and Ruiz 1995; Behrens Yamada et al. 2000; Figlar-Barnes et al. 2001). We are not certain when settlement of megalopae larvae occurred, but from the rapid growth rate observed in young crabs (Klein Breteler 1975c), we estimate that they could have settled during winter and spring. The anomalous El Niño ocean conditions of 1997 and 1998 provide a mechanism for the colonization event of 1998. The poleward currents along the coast lasted from September 1997 to April 1998 and exceeded 40 km/day (Huyer et al. 1998; Barth and Smith 1998). Thus, conditions were extremely favorable for larval transport from California to Oregon, Washington, and British Columbia.

In Oregon and Washington, crabs ranged in carapace width between 32 and 60 mm when they entered their first winter. From the recovery of tagged crabs, we learned that growth stops during the winter and resumes again in early May. By July 1999, smaller crabs (39–42 mm) had molted twice while larger crabs (50–55) had molted once. The size range of crabs entering their second winter was 50 to 80 mm (fig. 6b). By the fall of 2000, they ranged in carapace width from 60 to 92 mm.

The reproductive season on the west coast of North America is extended, as it is in the southern North Sea. In San Francisco Bay and Bodega Harbor, average monthly seawater temperatures rarely drop below 10°C for a whole month (USGS 1999; Scripps 2000). Under these conditions some female *C. maenas* are gravid most of the year (Cohen et al 1995; Ted Grosholz, unpublished data). In Oregon and Washington estuaries, where seawater temperatures typically drop below 10°C for two to four months of the year (Gilbert and Wyatt 1969; Scripps 2000; Figlar-Barnes et al. 2001), gravid females have been observed from August 1998 to July 1999.

Currently available information suggests that C. *maenas* on the west coast of North America are recruitment limited. Although females from the 1997/98 El Niño cohort produced viable eggs in Oregon and Washington estuaries during subsequent winters, recruitment of the 1999 and 2000 year classes was not strong enough to maintain the local populations. No young crabs settled out into shell bag collectors in Yaquina Bay, Oregon, or Willapa Bay, Washington (Christopher Hunt, unpublished

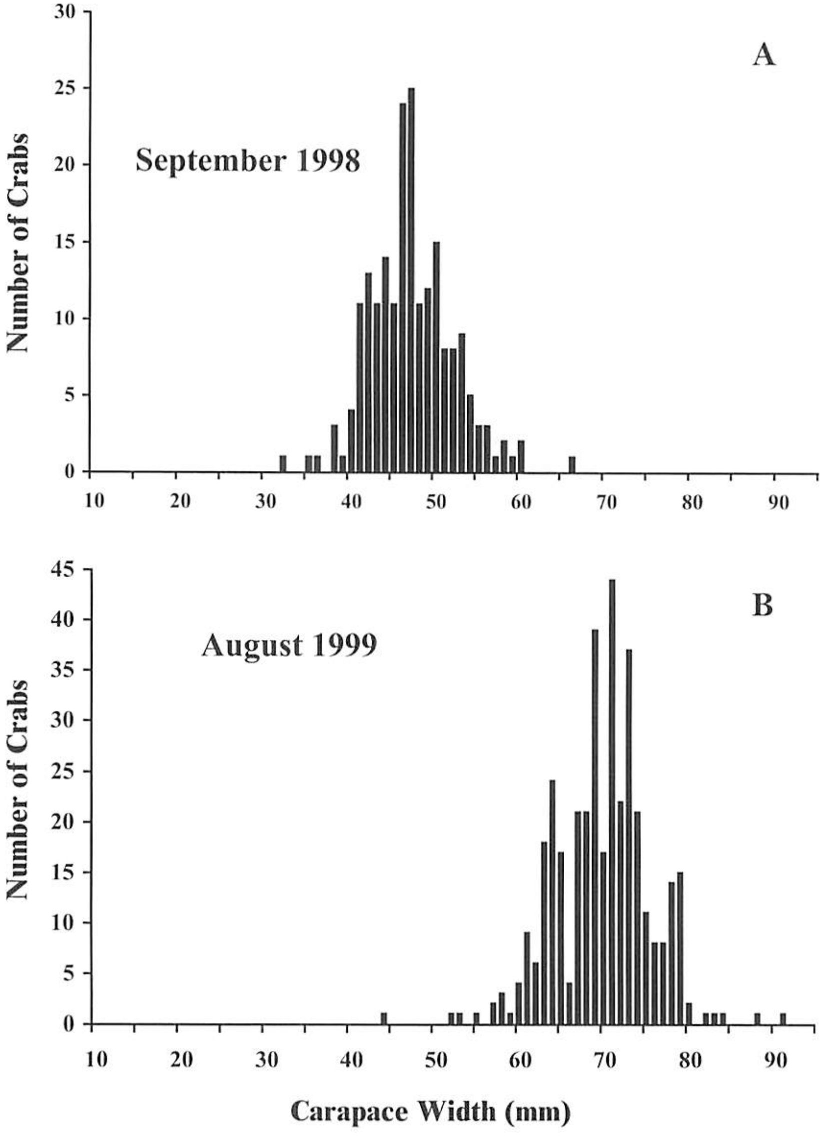


Fig. 6. Size frequency distribution of green crabs in Yaquina Bay, Oregon, in *(A)* September 1998 and *(B)* August 1999. Predominantly male crabs were trapped in the shallow subtidal and low intertidal zones in 1999. The majority of the crabs represent the 1998 year class. Data courtesy of Todd Miller and Christopher Hunt.

observation; Figlar-Barnes et al. 2001). The 1999 and 2000 year classes did not enter traps until early September (Washington Department of Fish and Wildlife, J.T. Hesse, unpublished observations). These two year classes were less abundant and smaller than the El Niño year class was at the end of its first summer. Since poleward coastal currents off the west coast of California, Oregon, and Washington were extremely weak during the winters of 1998/99 and 1999/2000 (Adriana Huyer and Robert Smith, personal communication), the chances of larval recruitment from the south were very low. Recruitment most likely was localized within each bay or estuary. If recruitment remains low in subsequent years, then *C. maenas* could die out until the next El Niño event transports more larvae from California. Similar patterns of temporary northward range expansion following El Niño events have been observed for marine fishes and invertebrates such as the mole crab, *Emerita analoga* (Schoener et al. 1985).

Visitors from Maine and Europe familiar with this crab species are impressed by the size of *Carcinus maenas* on the west coast of North America. The average size of green crabs in Oregon after the first summer was 47 mm carapace width (fig. 6a). Faster growth rates caused by an extended growing season and relaxed intraspecific competition may contribute to this pattern. One-year-old animals on the west coast of North America are similar in size to two-year-old animals in the North Sea and three-year-old animals in Maine (table 4). Minimum generation time on the west coast of North America is one year, while in central Maine it is three years. It should be noted that our initial estimates of growth rate and generation time for the Oregon population are based on only one year class, the cohort following the 1997/98 El Niño event. Preliminary data from subsequent year classes suggest that average size at the end of the first summer is around 37 mm, about one molt smaller.

Whereas the size distribution of crabs in a population may vary from area to area, the maximum size reached by *C. maenas* remains fairly constant: 70–79 mm carapace width for females and over 90 mm for males (table 4). Females are generally smaller than males after they reach sexual maturity because they cease to molt while brooding eggs. The largest green crab, a 100 mm male, was caught on the west coast of Sweden (Per-Olav Moksnes, unpublished observation).

Distribution and Abundance

Geographic Distribution

Carcinus maenas is native to the eastern shores of the Atlantic, the North Sea, and the western Baltic. Distribution records include Morocco (30° N) and Mauritania (21°N) to the south and the Faroe Islands (62° N) southern Iceland (64° N), and northern Norway (70° N) to the north, a latitudinal range of 49° (Crothers 1968; Christiansen 1969) (fig. 1). Introduced populations of *C. maenas* are at present established on the east coast of North America from Virginia to Prince Edward Island, the southern and eastern shores of Australia and eastern Tasmania, around Cape Town, South Africa, and on the Pacific coast of North America from California to Vancouver Island, British Columbia. Its sibling species, *Carcinus aestuarii*, inhabits the Mediterranean, Black, and Asov Seas and currently is expanding its range in Japan (fig. 1). The Strait of Gibraltar, with its high sill, prevents the water masses of the Atlantic and Mediterranean from freely intermixing, thus creating two basins with distinct water chemistry (Hopkins 1985). With only a limited amount of water flowing from the Atlantic into the Mediterranean in the surface layer and a limited amount of deeper, high-saline water flowing from the Mediterranean into the Atlantic, the Strait of Gibraltar acts as a partial barrier to larval exchange. Consequently, the Mediterranean and Atlantic populations of green crabs evolved into distinct forms (Demeusy and Veillet 1953; Zariquiey Alvarez 1968).

It is not clear whether *C. maenas* actually maintains viable, self-perpetuating populations over its entire native range, but the extremes in the range correlate with temperature limitations of the life stages of this species. Average seawater temperatures for southern Iceland are around 5°C in February and just above 10°C in August; those for Mauritania are 18°C and 25°C, respectively (Sverdrup et al. 1942).

Tolerance to Temperature Extremes

The geographic distribution of *C. maenas* is ultimately limited by its tolerance to physical factors such as temperature and salinity. Adult *C. maenas* tolerate temperatures between 0° and 33°C (Broekhuysen 1936; Eriksson et al. 1975). For adults to survive, grow, and reproduce and for larvae to develop, settle, and metamorphose, however, much narrower temperature ranges are needed.

The lowest critical temperature for short-term survival for many marine intertidal animals is the temperature at which ice crystals form within tissues. Once the temperature drops to that point, cell membranes are damaged and metabolic processes stop. Spaargaren (1984) found that spontaneous ice crystal formation in *C. maenas* blood did not occur until temperatures dropped as low as –9°C. Many vital functions, however, such as muscle movement and digestion, cease well before ice crystals form within tissues (Crisp 1964). Thus, prolonged exposure to low temperatures can lead to death indirectly by weakening an animal and making it more vulnerable to other factors such as predation and disease. Survival of green crabs is poor following severe winters when seawater temperatures remain below 3°C for two to three months (Beal 1998).

When temperatures drop gradually, crabs have time to seek out warmer subtidal refuges in which to shelter for the winter. When temperatures drop quickly, however, crabs can be caught out of water and exposed to subfreezing air (Welch 1968). During the winter of 1962/63, air temperatures around the British Isles dropped to as low as –5°C. Many large *Carcinus* not sheltering in the subtidal prior to the freeze washed up moribund or dead. Small crabs, however, were relatively unaffected (Crisp 1964). It thus appears that 5°C, the average winter seawater temperature for southern Iceland, is well within the lower temperature tolerance of *C. maenas*. The critical temperature for setting the northern distributional limit appears be the summer temperature. Berrill (1982) found that a minimum temperature of 10°C is needed for molting and growth to occur. The summer seawater temperature in southern Iceland is just above this critical limit (Sverdrup et al. 1942) (fig. 1).

The southern distributional limit of *C. maenas* in the Northern Hemisphere could be set either by 18°C, the maximum temperature tolerated for brooding, or by 26°C, the maximum temperature for long-term adult survival. Although seawater temperatures in Mauritania mirror these tolerances closely with an average of 18°C in February and 25°C in August, it appears that the critical distributional limit is 18°C, the maximum limit for brooding.

The northern limit of the distribution of *C. maenas* fluctuates greatly with long-term trends in winter water temperature. This pattern is best illustrated in the Gulf of Maine on the Atlantic coast of North America (Berrill 1982). During a series of warm years, as occurred around 1930, 1950, 1970, and 1998, *C. maenas* increased in abundance and rapidly spread northward to New Brunswick and Nova Scotia. After severely cold winters, with temperatures below 3°C for two to three months, populations are dramatically reduced and the range contracts (Beal 1998). Similar observations were made in the German and Dutch Wadden Sea (Buhr 1981; Beukema 1991). During cold trends, recruitment and growth rate are reduced while generation time increases (Berrill 1982). Thus, global warming will increase the potential range of the green crab.

By examining the temperature limitation of *C. maenas* in its native range, we can make predictions about its potential geographic range throughout the world. Although crabs survive well below 10°C, they cannot grow. Females need temperatures of 18°C or lower for at least part of the year to brood their eggs. Thus, for a population to thrive, water temperatures need to be above 10°C in the summer and below 18°C in the winter. By extending these isotherms, we can predict the potential temperature niche of *C. maenas* (fig. 1). It is not surprising that all introduced populations of green crabs, in both hemispheres, fall within these limits. There are, however, a lot of areas in the world where green crabs could still find suitable habitat.

Tolerance to Low Salinity

Adult *C. maenas* can tolerate a wide range of salinities (between 4 ‰ and 54 ‰) for short periods of time (Broekhuysen 1936; Eriksson et al. 1975). The cost of maintaining internal fluid concentrations is fairly low between 15 ‰ and 34 ‰, but energy requirements for regulating body fluid increase significantly with more extreme salinities (Spaargaren 1974). Although crabs are seldom challenged by salinities close to their upper limit, their lower tolerance determines how far they can penetrate an estuary. In their native habitat, *C. maenas* range from the Atlantic and North Sea to the Baltic Sea, a salinity range of 7 ‰ to 35 ‰. While crabs are found at 7 ‰ and below, the minimum salinity for long-term adult survival is 11 ‰. Males are often found in more marginal salinities while females choose more saline habitats close to the mouths of estuaries (Dries and Adelung 1982).

At marginal salinities, crabs need more favorable temperatures, and at marginal temperatures they need more favorable salinities. These two factors interact to create a two-dimensional space in which different life stages can persist. Adults need at least 10°C and 11 ‰ salinity for survival and growth (Ropes 1968). Broekhuysen (1936) showed that normal embryonic development requires at least 20 ‰ at 16–17°C or 26 ‰ at 10°C. Larvae from Baltic populations develop at 15 ‰ and 18°C or at 28 ‰ and 12.5°C (Dries and Adelung 1982). Anger et al. (1998) reared the larvae from a North Sea population of *C. maenas* at 15 ‰, 20 ‰, 25 ‰, and 32 ‰ at 18°C and found that survival was best above 25 ‰. Zoea 1 reared at 15 ‰ experienced difficulty in assimilating ingested food and converting it into tissue growth. Consequently, they showed signs of nutritional stress and died before molting to the Zoea 2 stage. Rasmussen (1973) observed that in Iselfjord, in eastern Denmark, new year classes of *C. maenas* established themselves only when salinities were above 17.8 ‰ during the breeding season. Conditions were favorable for recruitment in only 7 out of 20 years. In the Schlei, a fjord in the German Baltic, successful recruitment occurred in 1974 when salinities were between 15 ‰ and 17 ‰ and temperatures between 14°C and 17°C (Dries and Adelung 1982).

There is a cost associated with living at lower salinities. Theede (1964) found that Baltic populations of *C. maenas*, living in 15 ‰ salinity, had a significantly higher metabolic rate than North Sea populations living at 30 ‰. Reciprocal acclimation experiments suggest that these differences in metabolic rate are environmentally induced. It thus appears that Baltic populations, in their native low-salinity habitat, spend more energy osmoregulating than their North Sea counterparts. A higher maintenance cost would contribute to slower growth and longer generation time in the Baltic (table 4).

Recruitment

The persistence of a *C. maenas* population is dependent on continual recruitment from the plankton. Within the center of the range, conditions are favorable for survival, growth, and reproduction, and recruitment generally occurs every year. This may not always be the case at the extreme end of the range. As mentioned above, low winter temperatures can prevent recruitment in northern Maine and low salinities can prevent it in the Baltic (Berrill 1982; Dries and Adelung 1982). When recruitment stops for a few years in a row, the population eventually dies out. As soon as conditions improve, however, *C. maenas* can reestablish itself in the ecosystem (Dries and Adelung 1982). Colonization of depopulated habitats occurs through the transport of larvae from permanent populations in more favorable habitats. For example, in northern Maine, New Brunswick, and Nova Scotia, the source of larvae would be from the south.

Local Distribution

Young Juvenile Habitats

It appears that *C. maenas* megalopae prefer to settle in wave-protected habitats in the upper intertidal zone (Appendix B, plate 3). Newly settled crabs are found in sea grass *(Zostera)* beds, on filamentous green algae, in mussel beds, along cord grass *(Spartina)* banks, in muddy areas next to dikes, and in gravel in the upper intertidal zone (Klein Breteler 1976; Eriksson and Edlund 1977; Pihl and Rosenberg 1982; Ropes 1988; Zeng et al. 1997; Moksnes et al. 1998; Hedvall et al. 1998) (plate 3). Sandy areas, in contrast, receive very few recruits (Klein Breteler 1976). Moksnes et al. (1998) tethered small green crabs to monofilament lines in various habitats and found that mortality from predators was high (80–90%) in open sand habitats and much lower in the shelters provided by grasses, mussel beds, and filamentous algae. Günther (1996) reports that the highest abundance of newly settled *C. maenas* occurs in mussel beds with observed densities of over 1000 crabs/m^2. Thiel and Dernedde (1994) feel that mussel beds on mudflats act as a shelter and refuge from predators such as adult crabs, fishes, and birds. The abundance of *C. maenas* has increased in the North Sea in recent years in conjunction with the increase in mussel culture (Reise and Schubert 1987; Thiel and Dernedde 1994).

Eriksson et al. (1975) studied substrate preferences in young (20 mm carapace width) *C. maenas* and found that shelter and food both appear to play a role in substrate choice. In 10-minute trials, they offered individual crabs two-way choices between various substrates: sand, sand with plastic "eelgrass," sand and pebbles, plastic eelgrass and pebbles, and pebbles and cobble. They found that young *C. maenas* chose sand over pebbles, and artificial vegetation over sand or pebbles. Since *C. maenas* bury themselves in the sand and hide in the vegetation, the suggestion is that they choose the best available cover. When offered a choice between sterile, clean sand and natural sand with detritus, they chose natural sand. The authors actually observed *C. maenas* ingesting sediment and concluded that *C. maenas* can act as deposit feeders.

Older Juvenile and Adult Habitats

Adult *C. maenas* live in a variety of habitats. They occur on rocky shores, under rocks and boulders, in macroalgae or eelgrass beds, in marshes, inside burrows along *Spartina* banks, inside fouling communities on floating docks, and in lagoons and estuaries. Green crabs are highly nomadic and do not return to a permanent home shelter after foraging excursions, even when preferred food items are added (Singh 1991). Crothers (1967) reports a vertical distribution from the intertidal to 5.5 meters. On mud- and sand flats, they bury into the sediment at varying tidal levels, including weedy tide pools. In Wales, they are found on all shores except those with the most wave exposure (Crothers 1970). Young crabs can live inside marsh burrows above the high-water mark of neap tides. Some of these sites might not be covered by the tide for about a week, but as long as their burrows remains moist, crabs can tolerate emersion for up to 10 days. If gill membranes dry out, however, crabs lose the ability to respire and they die (Crothers 1968). *C. maenas* are also very tolerant of low oxygen concentrations and thus can survive at low tide in nearly oxygen-depleted tide pools (Klein Breteler 1981).

As crabs age, they move to lower tidal levels and into the subtidal zone. Crothers (1968) identifies three age groups of crabs in Wales. Group

1 crabs are in their first year of life. They range in size up to 34 mm carapace width and generally live in the intertidal zone. Group 2 crabs, adults >40 mm carapace width, spend most of their time in the subtidal but enter the intertidal during high tide to forage. Group 3, the oldest crabs, typically live permanently in the subtidal. Many of these subtidal crabs display the characteristic red coloration of crabs in late intermolt. These "red" crabs are competitively dominant over "green" crabs of similar size because their thicker claws are 29% stronger (Kaiser et al. 1990). "Red" crabs, however, are not as tolerant as "green" crabs to low salinity or low oxygen concentrations and thus are restricted to the deeper, more saline and cooler regions of estuaries (McGaw and Naylor 1992; Legeay and Massabuau 2000).

While group 2 crabs move into the intertidal zone with the flooding tide to forage, they also follow the tide in and out of estuaries (Mathieson and Berry 1997). Ameyaw-Akumfi and Naylor (1987) collected green crab in an estuary, clipped one of their anterio-lateral spines, and released them at high tide near the limit of tidal influence. During subsequent low tides, they checked baited traps at various points along the estuary. While some of the crabs remained in the estuary during low tide, a few of them reached the mouth of the estuary as the tide moved out, a distance of 2 km in only six hours.

C. maenas exhibit a seasonal pattern in distribution. Densities of crabs in the intertidal are typically highest in summer and early fall and lowest in winter (Aagaard et al. 1995). Thiel and Dernedde (1994) describe seasonal migrations of green crabs on the tidal flats of the northern German Wadden Sea. In the summer, adult green crabs undertake tidal foraging excursions over the mudflats, but small juvenile crabs stay in mussel clump shelters to avoid predation by adult crabs, shrimp, fishes, and birds. In early fall, adult green crabs leave the intertidal mudflats and migrate into deeper water. By the end of October, the other predators have also left the mudflats and the juvenile crabs leave their mussel clump shelters and start migrating over the mudflats into deeper water. By the end of December, all stages of the green crab population have migrated into the subtidal. There they remain until temperatures rise above 8°C (Atkinson and Parsons 1973). By late spring and summer, adult crabs become more active and resume their tidal foraging excursions over the mudflats.

In Oregon and Washington, the distribution of *C. maenas* appears to be limited to estuaries and bays. Although some crabs are found by rock turning, the best method for sampling *C. maenas* in their first summer is to set out baited minnow (crayfish) traps in the upper intertidal zone for one tidal cycle. Older crabs >50 mm carapace width are more efficiently sampled with rectangular, folding fish traps (60 x 45 x 20 cm, ordered from Aquatic Eco-Systems, Inc.) and steel mesh boxes with cone-shaped openings placed in the low intertidal or shallow subtidal. Traps set out overnight generally catch more crabs than those set out over a daytime high tide. We have caught green crabs in marshes, along tidal channels, on gently sloping gravel and boulder shores and in rip-rap. Larger crabs, >60 mm carapace width, enter baited crab rings set out by sportfishers and are raked up by cockle harvesters (John Schaefer, personal communication).

Feeding and Predation

Feeding

Carcinus maenas are opportunistic omnivores, feeding on prey items belonging to species in 158 genera in 19 phyla (Cohen et al. 1995). Green crabs are extremely tolerant to starvation. They survive prolonged periods of starvation up to three months by lowering their metabolic rate (Wallace 1973). The diverse food items in their diet include bacteria and foraminiferans ingested along with sediment, carrion, snail egg capsules, marsh vegetation, algae, worms, crustaceans (including crabs), insects, mollusks, urchins, fish, tunicates, and even stranded decaying jellyfish (Crothers 1968; Muntz et al. 1965; Rasmussen 1973; Brenchley 1982). *C. maenas* can feed on a range of food types, and its diet differs throughout the life cycle and from site to site.

Diet of Juvenile Crabs

On European mudflats, young *C. maenas* act as microcarnivores that extract their prey from the sediment. Eriksson and Edlund (1977) examined the feces from *C. maenas* in their first year of life and found shells and molts of small crustaceans along with sand grains. On the sand flats of the German North Sea, young *C. maenas* preyed heavily on nematodes, flatworms, and ostracods. The crabs extracted these prey items from the substrate by raking through the sediment with the tips of their legs and claws (Sherer and Reise 1981).

Jensen and Jensen (1985) determined that young *C. maenas* prefer young cockles (*Cerastoderma edule*) over other prey, such as the clam *Macoma balthica* and annelid worms. Crabs ate annelid worms only when no other prey was offered. Rangeley and Thomas (1987) offered juvenile and adult *C. maenas* a choice of barnacles (*Semibalanus balanoides*) or snails (*Nucella lapillus*, *Littorina littorea*, and *Littorina obtusata*). They found that juvenile crabs preferred barnacles whereas adults preferred snails. Cannibalism by larger crabs of smaller *C. maenas* can also be an important food source (Klein Breteler 1975b; Sherer and Reise 1981; Moksnes et al. 1998).

Diet of Adult Crabs

Adult *C. maenas* show strong regional and seasonal differences in their diet. In the Menai Strait, North Wales, green crabs ate mostly crustaceans and algae (Elner 1977) while in the Rance estuary, France, polychaetes and algae made up the greatest portion of their diet (Le Calvez 1987). In South Africa, *C. maenas* ate very little algae but ingested isopods, gastropods, and polychaetes (Griffiths et al. 1992). In the Bay of Fundy in Nova Scotia, green crabs ate mostly mussels (*Mytilus edulis*), clams (*Mya arenaria*), snails (*Littorina* spp.), barnacles (*Semibalanus balanoides*), and amphipods (*Gammarus oceanicus*). Diet composition varied with season. Barnacle consumption peaked in July, soon after their larvae settled from the plankton, with 90% of crab stomachs containing barnacle remains (Singh 1991). These regional and seasonal differences in the relative abundance of food items in the diet reflect prey availability in the immediate habitat (Elner 1981; Le Calvez 1987; Singh 1991).

While *C. maenas* can persist on whatever food is present, they do show a strong preference for bivalve mollusks. Ropes (1968) examined the stomachs of close to 4,000 *C. maenas* from Massachusetts and New Hampshire and concluded that this omnivore ate more animals than plants and that it preferred bivalve mollusks such as the mussel, *Mytilus edulis*, and the soft-shelled clam, *Mya arenaria*. Other bivalves, snails, and crabs were moderately important whereas marine worms, barnacles, and fish were less important items in the diet.

C. maenas become more carnivorous with age. Ropes (1968) divided crabs into two size classes, above and below 30 mm carapace width, and tabulated the frequency of food items found in their stomachs. Plant matter was found in 50% of the smaller crabs and in only 30% of the larger crabs, while animal remains were present in 90% of the larger and only 63% of the smaller crabs. Remnants of bivalves and gastropods were more prevalent in large crabs than in small crabs. Ropes (1968) observed that large crabs aggregated on clam beds when feeding, suggesting that they are attracted to bivalve prey. Similar preference of *C. maenas* for bivalve mollusks was found in Rhode Island (Ropes 1988), Nova Scotia (Elner 1981), and California (Grosholz and Ruiz 1995).

Predation

Prey Location

Crabs use chemical, visual, and tactile stimuli in foraging (Hughes and Seed 1995; Zimmer-Faust et al. 1995). Metabolites exuding from prey are detected at a distance by sense organs on the antennae. When currents carry prey odors, crabs follow the edge of the odor plume upstream by constantly comparing the chemical concentrations inside and outside the plume (Zimmer-Faust et al. 1995). Prey detection is most successful in quiet waters over smooth substrates and less successful in fast waters and rough bottoms when the odor plume is broken up by turbulence (Weissburg and Zimmer-Faust 1993). The presence of prey is detected by the funnel organs on the tips of the walking legs and claws when these appendages make contact with the prey. Crabs evaluate prey by manipulating it with their claws and mouth parts. Visual cues play a role in assessing the size of prey and in detecting moving prey (Hughes and Seed 1995).

Claw Morphology

The size, shape, and strength of a crab's claws often reflect its diet. Crabs that feed primarily on mollusks typically have more powerful claws than omnivorous crabs. For example, the claws of the predatory red rock crab, *Cancer productus*, are larger and have prominent molar teeth on the occlusal surfaces whereas those of the omnivorous purple shore crab, *Hemigrapsus nudus*, are more slender and have many fine teeth, or denticles (Behrens Yamada and Boulding 1998).

Biomechanical analyses of decapod crustacean claws have shown that it is mechanically impossible to design a claw lever system that is both fast and strong (Alexander 1968; Warner 1977). Strong claws with greater height and width have a higher mechanical advantage (MA) and have more slowly contracting strong muscles with long sarcomeres. Slender, long claws, on the other hand, have a high tip velocity but low MA (Alexander 1968; Atwood 1973; Warner 1977). Functional analogies of these two extremes in claw design are nutcrackers and tweezers. Most of our Pacific Northwest crabs have two equal-sized claws. For example, *Cancer productus* has two strong claws with an MA of 0.39, while *Hemigrapsus nudus* has two weak ones with an MA of 0.28 (Behrens Yamada and Boulding 1998). *Carcinus maenas*, on the other hand, has one of each: a strong "crusher" and a more delicate "cutter." The MA of the crusher is 0.36 and that of the cutter, 0.26 (Warner et al. 1982). Preston et al. (1996) measured the claw-closing forces generated at the tips of claws and found that the crusher claw of a 50-mm *C. maenas* is twice as strong as that of the cutter (88 vs. 44 Newtons). This dual "tool set" may contribute to the success of *C. maenas* as invaders by allowing them to exploit a larger spectrum of food types than our native crabs of similar size. By possessing both a strong claw and a fast claw, *C. maenas* can crush well-armored mollusks and possibly also catch fast-swimming fishes and crustaceans. In a lab trial in which we offered individual *C. maenas* and *Cancer productus* 15 snails a day, we observed no species difference in consumption rate for similar-sized crabs (Hauck 2000). Thus, size for size, *C. maenas* can be as devastating a predator on mollusks as *Cancer productus*. Shell breaking, however, is not the only way *C. maenas* gains access to mollusks. We observed that *C. maenas* can simply pull the soft tissue out of intact snail shells with their slender cutter claw and saw through the hinge ligaments of large mussels by using the serrated cutting surfaces of their claws (Hauck 2000; Michelle Cline, unpublished observation).

The hardness of a crab's diet can affect claw strength. Abby-Kalio and Warner (1984) fed *C. maenas* either hard prey, periwinkle snails (*Littorina littorea*), or soft fish flesh for six months. They found that the master claw of hard feeders was 30% stronger and the sarcomeres were 7% longer than those of soft feeders. Crabs living on the shore exhibited the same claw strength as hard feeders. The authors attribute the loss of strength and sarcomere length in soft feeders to lack of exercise.

Prey Handling Techniques

Crabs employ a variety of techniques to open mollusk prey, depending on the size and strength relationships between claw and prey (Elner 1978; Elner and Raffaelli 1980; Johannesson 1986). Small, thin-shelled prey that easily fit into the gape of the claw are steadied by the smaller claw or mouth parts and crushed outright in any plane by the larger claw. With larger shells, *C. maenas* seek out the weakest spots in the shell and often switch techniques if one technique proves fruitless (Elner 1978). Techniques used on mussels include umbone crushing, posterior crushing, boring, edge chipping, and hinge sawing. In edge chipping, the posterior valves are chipped until a claw can be inserted and the adductor muscle severed. Most oyster shells are crushed and fractured in a transverse or oblique plane with the master claw. Others are chipped at the margin or punctured in the middle of the shell (Dare et al. 1983).

Typical snail-opening techniques include apex severing, columella crushing, puncturing, lip peeling, and pulling (Johannesson 1986). In the pulling technique, the snail is held against the sternum with the larger claw. The smaller claw is inserted into the aperture and the entire soft body of the snail is jerked out, leaving an intact snail shell. Lab trials and field experiments using tethered snails on various beaches indicate that the puncturing and pulling techniques are characteristic of *C. maenas*. The native crabs *Cancer productus*, *Cancer magister*, and *Hemigrapsus* sp. primarily use the crushing or lip-peeling techniques (Behrens Yamada and Boulding 1998; Hauck 2000).

C. maenas learn to perfect their predation skills through experience. Cunningham and Hughes (1984) offered dogwhelk (*Nucella lapillis*) or mussels (*Mytilus edulis*) to naïve *C. maenas* and found that the time to break open a prey decreased by about 30% after the fifth or sixth prey of the same type had been eaten. Learning was delayed, however, when the two prey types were alternately presented.

Prey Size Selection

Although prey-handling experience and claw size and strength can limit the maximum size of mollusk a crab can open, crabs generally select prey at the lower end of their size spectrum (table 5) (Juanes 1992). For example, a *C. maenas* of 50 mm carapace width is capable of opening cockles of 20 mm shell height, but prefers 7 mm cockles (Sanchez-Salazar et al. 1987a; table 5). Likewise, *C. maenas* (70–75 mm carapace width) can easily open 27 mm-long mussels. When given a choice of prey sizes, however, they preferentially select 22 mm over 27 mm mussels (Elner and Hughes 1978; table 5). Starved crabs initially are less size selective, but after feeding for 30 minutes, they start rejecting larger mussels (Jubb et al. 1983). Although larger prey may appear to be more profitable, smaller prey require less handling time and are also less likely to damage the claws (Juanes and Hartwick 1990).

Dare et al. (1983) studied the predator-prey size relationship between *C. maenas* and Pacific oysters *(Crassostrea gigas)* and mussels *(Mytilus edulis)* in the lab and in the field at Menai Strait, U.K. They found that mussels were preferred over oysters and that the largest 75 mm crabs could open 55 to 60 mm oysters and 45 mm mussels (table 6). Prey in this size range, however, are not as vulnerable in the field as one might predict from these trials because crabs prefer smaller prey. Furthermore, crabs as large as 75 mm carapace width are very rare in the U.K. The authors thus suggest that juvenile oysters and mussels be protected from crab predators inside mesh cages until they reach 35 mm in length. On the west coast of North America, green crabs can attain 75 mm at the end of their second summer (Hunt, personal communication). Thus, shellfish larger than 35 mm would be vulnerable to these larger predators.

Table 5. Prey size selection exhibited by *Carcinus maenas* on various species of molluscan prey. Prey sizes are given as shell length (SL) or shell height (SH). The table was adapted from Juanes (1992).

Prey species	***Carcinus maenas* carapace width (mm)**	**Prey size offered (mm)**	**Prey size preferred (mm)**	**Reference**
Mytilus edulis (bay mussel)	50–55	10–35 SL	12.5	Elner and Hughes (1978)
	60–65	10–35	17.5	
	70–75	10–35	22.5	
	60	35–45	35	Ameyaw-Akumfi & Hughes (1987)
	65–75	45–55	45	
Mercenaria mercenaria (hard-shelled clam)	33	4–7 SL	4	Walne and Dean (1972)
	33	5–9	5	
	37	5–9	5	
	38	7–11	7	
	46	7–13	7	
	46	7–20	7	
Cerastoderma edule (cockle)	40	5–35 SL	6	Sanchez-Salazar et al. (1987b)
	50	5–35	7	
	70	5–35	9	
Modiolus modiolus (horse mussel)	50–65	7–99 SL	7–50	Seed & Brown (1975)
Pecten maximus (scallop)	45–75	40–60 SH	40–50	Lake et al. (1987)
Argopecten irradians (scallop)	41–65	17–32 SH	17–23	Tettelbach (1986)
Nucella lapillus (whelk)	60–70	6–16 SH	6–16	Hughes & Elner (1797)
	60–70	11–23	11–15.5	
	60–70	15–30	15–20	
Littorina saxatilis (periwinkle snail)	22–25	2–8 SH	2–4	Johannesson (1986)
Littorina sitkana (Sitka periwinkle)	30–42	5–13	5–8	Mahaffy and Behrens Yamada, unpublished data

Table 6. Largest intertidally grown Pacific oyster (*Crassostrea gigas*) and mussel (*Mytilus edulis*) that could be opened by *Carcinus maenas* of a given carapace width in laboratory trials. The table was adapted from Dare, Davies, and Edwards (1983).

Carcinus maenas **Carapace width (mm)**	**Largest oyster opened Shell length (mm)**	**Largest mussel opened Shell length (mm)**
25	24	25
35	31	28
55	45	38
75	60	45

Natural enemies

Predators

While *C. maenas* is an important predator in marine communities, it is also prey for other species. Predators on *C. maenas* in its native range include other crabs, octopods, cuttlefish, 26 species of fishes, 35 species of birds, and 5 species of mammals (Crothers 1968). Larval *C. maenas* are eaten by postlarval whiting (*Gadus merlangus*) and various other fish species (Nagabhushanam 1964; Crothers 1968). In Isefjord, Denmark, the brittle star, *Ophioglypha texturata*, traps the planktonic zoea larvae of green crabs on the sticky tube feet on its arms (Rasmussen 1973) while in western Sweden the shrimp *Crangon crangon* preys on newly recruited green crabs (Pihl and Rosenberg 1984; Moksnes et al. 1998).

C. maenas escape predation by sheltering in complex habitats. Birds, adult crabs, shrimp, and fishes are common predators on juvenile *C. maenas* on the extensive tidal flats of the Dutch and German North Sea coast (Thiel and Dernedde 1994). Juvenile and postmolt *C. maenas* are most abundant inside the shelter of mussel beds and eelgrass beds (Klein Breteler 1976; Reise 1978). Once the young crabs leave these structured habitats, however, they are preyed on by adult *C. maenas*, shrimp and fishes at high tide, and wading birds and gulls at low tide (Thiel and Dernedde 1994). Small gulls (*Larus ridibundus* and *L. canus*) feed on crabs between 10 and 30 mm carapace width while the herring gull (*Larus argentatus*) prefers larger crabs between 30 and 50 mm (Dernedde 1993). Dumas and Whitman (1993) followed the survival of tethered crabs in midintertidal pools with and without refuges. Gull (*Larus argentatus*) predation was 70% per day in pools without algal cover but only 10% per day when algae were present. Survival of crabs increased with crevice depth. When crevices inside pools were deeper than 6 cm, over 90% of the tethered crabs survived a 48-hour trial period.

Other birds frequently observed to feed on *C. maenas* include the lesser black-backed gull *(Larus fuscus)*, the velvet scoter (*Melanitta fusca)*, the scaup (*Aythya marila)*, the goldeneye *(Bucephala clangula)*, the curlew (*Numenius arquata*), the oystercatcher (*Haematopus ostralegus*), the shag *(Phalacrocorax aristotelis)*, the grey plover *(Pluvialis squatarola*), the common sandpiper *(Actitis hypoleucos)*, eiders *(Somateria mollissima* and *S. spectabilis*), and sandpipers (*Tringa nebularia* and *T. totanus*) (Crothers 1968; Gross Custard et al. 1977; Zwarts 1981; Le Calvez 1987; Moreira 1999). On the west coast of North America, the western gull (*Larus occidentalis*) appears to be a common bird predator on *C. maenas* (Christopher Hunt, unpublished observation)

Fishes are also important predators on *C. maenas*, especially on smaller and newly molted individuals. The most frequently observed predators on *C. maenas* are perch (*Dicentrarchus labrax*), dragonet *(Callionymus lyra)*, flounder *(Platychthys flesus)*, eel (*Anguilla anguilla*), conger eel (*Conger conger*), pout *(Gadus luscus*), whiting *(Gadus merlangus)*, cod (*Gadus morhua*), dab *(Limanda limanda)*, bass *(Morone labrax*), dogfish *(Scyliorhinus canicula)*, and the rock goby (*Gobius paganellus*) (Crothers 1968; Le Chalvez 1987; Isaksson et al. 1994). The commercial landings of the goby (*Gobius ophiocephalus*) and *Carcinus aestuarii* in the Lagoon of Venice exhibit an inverse relationship, typical of a predator-prey system. This goby is the main predator on newly molted *C. aestuarii* (Varagnolo 1968).

While it is plausible that other crab species can prey on *C. maenas*, the available evidence from field studies is only circumstantial. Adult lobsters *(Homarus americanus)*, rock crabs *(Cancer irroratus)*, and velvet swimming crabs (*Necora puber*) all prey on adult green crabs in the lab (Elner 1981; ap Rheinallt 1986). Ropes (1988) examined the stomach contents of five coexisting crab species at the Pettaquamscutt River, Rhode Island, and noted that the blue crab, *Callinectes sapidus*, and the lady crab, *Ovalipes ocellatus*, appear to be competitors and possible predators of *C. maenas*. When these three portunids coexist, *C. maenas* eat fewer bivalve mollusks, its preferred prey, than do the other two species. The fact that 40% of blue crabs and 28% of the lady crabs had crab fragments in their stomachs suggests that these larger swimming crabs may actually feed on *C. maenas*. When the velvet swimming crab, *Necora puber*, was offered different size classes of green crabs, they preferred larger crabs (ap Rheinallt 1986).

On the west coast of North America, green crabs may be restricted to less saline and warmer upper estuary sites by more aggressive native rock crabs. Hunt (2000, 2001) found very little overlap in the distribution of green crabs and red rock crabs (*Cancer productus*) in Yaquina Bay, Oregon. Red rock crabs dominate the more saline, cooler, lower estuary, and green crabs dominate the warmer and less saline upper estuary. In seven-day laboratory trials in which individual crabs were paired with crabs of their own species, all crabs survived well. Survival was around 90%, even in the presence of larger conspecific crabs. Smaller red rock crabs survived well in the presence of larger green crabs, but the reverse was not true. When 65 mm green crabs were matched with 95 and 105 mm red rock crabs, their survival dropped to 48% and 24%, respectively. McDonald et al. (1998) present compelling indirect evidence of native crab predation on *C. maenas* in Bodega Harbor, California. Eighty percent of the green crabs were missing limbs and 40% were missing claws at a site near the mouth of the harbor where they coexist with large Pacific and red rock crabs (*Cancer antennarius* and *Cancer productus*). Limb damage in green crabs was only 44% and claw loss 20% in a high marsh site where they are the only crab species.

Cannibalism by larger green crabs of smaller ones may be an effective density-dependent mortality factor. Klein Breteler (1975a) observed that young crabs from the first settlement pulse in June grow and survive better than those from subsequent settlement pulses. Laboratory experiments designed to look at the role of juvenile crab density and the presence of adult crabs on the growth rate of juveniles were unsuccessful because of cannibalism (Klein Breteler 1976). Scherer and Reise (1981), likewise, observed cannibalism in the new year class of *C. maenas*. Out of 300 crabs held in field enclosures, only 136 survived. Moksnes et al. (1998) concluded that the most efficient predators on megalopae and first-stage crabs were slightly larger green crabs that had settled from the plankton a few weeks earlier. Elner (1981), Le Roux et al. (1990), and Singh (1991) found the remains of conspecifics inside the stomachs of *C. maenas* from Nova Scotia and South Africa.

Crothers (1968) lists the following mammals as predators on green crabs: grey seal (*Halichoerus gryphus*), pygmy sperm whale (*Kogia breviceps*), otter (*Lutra lutra*), and common seal (*Phoca vitulina*). Seals have also been observed to feed on green crabs in Maine (Brian Beal, unpublished observation). On the west coast of North America, raccoons (*Procyon lotor*) patrol marsh banks during low tide for crabs not hiding in burrows or sheltering under clumps of sod. Raccoons have been observed to eat green crabs in San Francisco Bay (Jim Carlton, unpublished observation). Dunstone and Birks (1987) reports that mink (*Mustela vision*), and even foxes, forage on green crabs during the onshore migration of large crabs during the mating season.

There is a minor fishery for green crabs in Spain, Portugal, France, the U.K., Italy, and Greece (Varagnolo 1968; Crothers 1968; Gomes 1991; FAO 1999). Around 1,770 metric tons (3.9 million lbs) of *C. maenas* and *C. aestuarii* are harvested annually. This figure is an order of magnitude less than the average annual landings of the Dungeness crab (*Cancer magister*) on the west coast of North America of 25,000 metric tons and the edible crab (*Cancer pagurus*) in Europe of 30,000 metric tons (FAO 1999). In Britain, people used to eat green crabs in the 1800s, but today they are used mainly for bait (Crothers 1968). In France they are used in soup, and in Spain, in paella (Armand Kuris, personal communication). Varagnolo (1968) describes the *C. aestuarii* fishery in the Lagoon of Venice in the middle of the twentieth century. This fishery is based on two products: soft-shelled crabs in the spring (molecche) and females with ripe ovaries in the fall (masanette). Between 100,000 and 200,000 kg (220,000 to 440,000 lbs) were harvested annually for local consumption between 1946 and 1966. During the 1700s, annual catches exceeded 7 million kg (15 million lbs), including 6 million kg (13.2 million lbs) used for pilchard bait.

In the Ria de Aveiro Lagoon in Portugal, dozens of families depend on the green crab fishery for their year-round livelihood. The minimum commercial size is 50 mm carapace width. Although this traditional fishery has been in existence for a long time, fishery scientists only started studying it the late 1980s when green crabs started to decline, possibly because of overfishing. An average of 1,200 tons (2.6 million lbs) is harvested annually. Most of the crabs are exported live to Spain, where they are either consumed or processed for export (Gomes 1991).

On the east coast of North America, the green crab is considered a pest. Some communities in Maine and Massachusetts offer a 30-cent bounty per crab. These crabs are taken to garbage dumps or sold to bait dealers. In some communities, clammers must spend three low tides collecting green crabs before they can receive a harvesting permit. In one community, special licenses are given to individuals to trap green crabs for the Asian market (Beal 1998). On the west coast of North America, larger male green crabs (>90 mm) are gaining popularity with some sportfishers. They report that the steamed meat is quite tasty.

Parasites and Egg Predators

In its native habitat, *C. maenas* plays host to a number of parasites and egg predators. These include the protozoan *Thelothania maenadis*, the flatworms *Fecampia erythrocephala* and *Microphallus similis*, the acanthocephalan *Profilicollis botulus*, the nemertean *Carcinonemertes carcinophila*, the parasitic barnacle *Sacculina carcini*, the isopod *Portunion maenadis*, and nicothoid copepods (Crothers 1968; Johnson 1957). *Thelothania maenadis* attacks striated muscle, *Fecampia erythrocephala* lives in the body cavity, and *Carcinonemertes carcinophila* is an egg predator.

Microphallus similis is a fluke parasite with a circumpolar distribution in the Northern Hemisphere. Three hosts are needed to complete its life cycle: a snail, a crab, and a gull. In addition to being present in Europe, this parasite has also been found in *C. maenas* from Woods Hole, Massachusetts (Stunkard 1956). Ching (1965, 1991) isolated the metacercaria (larvae) of *Microphallus similis* from the digestive gland of the crab *Cancer magister* and adults from the intestine of the gull *Larus glaucescens* in Washington and British Columbia. Since this parasite is already established on the west coast, one might expect *C. maenas* to also acquire it. So far none of the *C. maenas* in Bodega Bay have acquired this or any of the native microphallids, even though native *Hemigrapsus oregonensis* is often "loaded with them" (Armand Kuris, personal communication).

Another worm parasite with circumpolar distribution is the acanthocephalan *Profilicollis botulus*. Two hosts are needed to complete its life cycle: a crab and a duck. *Profilicollis botulus* has been found in pouches near the rectum and in body cavities of *C. maenas* from Scotland, Russia, and eastern North America. *Profilicollis botulus*, or a related species, has been found in the crab *Hemigrapsus oregonensis*, from British Columbia and Bodega Bay (Ching 1989). This west coast acanthocephalan does not appear to cross over from *H. oregonensis* to *C. maenas* (Kuris, personal communication).

Sacculina carcini and *Portunion maenadis* are female crustacean parasites that feminize and castrate their host. The mode of this sexual transformation is thought to be hormonal (Rasmussen 1973). Parasitic barnacles of the genus *Sacculina* infect crabs of the family Portunidae. Adult parasitic barnacles are so specialized that they bear no resemblance to their shore-dwelling counterparts. Only the free-living larval stages allow them to be classified as barnacles. Both a female and a male parasite are needed to complete the life cycle of *Sacculina carcini* in *C. maenas* (Thresher 1996). In the first phase of the infection, a free-swimming female larva metamorphoses and settles on the integument of a small crab. Glenner and Werner (1998) found that more larvae settle on recently molted crabs than on those with hard carapaces. The parasite then penetrates the integument of its host via a syringelike structure. Once inside, the parasite develops roots throughout the nervous tissue of its hosts, disrupts the neuroendocrine controls, and sends branching projections throughout the body (Rubiliani et al. 1980; Payen et al. 1981).

Not only does the parasite rob its host of nutrients and retard molting, it also neuters it, regardless of sex. The second phase of the infection is characterized by the formation of an external sac at the base of the abdomen in both male and female *C. maenas*. A male *Sacculina carcini* larva is attracted to the parasitized crab and attaches itself to the sac. The sac may resemble an egg mass, but instead of crab eggs it contains the gonads of the parasites. Both parasitized male and female *C. maenas* exhibit brooding behavior. They clean and aerate the sac and protect their "brood" by covering it with their appendages when handled. Parasite larvae are released whenever conditions are favorable (Crothers 1968). The parasitic sac can remain attached to the crab for six months. When the sac drops off, the crab often dies (Rasmussen 1973). In rare cases, a new sac regenerates from the parasitic root system (Luetzen 1981). Hoeg et al. (1997) dissected 438 *C. maenas* from the west coast of Sweden and found that 47% of the crabs were infected with *Sacculina carcini*. Fifty of the crabs (11%) exhibited scars, indicating that they had lost their parasitic sac. While some green crab populations are heavily parasitized by *Sacculina carcini*, others, such as those of the Somerset coast of the British Channel, and the Schlei estuary in the German Baltic Sea, never exhibit an infection (John Crothers, personal communication; Dries and Adelung 1982).

The parasitic isopod *Portunion maenadis* also feminizes its crab host. Rasmussen (1973) reports that infected male crabs exhibit bulging carapaces, small claws, and broad, segmented abdomens. Most of the infected crabs examined by Rasmussen (1973) contained only one female isopod in the digestive gland. He reports that in August, 50% of the isopods contain embryos and larvae ready to hatch. The first and third larval stages are planktonic while the second lives attached to a copepod (Crothers 1968). Hoeg et al. (1997) observed a 2% infection rate for a crab population in western Sweden. A parasitic isopod from the west coast of North America, *Portunion conformis*, destroys the ovaries of female *Hemigrapsus oregonensis* and feminizes the males (Kuris 1975). So far, this isopod has not crossed over to *C. maenas* (Kuris, personal communication).

Egg predators can make a significant contribution to egg mortality in crustaceans (Kuris 1991). Nemertean worms and nicothoid copepods, small crustaceans that complete their development as symbionts of crabs, fall into this category. Nemerteans of the genus *Carcinonemertes* are thin, elastic, nonsegmented worms that feed on crustacean eggs. The planktonic larvae settle on crabs and develop on the gills, in the limb axillae, or in the abdominal furrow of their host. When a female crab deposits eggs, the worms migrate to the egg mass. There they prey on the embryos and also lay their own eggs inside mucus tubes among their host's eggs (MacGinitie and MacGinitie 1968; Torchin et al. 1996). While *Carcinonemertes carcinophilia* parasitizes *C. maenas* in Europe, it does not do so on the east coast of North America (MacGinitie and MacGinitie 1968).

Carcinonemertes epialti is native to the U.S. west coast and is found in *Hemigrapsus oregonensis*, *H. nudis*, and *Pugettia producta*. Torchin et al. (1996) report that this parasite has already infected the *C. maenas* population in Bodega Harbor.

An adult female nicothoid (*Choniosphaera cancrorum*) resembles a green crab egg in color, shape, and size (0.35–0.42 mm in diameter). The only clue that this organism is an egg mimic rather that an egg is the presence of the small segmented antennae, legs, and tail and the attached embryo sac that protrude from the base of the spherical "egg." Female nicothoids and their attached balloonlike egg packets of one to four fertilized embryos move around freely within the crab's egg mass. While they appear to be part of the brood, these egg predators actually suck out the contents of the crab eggs. At a later stage, the egg packets are found attached to crab's eggs and the hairs of the pleopods. Larval development resembles that of other copepods with typical nauplius and copepodite stages. However, instead of living freely in the plankton, these stages live in the crab's egg mass (Johnson 1957; Armand Kuris, personal communication).

Microorganisms

Brock and Lightner (1990) provide the most comprehensive review of crustacean diseases caused by microorganisms such as viruses, bacteria, and fungi. The following summary of diseases found in *C. maenas* and *C. aestuarii* is based on their review.

Viruses are the most numerous and diverse groups of microorganisms affecting arthropods, including marine crustaceans. Many of the viruses found in crustaceans do not lead to disease. Virulence depends on other stressors, such as pollution, high temperatures, or the presence of other disease organisms. For example, cultured shrimp are especially vulnerable to viruses when they are combined with bacterial, protozoan, or fungal infections. The type of viral infections reported from *C. maenas* and *C. aestuarii* include baculoviruses, a parvovirus, reoviruses, and a bunyalike virus. It should be noted that little is known of the role of these viruses in wild populations.

Baculoviruses infect the nuclei of blood cells and the epithelial cells of digestive glands. They have been found in *C. maenas* from Europe and eastern North America and in *C. aestuarii* from the Mediterranean. Healthy crabs acquire the disease by ingesting infected tissue. An experiment was conducted in which *C. aestuarii* were either injected with the bacolovirus Tau or fed infected digestive gland. All injected crabs lost their appetite, became lethargic, and died within 25 days, but only 20% of the crabs fed infected tissue died. The onset of the disease was slower in crabs held at 18°C than those held at 23°C (Pappalardo et al. 1986).

Parvovirus PC84 is reported for *C. aestuarii* from a lagoon on the Mediterranean coast of France. This virus infects the epithelial cells of the gills, midgut, and digestive gland. Infected crabs are weak, lethargic, and anorexic. Crabs that were artificially infected by injecting a viral suspension into their body fluids died within 25 days (Mari and Bonami 1988).

Three reoviruses were identified by Bonami (1976) and Mari and Bonami (1986). The first destroys the gill epithelium of *C. aestuarii*, while the second, termed W2, infects interstitial cells of the digestive gland, midgut, gills, and blood cells. The third, termed W, infects the digestive gland of *C. maenas*.

A bunyalike virus has been reported to cause disease in *Carcinus*: the crab hemocytopenic virus (CHV). CHV was found in 1 out of 700 *C. maenas* collected from Roscoff, France. This virus was shown to inhibit blood clotting (Bang 1971).

Two nonviral diseases have been identified in *C. aestuarii* from the French Mediterranean coast: a rickettsialike infection and *Streptococcus faecalis liquefaciens*. Rickettsia are small rod-shaped microorganisms found within the cells of the connective tissue of the digestive gland, gut, gonad, and gills. Although crabs experimentally infected with this pathogen die within 15 days, its impact in the wild is not known (Bonami and Pappalardo 1980). The bacterial disease caused by *Streptococcus faecalis liquefaciens* is typically found in fish such as salmon. In green crabs the bacteria were found in the digestive gland and in the connective tissue of the digestive tract, gills, and gonads. Infected crabs appeared weak but exhibited no lesions. The disease is spread through wounds and through ingesting infected tissue. The impact and distribution of the infection in wild populations are not known (Pappalardo and Boemare 1982).

Ecosystem Impact

The role of *Carcinus maenas* in marine ecosystems is very complex. The free-swimming larvae feed on plankton and are preyed upon by predators in the water column. The benthic crab stages feed on algae, marsh vegetation, mollusks, crustaceans, marine worms, carrion, and organic matter in sediment and thus act as grazers, carnivores, scavengers, and deposit feeders (Eriksson et al. 1975). In turn, *C. maenas* is also prey for other invertebrates, fishes, birds, and mammals. They interact with other crab species for food and shelter. Furthermore, the digging activities of green crabs on mudflats disrupt surface-dwelling organisms and tube-building worms. The studies below describe how *C. maenas* can control the distribution, abundance, size, morphology, and behavior of prey populations and the species composition of rocky shore and soft-bottom communities.

Prey Populations

C. maenas has the potential to dramatically affect the abundance, size structure, and defense responses of its prey populations. In sites where *C. maenas* is abundant, mussels, urchins, cockle beds, and barnacles cannot establish themselves because crabs prey on newly recruited prey (Kitching et al. 1959; Muntz et al. 1965; Beukema 1991; Leonard et al. 1999a). For example, Seed (1969) found that a 64 mm *C. maenas* could consume 34 medium-size mussels (1.5–2.5 cm) or 65 small ones (0.5–1.5 cm) per day. Such high predation rates on young mussels preclude their establishment in sites of high *C. maenas* abundance (Kitching et al. 1959; Seed 1969; Janke 1990).

Prey populations, however, can escape their predator by finding refuge in size, time, and space (Richards et al. 1999). On the extensive mudflats of the North Sea, *C. maenas* and the cockle *Cerastoderma edule* settle out from the plankton in the early summer. In July, densities of cockles typically range between 34,000 and 60,000/m^2, while young crabs range from 200 to 700/m^2 (Jensen and Jensen 1985). *C. maenas* grow rapidly and during the month of August consume most of the young cockles. Lab feeding rates confirmed that crabs in their second to fourth stages (mean size 4 mm) can consume six cockles (<4 mm) per day. After August, however, the remaining cockles have reached a size (>5 mm) too large for the young crabs to open and thus remain fairly resistant to further crab predation. After an unusually cold winter, it is common for cockles and other bivalves to establish very strong year classes. This pattern is due to the fact that cold temperatures delay crab settlement to a greater extent than that of bivalves. Bivalves then outgrow their predator and reach an invulnerable stage before the crabs are large enough to prey on them (Jensen and Jensen 1985; Beukema 1991).

In addition to escaping their main predator in size and time, cockles also find a spatial refuge from crab predation in the mid and high intertidal zones and in eelgrass beds. Since cockles in the higher tidal zones are covered by the tide less often, they are exposed to crab predation for shorter time periods than those in the lower zone (Sanchez-Salizar et al. 1987b). The complex structure of the eelgrass root system retards the foraging activities of crabs (Reise 1978). The soft-shelled clam (*Mya arenaria*) finds a refuge from green crab predation by burying deep into the sediment (Whitlow 2000).

Some fouling organisms attached to prey can deter a predator. Wahl et al. (1997) offered clean mussels or mussels fouled with barnacles or hydroids to *C. maenas* and noted the survival of the mussels. They found that crabs preyed on both the barnacles and the underlying mussels but avoided mussels covered with hydroids.

While intense predation can result in the total elimination of a prey population from part of its range, less intense predation can act as a powerful selective agent for predator-resistant prey. The mussel *Mytilus edulis* and the snails *Littorina saxatilis* and *Nucella lapillus* possess thicker shells in sites where *C. maenas* is abundant (Currey and Hughes 1982; Vermeij 1982; Johannesson 1986; Leonard et al. 1999b). The arrival of *C. maenas* in northern New England between 1871 and 1982 has been linked with thicker and more globose shells in *Nucella lapillus* and *Littorina obtusata* (Vermeij 1982; Seeley 1986; Trussell 1996). Field and lab experiments confirm that high-spired, thin-shelled *Littorina obtusata* are more vulnerable to *C. maenas* predation than globose, thick-shelled ones (Seeley 1986).

Many prey defenses observed in marine systems are induced by water-borne chemicals that exude from the predator or from the damaged prey (Harvell 1990). When an alarm substance from crushed conspecific snails is present in the water, the mudsnail, *Ilyanassa obsoleta*, rapidly burrows into the sediment, and the common periwinkle, *Littorina littorea*, crawls into crevices or hides under algal fronds (Ashkenas and Atema 1978; Hadlock 1980). Waterborne cues from green crabs induced stronger, thicker shells in the snail *Littorina obtusata* (Smith and Trussell 2000). Furthermore, mussels transplanted from a low green crab predation site to a high predation site produced more byssal threads and attached themselves more firmly to the substrate (Leonard et al. 1999b). The advantage of these inducible defenses over purely genetic ones is their flexibility. Prey spend energy on a defense only when a predator is present in space or time.

Competitors

Although the role of *C. maenas* as predator on hard-shelled prey is easy to document, its impact on competitors is more subtle and thus not as easily studied. Because the role of *C. maenas* in marine ecosystems is so complex, it potentially can compete with many different species at various trophic levels. For example, young plaice grew very poorly on the mudflats of the German Wadden Sea in 1981 when an abundant year class of green crabs depleted the cockle population, a common food resource for both predators (Bergham 1987). A similar scenario could develop in other habitats when green crabs become very abundant. At present, green crabs and wading shorebirds feed on the small clam *Nutricula* spp. and other species on the mudflats of Bodega Harbor. Grosholz et al. (2000) fear that wading birds could be affected adversely once green crabs increase their range and their abundance along the west coast of North America.

Green crabs will compete most intensely for food and shelter with other crabs. Grosholz et al. (2000) note that since the arrival of the green crab in Bodega Harbor, California, in 1993, the abundance of the native shore crab, *Hemigrapsus oregonensis*, has decreased on sandy intertidal mudflats. *H. oregonensis*, however, still remains the dominant crab in structured habitats where shelter is provided by rocks or oyster shells (Greg Jensen, personal communication).

To evaluate interspecies interactions between green crabs and native crabs, Jensen et al. (2000) and McDonald et al. (2001) set up laboratory trials in which individual green crabs were matched with *H. oregonensis* or with the Dungeness crab, *Cancer magister*, of a similar size. Crab pairs were introduced into arenas containing either a food item or an oyster shell for shelter. *C. maenas* invariably was the first crab to exploit the food. When crabs were forced to compete for shelter, green crabs "won" over Dungeness crabs, but *H. oregonensis* "won" over green crabs.

Community Effects

Hard-Bottom Communities

On the sheltered rocky shore of the North Sea island Helgoland, *C. maenas* is the only crab species. Janke (1990) constructed field cages (0.5 x 0.5 x 0.1 m) with and without green crabs at three tidal heights and monitored changes in community structure. He found that *C. maenas* plays an important role in structuring the species composition by preying on mussels (*Mytilus edulis*) and two species of grazing snails (*Littorina littorea* and *Littorina fabalis*) and by consuming blades of the alga *Fucus* sp. In the mid and low intertidal zone, *C. maenas* was able to control the abundance of *Littorina littorea*, but the resulting reduction in grazing pressure had no effect on algal growth. The most profound effect of *C. maenas* was the total exclusion of mussels from the low zone. Any mussels that settled were soon eliminated by this crab, thus creating space for algae to flourish and to dominate the low intertidal zone.

Kitching et al. (1959) came to a similar conclusion about the role of *C. maenas* in preventing the establishment of mussels after studying the distribution patterns of crabs and their prey in Lough Hine, Ireland. They transplanted mussel clumps from the open coast to various stations in the lough and found the lowest mussel survival in sites with the highest *C. maenas* abundance. Seed (1969) noted that mussels were nearly absent from the low intertidal zone of semi-wave-exposed rocky shores on the southwest coast of England. He marked and measured individual mussels at three tidal heights and recorded significantly higher survival rates in the mid and high intertidal than in the low zone. High predation rates by the crabs *C. maenas* and *Cancer pagurus* most likely produced this pattern. The distributions of dogwhelks (*Nucella lapillus*) and sea urchins (*Paracentrotus lividus*) also appear to be controlled by *C. maenas* (Kitching et al. 1959; Muntz et al. 1965).

Menge (1983) looked at the relative importance of five species of predators, a drilling snail (*Nucella lapillus*), a starfish (*Asterias forbesi*), and three species of crabs (*C. maenas, Cancer irroratus*, and *Cancer borealis*) in the low intertidal zone of New England shores. He found that all predators were more effective in controlling mussel and barnacle distributions on wave-protected shores than on exposed headlands. *C. maenas* was the most important predator, eating up to seven mussels per day. This crab ate mussels 25 times faster than *Nucella* and 4 times faster than *Cancer borealis*. On some beaches, *C. maenas* removed 80% of the mussels during the growing season. By eliminating mussels and barnacles from sheltered shores, these five predators created bare substrate for the establishment and maintenance of the alga *Chondrus crispus*.

Soft-Bottom Communities

The impact of *C. maenas* on soft-bottom communities has been well studied on the Wadden Sea, the extensive tidal flats and channels bordering the Dutch, German, and Danish North Sea coasts. During the summer months, newly settled *C. maenas*, along with other predators, such as shrimp and fishes, prey heavily on the infauna of the mudflats (Reise 1977, 1978; Jensen and Jensen 1985; Beukema 1991). Prey organisms include the commercial cockle, *Cerastoderma edule*, the soft-shelled clam, *Mya arenaria*, the hard-shelled clam, *Mercenaria mercenaria*, and tube-dwelling polychaetes. When prey organisms were protected from predators inside 1 mm mesh cages, they survived from 4 to 23 times as well as unprotected prey (Reise 1977).

In the summer of 1982, Jensen and Jensen (1985) were able to evaluate the predatory effects of newly settled *C. maenas* on cockles since these two species were the dominant predator and prey species on the mudflat that year. Both species settled simultaneously in early summer. Young cockles were as dense as 60,000/m^2 but decreased in abundance dramatically over July and August. Between July 22 and August 15, the growth of the crabs accounted for 26% of the loss of cockles. The authors concluded that predation by young *C. maenas* promotes a more diverse community by preventing the establishment of dense cockle beds. By preventing cockles from dominating the mudflat, *C. maenas* indirectly create habitat for other species, such as the tube-building amphipod *Corophium volutator*.

Habitat Disturbance

The digging activities of *C. maenas* while foraging and searching for shelter have the potential to disrupt soft-bottom communities. Mudflats in Massachusetts present an even, level surface during the winter and early spring. As soon as temperatures rise and green crabs become active, however, the flats become completely covered with excavations (Smith 1954). Many large crabs, including our native red rock crab, *Cancer productus*, use their walking legs and claws to excavate clams from the sediment (Smith et al. 1999). *C. maenas* rapidly dig up jackknife clams (*Ensis directus*) and soft-shell clams (*Mya arenaria*) on the east coast (Elner 1981). Auster and Crockett (1984) observed green crab digging activities while diving and counted as many as nine crabs excavating different edges of a large pit. This digging activity often attracts secondary predators such as sand shrimp (*Crangon septemspinosa*), winter flounder (*Pseudopleuronectes americanus*), killifish (*Fundulus* spp.), and smaller crabs. The digging activities of green crabs also interfere with attempts to reestablish the eelgrass, *Zostera marina*, to New Hampshire estuaries (Davis et al. 1998).

The effect of the digging and predation activities of *C. maenas* on soft sediment infauna depends on the size of the crabs and sediment composition. Gee et al. (1985) set up cages containing 15 juvenile crabs (11–13 mm), 1 adult crab (50 mm), or no crabs on the mudflats of the Lyner estuary in Cornwall, U.K. They found that juvenile crabs had a negative effect and adult crabs a positive effect on the abundance of various species of small, burrowing annelid worms. Their results suggest that juvenile crabs prey on the small annelids and that annelids benefit from the digging activities of adult crabs.

Schratzberger and Warwick (1999) examined the effect of predation and biological disturbance by *C. maenas* on free-living, estuarine nematode (roundworm) communities in both sand and mud habitats. They found that predation was most important in sand habitats whereas biological disturbance was most important in mud habitats. The structure of sand substrates was not affected by the digging activities of *C. maenas*, since the whole sediment column was well aerated in both crab and no-crab treatments. Nematode abundance in sand habitats with *C. maenas*, however, was significantly lower than when crabs were absent. The authors attribute this reduction to predation. Scherer and Reise (1981), likewise, concluded that *C. maenas* predation was responsible for a dramatic reduction in nematode abundance in the top 5 mm of sediment. Predation on nematodes, however, was not a factor in muddy habitats because alternative prey such as annelid worms and detritus were very abundant. Undisturbed muddy habitats consist of a thin layer of oxygenated mud on top of a black anoxic layer. The digging activities of *C. maenas* aerate the sediment and allow nematodes to penetrate deeper into the substrate. It thus appears that infaunal organisms can benefit from the digging activities of *C. maenas* as long as they are not the preferred prey.

CHAPTER TWO

Global Invasions

Case Studies of Green Crab Invasions

The European green crab has a long history of range expansion. During the last two centuries, sustainable populations of *Carcinus maenas* established themselves on the east coast of North America; in Australia, Tasmania, South Africa; and most recently, on the west coast of North America (see Grosholz and Ruiz 1995). Reports of green crab sightings in Brazil and Hawaii could not be confirmed (Almaça 1962). The Mediterranean green crab, *C. aestuarii*, established itself in Tokyo Bay, Japan (Furota et al. 1999). By studying these case histories, we may be able to identify common patterns of establishment, spread, and impact and thus make predictions for future introductions. Knowing what the common patterns are could help us implement appropriate preventive and control measures.

Atlantic North America

The oldest nonnative green crab population exists on the east coast of North America. A founder population established itself somewhere between New Jersey and southern Massachusetts prior to 1817 (Say 1817). Most likely they arrived from Europe on wooden ships, either with rock ballast or with fouling communities on the hulls (Beal 1998). Before 1900, green crabs were rare and restricted in their distribution from Delaware

Bay, New Jersey, to Cape Cod, Massachusetts (MacPhail et al. 1955). In the early 1900s, however, they responded to a long-term increase in seawater temperature by spreading north of Cape Cod. Subsequent episodes of population buildup and range expansion also reflect warm temperature trends. The northern range expansion was episodic rather than gradual: Portland, Maine, in 1905, Port Clyde in 1930, Bar Harbor in 1937, Lubec in 1951, and the Gulf of Fundy in 1953 (Glude 1955; Beal 1998). In 1961 *C. maenas* reached Sable Bay in Nova Scotia, and at present, it ranges from Virginia to the southeastern shores of Prince Edward Island (Gillis et al. 2000).

The recent appearance of green crabs on Prince Edward Island is linked to a series of years with unusually warm water temperatures. It is believed that green crab larvae crossed the Northumberland Strait around 1995 and colonized a number of estuaries on the southeastern shores of Prince Edward Island (Gillis et al. 2000). Whereas warm temperature trends are associated with high green crab abundance, severe winters are correlated with mass mortality and range contraction (Welch 1968; Berrill 1982). Thus, global warming would result in a poleward expansion of the green crab's range.

Australia and Tasmania

The first reported sighting of green crabs in Australia occurred in Port Phillip Bay near Melbourne in 1900 (Fulton and Grant 1900). It is believed, however, that the actual introduction occurred much earlier, possibly during the gold rush in the 1850s. The most likely mechanism for the arrival of this invader was as a hitchhiker on semidry ballast rocks from Europe. In 1971, *C. maenas* spread 550 km east to Mallacoot Inlet in far eastern Victoria, and by 1978 they had spread another 150 km north to Narooma. Green crabs also spread east to the Adelaide area in South Australia: to Port River in 1978 and to Coorong and Onkaparinga estuaries in 1985 (Zeidler 1988). Although *C. maenas* is moderately abundant in southern Australia, it does not appear to have a significant negative effect on seven species of grapsid crabs (Sinclair 1997). In deeper waters, *C. maenas* appears to be competitively displaced by the heavily armored native crab, *Ozius truncatus* (Zeidler 1997).

In 1993, green crabs crossed the Bass Strait into northern Tasmania. It is not known whether they dispersed by larvae on ocean currents or through ballast water transport. At present, they are found in many sheltered locations in northern and eastern Tasmania, including Flinders Island and the D'Entrecasteaux Channel, south of Hobart (CRIMP 2000a). Currently, the range of the green crab in Tasmania is still expanding, aided by strong poleward currents as well as by shellfish transports (Ron Thresher, personal communication).

Scientists from the Center for Research on Introduced Marine Pests (CRIMP) in Hobart are monitoring the Tasmanian situation closely. They have observed that the green crabs in Tasmania are more numerous and have a more damaging effect on native bivalves and crabs than their mainland counterparts. It is feared that green crabs could threaten some of the shallow-water endemic species in southwestern Tasmania. The mainland green crabs are less abundant and spend more time hiding under rocks or buried in sediment. This secretive behavior could be an avoidance adaptation to a suite of predators, including the aggressive swimming crab, *Portunus pelagicus*, skates, and rays. These predators are absent in Tasmania. Furthermore, mainland green crabs are hosts to a number of parasites that are only now appearing in the Tasmanian population (Ron Thresher 1997 and personal communication). While the impact of *C. maenas* on mariculture operations so far has been minimal, this could change as the crabs extend their range and the mariculture industry grows (CRIMP 2000a).

South Africa

The first green crab sighting in South Africa occurred in Table Bay Docks in Cape Town in 1983. The largest crab was 84 mm carapace width, suggesting that it may have been in its second or third year of life. Subsequent sampling in 1984 revealed the presence of a breeding adult population ranging from 42 to 84 mm carapace width. The crabs could have arrived as adults inside the fouling communities on the feet of semisubmersible exploratory oil-drilling vessels that started to call in South African ports after 1969. Another possibility is that they arrived as larvae inside the ballast water tanks of cargo ships (Le Roux et al. 1990). Between 1986 and 1988, green crabs spread 10 km south to Camp Bay and 17 km north to Melkbosstrand, most likely via larval transport by currents. In 1990 a single mated pair was found under a boulder in Langebaan Lagoon in Saldanha Bay, a range extension of 100 km. These two crabs were found inside a semi-enclosed lagoon used for culturing mussels. Over the next 10 years, however, the range of the green crabs contracted and at present extends only 30 km north of Cape Town. Thus, after 17 years, there remains only one large, self-perpetuating population in Table Bay and a few smaller ones in harbors and lagoons (Charles Griffiths, personal communication).

The limiting factor to green crab spread in South Africa is suitable sheltered habitats, a rare resource on the extensive wave-exposed shores.

The impact of green crabs in South Africa thus will be most intense in sheltered areas. Green crabs are predicted to have no major effect on the two common species of native crabs (*Cyclograpsus punctatus* and *Plagusia chabrus*) because their diets do not overlap (Griffiths et al. 1992). While green crabs feed on isopods, limpets, polychaetes, barnacles, and whelks, their most noticeable effect has been inside Table Bay Docks. There the crabs have removed all the mussels that used to grow on the wharf. The main concern now is to keep green crabs from establishing breeding populations inside sheltered lagoons, as these serve as marine preserves and mariculture centers (Griffiths et al. 1992).

Japan

Carcinus aestuarii was discovered in Tokyo Bay, Japan, in 1984. Tokyo Bay is extremely polluted and experiences periods of oxygen depletion during the summer. Green crabs are able to maintain large populations under these conditions by migrating to shallow oxygenated waters during the summer. So far, green crabs have spread from Tokyo Bay to adjacent Sagami Bay and to the polluted Osaka Bay and Dokai Bay (Furota et al. 1999). It is not known whether the high diversity of native crab species outside of these polluted bays (A.W. Lohrer, personal communication) will play a role in limiting the abundance and spread of green crabs along the Japanese coast. At this time, green crabs are not considered a nuisance species in Japan (Lafferty and Kuris 1996).

Western North America

A self-perpetuating, breeding population of *C. maenas* was discovered in San Francisco Bay in 1989 (Cohen et al. 1995). The crabs had most likely arrived much earlier and had built up their population size inside lagoons and tidal sloughs for several generations (Cohen et al. 1995). Molecular genetic analysis indicates that the founding colonists originated from the east coast of North America (Bagley and Geller 2000). Possible vectors for this introduction include seaweeds used in packing Atlantic sea food products such as lobsters or bait worms and ballast water transport of larvae.

By 2000, the green crab had spread to coastal embayments 1,390 km north to Nootka Sound on Vancouver Island and 320 km south to Morro Bay (Ted Grosholz, John Morrison, and Glen Jamieson, personal communication) (fig. 7). It should be noted that population densities in bays and estuaries north of Yaquina Bay, Oregon, are still sparse. Because coastal currents generally flow south in the summer and north in the winter, larval dispersal by ocean currents is a plausible mechanism for this rapid

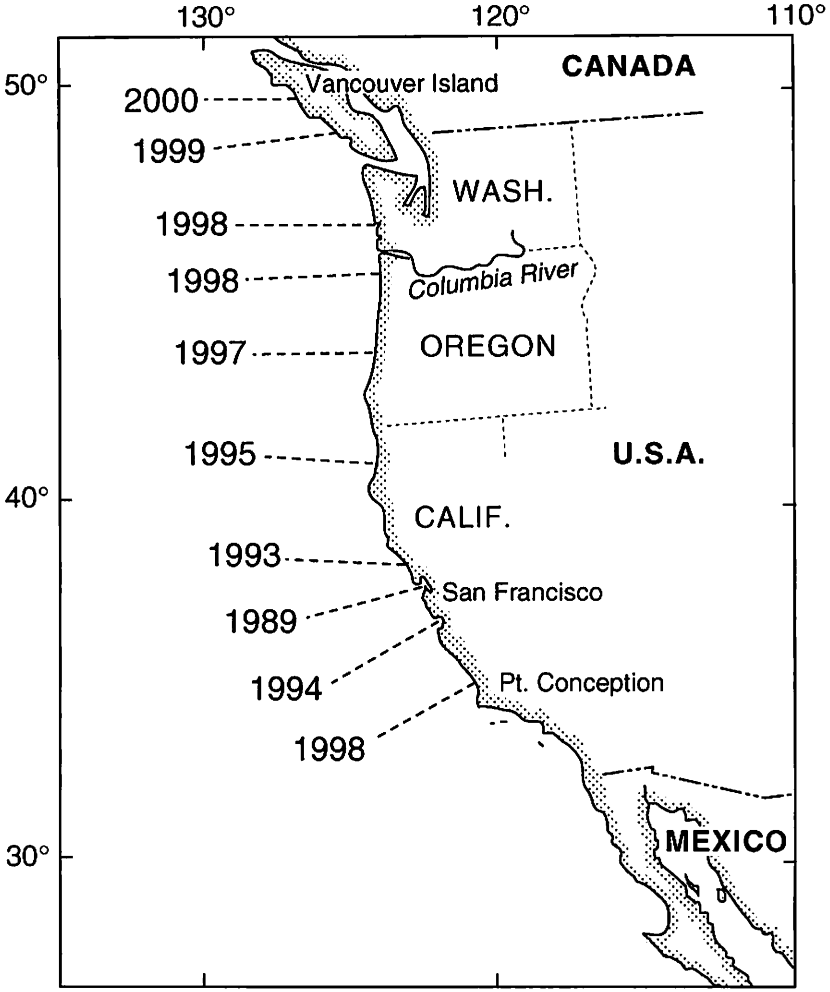


Fig. 7. Sitings of the European green crab on the west coast of North America. As of the year 2001, they ranged from Morrow Bay, California, in the south, to Nootka Sound, on Vancouver Island in the north.

range expansion (Grosholz and Ruiz 1995; Behrens Yamada and Hunt 2000).

From sightings and growth rate measurements, it appears that the northern range expansion was not gradual, but occurred episodically in waves at two- to three-year intervals. The first green crab sighting, outside of San Francisco Bay, occurred 70 km to the north in Estero Americano in 1989. This specimen was an 85-mm male caught in a gill net (Cohen et al. 1995). It is possible that this sighting represents the first wave of range expansion. In 1993, newly recruited green crabs arrived in Bolinas Lagoon, Drakes Estero, Tomales Bay, and Bodega Harbor, a distance of 80 km from the source population in San Francisco Bay (Grosholz and Ruiz 1995). From growth studies, we deduce that the large green crabs that were discovered in Humboldt By in 1995 most likely arrived as larvae in 1993 (Miller 1996; Behrens Yamada and Hunt 2000). Thus, in the spring and summer of 1993, green crabs simultaneously colonized five northern California estuaries, a distance of 380 km. From the discovery in 1997 of one- or two-year-old crabs in Coos Bay and other crab sightings from the same cohort in six more estuaries—five in Oregon and one in Washington—we deduce that a second colonization event occurred in 1995 or 1996.

The most recent and most dramatic range expansion, however, occurred after the 1997/98 El Niño when ocean conditions were extremely favorable for northward larval dispersal. During the summer of 1998, a strong new year class of green crabs appeared simultaneously in Humboldt Bay, California, seven Oregon estuaries, and two Washington estuaries. Subsequently, the same year class was found in Price Bay near Victoria, Barkley Sound, Lemmens Inlet, and Nootka Sound on Vancouver Island. In 1997, a northward-moving current of 10 km/d was measured off Newport as early as September. By November, it had intensified over the whole shelf and slope, from northern California to Oregon. The northward currents were especially strong off Crescent City, California, and Coos Bay, Oregon, measuring > 40 km/d. Such strong currents lasted until April 1998 (Huyer et al. 1998). Drifters released off Newport, Oregon, in January 1998 moved north to the west coast of Vancouver Island at an average velocity of 50 km/day (Barth and Smith 1998). These observations support the view that strong northward currents were a coastwide phenomenon during the fall, winter, and spring of 1997/98. If we use 55 days as the developmental time for *C. maenas* larvae at 14°C (Dawirs et al. 1986), then it is possible for larvae to be transported 2,200 km by ocean currents, a distance from San Francisco to the Queen Charlotte Islands. It is thus feasible that *C. maenas* larvae from San Francisco Bay and northern California could have seeded Oregon, Washington, and Vancouver Island estuaries between September 1997 and April 1998. Shore station data provide supporting evidence that larval colonization plays a dominant role in the range expansion of green crab on the west coast of North America. Favorable northward currents occurred during the first four months of 1993 and 1998 when green crab recruitment north of the source population was good, but not in 1997, 1999, or 2000 when it was not (Anonymous 2000; A. Huyer and R.L. Smith, personal communication).

Observations and Predictions of Spread and Impact

From the above case studies of green crab invasions, a number of common patterns emerge. These patterns can help us predict where future invasions of green crabs might occur, how they are most likely to spread, and what their ecological and economic impact might be.

Observed and Predicted Patterns of Spread

Green crab populations, like many other invasive species, establish themselves in large, international shipping ports. For example, the current count of established marine species in Port Phillip Bay, Australia, is 100 and in San Francisco Bay, 234. Over 10% of the species in Port Phillip Bay and 95% of the species in San Francisco Bay are nonnatives. It is estimated that every year, one or two new species establish themselves in Port Phillip Bay and four or five in San Francisco Bay (CRIMP 2000b; Cohen and Carlton 1998 and personal communication). Ships and exploratory oil-drilling vessels are notorious for transporting species from port to port. Green crabs could have hitchhiked on ballast rocks, in the fouling communities on hulls or drilling platforms, and inside ballast water tanks. Because these ports are associated with large metropolitan areas, human-mediated vectors other than ship traffic could also come into play. For example, Atlantic lobsters, bait worms, and scientific specimens are kept moist during their plane flight by wrapping them in seaweed. Small green crabs, snails, and other invertebrates have all been observed on the seaweed (Gregory Jensen, personal communication).

Green crab populations build up in sites where larvae are retained and not flushed out to sea. Cohen et al. (1995) suggest that microhabitats inside San Francisco Bay, such as lagoons and tidal sloughs, acted as “incubators” for the establishment of the founding population. Thus, the whole life cycle, including larval development, settlement, and growth to breeding adult would occur within these microhabitats. Port Phillip Bay, Australia, Tokyo Bay, and Table Bay, South Africa are large bays with structures such as lagoons, canals, or docks that limit water exchange and thus aid larval retention.

Once a founding population has reached a critical size, it can produce sufficient larvae to “seed” adjacent sites. Range expansion by larval dispersal appears to be the dominant mechanism for range expansion. Other possible vectors for spread include shellfish transfers between sea farms and transport via local ship traffic. Young crabs could hitch rides on seed stock, in bilge water, or in bait wells.

The spread of green crabs is not gradual but episodic. The species might not spread for many years and then one year spread rapidly over great distances. Once a green crab population is established, it may take decades before it builds up a large enough larval pool to expand its range. Green crabs arrived on the Atlantic coast of North America in the early 1800s, but their range did not expand north of Cape Cod until around 1900. It took another 50 years before they were observed to be a pest on clam beds in Massachusetts and Maine. We see a similar pattern of delayed spread in Australia. If green crabs were introduced to Phillip Bay in the 1850s, then it took 80 years before they were discovered in Mallacoot. Crabs from the mainland population did not reach Tasmania until around 1990, despite favorable currents. If this episodic pattern of range expansion also holds for the west coast of North America, it could take decades, perhaps even a century, for green crabs to establish large, viable populations throughout their potential geographic range from northern Baja California to Alaska (fig. 1).

Green crabs can exhibit cycles of range contractions and expansions. In the Western Baltic, green crabs die out after a number of years of low salinity but re-invade as soon as conditions become more favorable. On the east coast of North America, green crab ranges contract after an unusually cold winter but expand again when temperatures are milder. Although at present the range of green crabs has stabilized in South Africa, it could increase in the future. A large larval pool, combined with favorable currents, is all that is needed to seed the lagoons north of Table Bay.

Green crabs have not colonized all of the regions in the world where temperatures are favorable for their growth and reproduction (fig. 1). For example, so far, green crabs have not established themselves in South America or New Zealand. Any international port with salinities above 17 ‰ and temperatures above 10°C and below 18°C, for at least part of the year, is vulnerable to receiving an inoculation of green crabs. Sheltered habitats are most at risk for green crab colonization. Since green crabs cannot forage on shores exposed to extreme waves, they thrive best in sheltered areas (Crothers 1970). The relative amount of sheltered to wave-exposed habitat thus will allow us to predict how successful green crabs will be in a new area. Green crabs were very successful in establishing themselves on the extensive sheltered shores of Atlantic North America, but not very successful in South Africa with its extensive wave-exposed beaches.

On the west coast of North America and in Tasmania, green crabs are not using rocky shore habitats to the same extent as they do in their native habitat and on the east coast of North America. So far, they are primarily found in soft sediment in estuaries, bays, and inlets (Grosholz and Ruiz 1996; Proctor 1997a). This pattern may indicate that green crab densities on the west coast of North America (0.04–0.4 crabs/m^2 in Bodega Harbor) are still too low to disperse to rocky shores. It is also possible that native crab species are keeping them out of rocky habitats (Hunt 2000, 2001).

It is difficult to predict the future fate of *C. maenas* in Pacific Northwest estuaries. Recruitment during the summers of 1999 and 2000 was sparse. The next few years will be critical in determining the fate of these satellite populations. If the trend of low recruitment continues, the colonizing 1997/98 El Niño cohort could die of old age without leaving sufficient numbers of offspring to maintain the populations. The trend could also reverse for two reasons. First, females from the year El Niño cohort are now at the peak of their reproductive life and could produce more than one brood a year (d'Udekem d'Acoz 1993). Second, another coastwide colonization event could occur with the next El Niño. A series of warm years with favorable currents have been linked to range expansion and population buildup in green crabs. El Niño events may provide two crucial components for spread: a large larval pool and a dispersal vehicle. The unusually warm ocean temperatures during an El Niño could aid reproduction and larval survival while strong currents could transport the larvae great distances. In the future we may see range expansions and contractions that mirror ocean conditions. If we should experience global warming, with El Niño events increasing in frequency, green crabs will thrive. A series of cooler years with weak poleward currents could result in the temporary extinction of satellite populations.

While currents on the open west coast of North America have been the dominant mechanism of spread, human-mediated transport could play a critical role in accelerating the spread into the inland sea between Vancouver Island and the mainland (fig. 7). So far, no green crabs have been found in the Strait of Georgia, Puget Sound, or Hood Canal. These shores consist of many wave-protected bays, lagoons, and mudflats where green crabs would thrive. Once a satellite population of green crabs gets established there, they could spread very quickly through natural larval dispersal. It is thus very important to prevent an introduction into these waters via shellfish transport, ballast water discharge, boat traffic, or other means. It is predicted that green crabs will be most abundant in shallow, wave-protected bays where water temperatures rise well above 11°C in the summer, salinities are above 17%, and large predatory crabs, such as *Cancer productus*, are rare.

Ecological Impact

The role of green crabs in communities is summarized in chapter 1. Although it is not always possible to isolate the effect of green crabs from that of other predators, the available evidence indicates that when green crabs are abundant, they can prevent the establishment of mussel and cockle beds. By preventing these bivalves from dominating a habitat, green crabs indirectly allow other species, such as algae and tube-building amphipods, to flourish (Kitching et al. 1959; Menge 1983; Jensen and Jensen 1985; Janke 1990). The potentially devastating effect of a large green crab population on bivalves has been reported throughout the world. On the Atlantic coast of North America, green crabs are implicated in the decline of the soft-shelled clam fishery (Glude 1955; Welch 1968). Inside Table Bay Dock in South Africa, the green crabs have removed all the mussels that once grew on the walls of the wharf (Charles Griffiths, personal communication).

There is evidence that green crabs in Tasmania are having an effect on bivalves and native crabs. From caging experiments, Walton (1997) showed that large male green crabs (50–60 mm) are more important predators on juvenile clams (*Katelysia scalarina*) (6–15 mm) than are a native crab (*Paragrapsus* sp.) and a native whelk (*Columinella* sp.). However, no evidence was found that green crabs controlled the abundance of the clams. MacKinnon (1997) examined mussel survival inside and outside the present range of the green crab and found that survival was much better in the absence of green crabs. Whereas bivalves were found to be potential prey of green crabs, the mudsnail *Batillaria australis* was not (Rodriguez 1997). Ruiz and Rodriguez (1997) found a negative correlation between the abundance of green crabs and that of three species of native crabs. The authors suggest that green crab predation was responsible for the decline in the abundance of native crabs.

On the west coast of North America, studies designed to document and predict the impact of green crabs on resident prey species have been carried out in San Francisco Bay, Bodega Bay, California, and Yaquina Bay, Oregon. Cohen et al. (1995) set up laboratory feeding trials with 10 female green crabs (55–60 mm carapace width) and three species of bivalves (10–20 mm shell length). They found that green crabs preferred the softer-shelled Asian clam (*Potamocorbula amurensis*) to the harder Manila clam (*Venerupis philippinarum*).

Grosholz and Ruiz (1995) placed cages (0.3 m x 0.3m) on a mudflat in Bodega Harbor. They added one crab (38–52 mm) to half the cages and after 12 days noted the abundance of microfauna in sediment samples. Two species of small native clams (*Nutricola confusa* and *N. tantilla*) and two species of small crustaceans were significantly reduced in number when a crab was present in a cage, whereas two crustacean, four annelid, and one phoronid species were unaffected. A subsequent laboratory feeding trial revealed that green crabs preferred larger *Nutricula* (>3 mm) over smaller ones (<1 mm) as predicted from the field experiment.

Long-term monitoring studies in Bodega Harbor by Grosholz et al. (2000) show a negative correlation between the abundance of green crabs and that of *Nutricula* sp. but a positive correlation with two species of polychaetes and a tube-building crustacean. They also observed a decline in the number of the shore crab *Hemigrapsus oregonensis* in pitfall traps after the arrival of green crabs in 1993. Shore bird abundance, however, was not affected, even though green crabs may have reduced the abundance of the small *Nutricula* clams, an important food source for shore birds. The impact of green crabs could increase if their densities increase from the current level of 0.04 to 0.4 crabs/m^2.

Bassett (2000) examined the possible effect of *C. maenas* foraging activities on the species composition of mud-dwelling invertebrates in Yaquina Bay, Oregon, by setting up a caging experiment. Square mesh cages (0.25 x 0.25 x 0.20 m) were embedded in the sediment and crabs (60–67 mm) added to half the cages. After 10 days, sediment cores were taken from each cage and the species composition and abundance were tabulated. Two out of four small crustacean species showed a significant decrease in numbers when a green crab was present in a cage whereas two crustaceans, a bivalve, two annelids, and one nematode species showed no effect.

Other studies seek to define the position of the green crab in the hierarchy of native crab predators. Hauck et al. (2000) compared prey size selection and prey consumption rates of green crabs and five native crab species. Individual crabs were housed inside perforated plastic chambers in seawater tanks and offered five small (5–8 mm), five medium (8–10 mm), and five large (10–13 mm) snails (*Littorina sitkana*) per day. Green crabs ate significantly more snails than the shore crabs *Hemigrapsus oregonensis* and *H. nudus* of similar size. While all three crabs preferred smaller snails, only green crabs ate the largest ones. They simply inserted the slender tips of their minor claw into the snail's aperture and pulled out the soft tissue. Green crabs exhibited the same feeding rates as red rock crabs (*Cancer productus*) and Dungeness crabs (*Cancer magister*) of similar size (Hauck et al. 2000; Tim Davidson, unpublished data). These comparisons suggest that the per capita impact of green crabs on hard-shelled prey is significantly higher than that of native shore crabs and of the same order of magnitude as that of red rock crabs and Dungeness crabs of similar size.

Hunt (2001) observed that green crabs in Yaquina Bay, Oregon, are not abundant in the lower estuary where a dense population of red rock crabs (*Cancer productus*) forages. He set up interaction trials in which a small or medium green crab was matched with another green crab or red rock crab of various sizes. Larger *C. productus* ate smaller *C. maenas*, but not the reverse. Little or no cannibalism occurred within either species, regardless of the size difference between partners.

To evaluate interspecies interactions between green crabs and native crabs, Jensen et al. (2000) and McDonald et al. (2001) set up laboratory trials in which individual green crabs were matched with *Hemigrapsus oregonensis* of a similar size or with the Dungeness crab, *Cancer magister*. Crab pairs were introduced into arenas containing either a food item or an oyster shell for shelter. *C. maenas* invariably was the first crab to exploit the food. When crabs were forced to compete for shelter, green crabs won over Dungeness crabs, but *H. oregonensis* won over green crabs. While these laboratory trials can give us an indication of where the green crab fits into the dominance hierarchy of the native crab guild, it should be noted that interactions between crabs in the field are more complex. The outcome of crab-crab interactions depends on many factors, including the relative densities, size frequency distributions, species, sex, hunger level, physiological stress, and molt status of the crabs.

Case studies of green crab introductions throughout the world suggest that the ecological impact of this crab depends on habitat type, larval supply, and the degree of resistance offered by the native community. In South Africa and on the mainland of Australia, the impact is judged to be minimal whereas in Atlantic North America and in Tasmania it is substantial. Lack of suitable habitat along the extremely wave-exposed coast of South Africa limits green crab populations to Table Bay and to a few isolated lagoons and sheltered bays. So far, a dense enough larval plume has not reached Langebaan Lagoon, to the north of Cape Town, to start a self-perpetuating population there. On the east coast of North America, extensive wave-sheltered habitats for green crabs are provided by barrier islands and by many bays. Under these conditions, large populations can build up to over 500 crabs/m^2 and catches of over 300 crabs/trap/day (MacPhail et al. 1955).

The degree of resistance offered by the native community may be an important factor in determining the ecological impact of an introduced green crab population. Although we lack data from controlled experiments, the comparison of Tasmanian and Australian mainland populations suggests that predators, competitors, and parasites can keep green crab populations low and their impact small. Thus, the more diverse native communities on the west coast of North America, with a total of 23 crab species, could offer more resistance to the green crab invasions than did the native communities on the east coast with only 9 crab species (Jamieson et al. 1998). It appears that larger predatory crabs such as the red rock crab (*Cancer productus*) can prevent green crabs from using the more saline parts of estuaries as well as rocky sheltered shores. The smaller shore crabs, *Hemigrapsus oregonensis* and *H. nudus*, may prevent young green crabs from seeking shelter under rocks and boulders. Thus, it is possible that on the west coast of North America, native crabs could limit green crabs to soft sediment beaches in estuaries.

So far, there is no record of green crabs causing the extinction of any native species. If green crab densities were to increase on the west coast of North America, they could endanger small local populations of small snails as well as recovering populations of native oysters (*Ostrea conchaphila*). The snails *Littorina sitkana* and *L. subrotunda* live in the upper zone of salt marshes. Their thin shells make them susceptible to being crushed even by small crabs (Boulding and Van Alstyne 1993). If green crabs were to become abundant, they could cause the local extinction of isolated populations of these snails. Since these snails hatch from eggs as miniature adults, recruitment from other populations would not occur readily. The native oyster (*Ostrea conchaphila*) is gradually building up its numbers in Coos Bay, Oregon, after a high-saline habitat was created in the deep shipping channel by a recent dredging operation (Baker et al. 2000). The facts that adult green crabs prefer native oysters over other bivalves and that adult green crabs overwinter in these deep channels puts these recovering oyster populations at risk (Palacios and Ferraro 2001; Neil Richmond, personal communication).

Economic Impact

Although the economic impact of green crabs on commercially and recreationally harvested species is difficult to quantify, many studies identify *C. maenas* as an important predator on valuable bivalve species. On the extensive mudflats of the North Sea, young green crabs feed on newly settled bivalves such as cockles (*Cerastoderma edule*) and clams (*Macoma balthica* and *Mya arenaria*). These bivalves typically settle at great densities in the spring, but numbers drop sharply by late summer because of predation by green crabs and other predators (Jensen and Jensen 1985; van der Veer et al. 1998). This negative effect on newly recruited bivalves is most noticeable after mild winters, when green crab recruitment precedes that of the bivalves (Jensen and Jensen 1985; Beukema 1991).

The most quoted impact of green crab on a native species is that on the soft-shelled clam (*Mya arenaria*) in New England. The declines in clam landings from a high of 14.7 million pounds in 1938 to a low of 2.3 million pounds in 1959 have been attributed to the range extension of green crabs. The downward trend in clam harvest occurred eight years earlier in Massachusetts than in Maine, corresponding to the northward spread of green crabs (Glude 1955). MacPhail et al. (1955) set out marked soft-shelled clams (12–15 mm) in three sites in New Brunswick varying in green crab abundance. After one month, mortalities ranged from 17% to 57% compared to 10% before the arrival of the green crabs. While it is plausible that an increase in foraging crabs can severely affect the recruitment of young clams, it should be noted that other factors might have contributed. These factors include the direct effects of warm temperatures on *Mya arenaria*; disease; increase in other predators, such as horseshoe crabs, herring gulls, ducks, and flounders; and overfishing (Smith 1950, 1954; Glude 1955).

At present, there is little evidence that green crabs are significantly affecting shellfish-growing operations in Tasmania or on the west coast of North America. Tasmanian shellfish growers are not concerned that green crabs could affect their $14 million oyster (*Crassostrea gigas*) and $1.2 million mussel (*Mytilus edulis*) industries. Because these species are grown off the bottom, in racks and longlines, they are not accessible to foraging green crabs. Right now green crabs are feeding on organisms in the sediment and do not climb up into the oyster racks (Procter 1997b). So far, there is only one report of adverse effects of green crabs on mariculture operations on the west coast of North America. A strong year class of green crabs arrived in Tomales Bay, California, in 1993. The larvae settled inside the 8 mm mesh bags in which Manila clams (*Venerupis philippinarum*) are grown and preyed on a wide size range of clams. Average clam production that year was around 10 lbs per bag, down from a typical previous yield of 12–15 lbs (Finger 1998). In Tillamook Bay, Oregon, where oysters are grown on the mudflats, adult green crabs (86 mm) seek shelter in the mud and under oyster clusters but do not appear to attack two- to three-year-old oysters (John Faudskar and Jesse Hayes, personal communication).

The ecological and economic impact of green crabs depends on their feeding rate and abundance. Some studies have compared the feeding rate of green crabs to that of other predators. On New England rocky shores, green crabs are the most important predator, eating up to seven mussels per day. This crab ate mussels 25 times faster than snails of the genus *Nucella* and four times faster than the rock crab, *Cancer borealis* (Menge

1983). On New Brunswick mudflats, green crabs eat five times as many clams as the shell-drilling northern moon snails (*Lunatia heros*) (MacPhail et al. 1955). Reported densities of green crabs range from as high as over $500/m^2$ on the east coast of North America to as low as 0.04–0.4 crabs $/m^2$ for Bodega Harbor, California (MacPhail 1955; Grosholz et al. 2000). Densities in Oregon, Washington, and Vancouver Island, British Columbia, are lower than in Bodega Bay. Catches of green crab in Yaquina Bay, Oregon, during the summer of 1999 were less than 3 crabs/trap/day in prime green crab habitat (Christopher Hunt, personal communication). This compares to up to 343 crabs/trap/day for the Atlantic coast and 300 crabs/trap/day for Tasmania (MacPhail 1955; Walton 2000; Proctor and Thresher 1997). If, however, populations on the west coast of North America were to build up within this century to levels found on the east coast, then many species could be at risk (table 7).

All mollusks, no matter how large or thick their shell as adults, are vulnerable to crab predators right after they settle from the plankton. At this stage, a large green crab population has the potential to prevent newly recruited clams from reaching harvestable size (Jensen and Jensen 1985). Studies were designed to evaluate the susceptibility of various species of

Table 7. Commercial and sports species on the west coast of North America that could be affected by *Carcinus maenas*. Annual landings and estimated value of fisheries are based on 1998 and 1999 data obtained from FAO (1999), BC Fisheries (1998), PSMFC (1998), and PSMFC (2000). British Columbia shellfish landings were provided by J. Davidson and C. Matthews.

Common Name	**Scientific name**	**Landings in metric tons**	**Estimated value $US**
Pacific or Japanese oyster	*Crassostrea gigas*	8,400	25,000,000
Manila clam	*Venerupis philippinarum*	3,448	14,800,000
Geoduck	*Panopea abrupta*	4,027	34,500,000
Native littleneck	*Prothaca staminea*	164	320,000
Butter clam	*Saxidomis gigantes*	1,280	113,000
Cockle	*Clinocardium nuttallii*		
Bent–nose clam	*Macoma nasuta*		
Baltic *Macoma*	*Macoma balthica*		
Eastern soft-shell, or steamer clam	*Mya arenaria*		
Gaper clam/ horse clam	*Tresus* sp.	8	10,000
Dungeness crab	*Cancer magister*	25,000	133,000,000
English sole	*Pleuronectes vetulus*	2,100	1,500,000

Pacific coast bivalve species to green crab predation. Palacios and Ferraro (2001) offered male green crabs (60–70 mm) native oyster (*Ostrea conchaphila*) and three clam species ranging in size from 10 to 37 mm. They found that size is not as significant a factor in predicting prey vulnerability to these large predators as species and burrowing behavior. The softer-shelled native oysters were preferred over the thicker-shelled Manila clams (*Venerupis philippinarum*) and bent-nosed clam (*Macoma nasuta*). A hungry crab ate as many as 40 small native oysters (10–14 mm) in a 16-hour trial. Bassett (2000) set up similar lab feeding trials in which she offered green crabs (52–62 mm) a choice of three size classes (10, 20, and 30 mm shell length) of Pacific oysters (*Crassostrea gigas*), bent-nose clams (*Macoma nasuta*), and bay mussels (*Mytilus trossulus* and *M. galloprovincialis*). She found that the crabs preferred the small and medium oysters and bent-nose clams to the larger ones, but all sizes of bay mussels were vulnerable. When medium-size oysters, bent-nose clams, and mussels were offered, crabs preferred mussels over oyster and bent-nose clams.

If green crabs were to become abundant in northern California, Oregon, Washington, and British Columbia, there is concern that they could threaten valuable Dungeness crab and flatfish fisheries (Lafferty and Kuris 1996; Jamieson et al. 1998). Currently, 25,000 metric tons of Dungeness crab (*Cancer magister*) and 2,100 metric tons of English sole (*Pleuronectes vetulus*) are landed annually in west coast ports (FAO 1999; PSMFC 1998). Both Dungeness crabs and English sole rely on estuaries as nursery areas for growth and survival (Gunderson et al. 1990). Dungeness crabs feed on small crustaceans, polychaete worms, and bivalves, species that are also eaten by green crabs. If green crabs were to become abundant, they could be potential predators and competitors of Dungeness crabs. McDonald et al. (2001) found that 15 mm green crabs are better competitors for food and shelter than similar-sized Dungeness crabs, but that predation of green crabs on Dungeness crabs did not occur. The authors observed, however, that the two species use different nursery habitats in Washington bays. Young green crabs were captured in the high intertidal zone near marsh vegetation whereas young Dungeness crabs seek out shelters in the mid and low intertidal zone. The foraging ranges of adult green crabs and larger juvenile Dungeness crabs (>40 mm) do appear to overlap as both species enter baited traps set out in the lower intertidal and shallow subtidal zones of estuaries (Christopher Hunt, personal communication). More research is needed to evaluate the potential impact of green crabs on Dungeness crab and English sole landings. Since estuaries are complex interacting systems, predictions are difficult to make.

Control Measures

Avoiding Introductions

Humans have moved species around throughout history. Intentional introductions include our agricultural crops and livestock. Polynesians brought pigs to the Hawaiian Islands, seafarers left goats on oceanic islands to assure a fresh meat supply for future voyages, and fisheries agencies stocked trout in lakes that lacked them. Not all of our intentional introductions have focused on food, however. English colonists in North America attempted to introduce all the birds mentioned in the collected works of Shakespeare, and our cosmopolitan domestic cat traces its roots to the sand cat of Egypt. Although introductions can benefit humans, they can also be very damaging to native species and communities. Most nations now carefully screen species before they introduce them for agricultural and maricultural purposes. While intentional introductions are still a concern, the major problem today is to identify the vectors for unintentional ones, especially for those species that we consider invasive. In the aquatic environment, invasive species include the zebra mussel, toxic marine algae responsible for paralytic shellfish poisoning, disease organisms such as cholera bacteria (*Vibrio cholerae*), the western Atlantic comb jelly (*Mnemiopsis leidyi*), and voracious predators such as the northern Pacific starfish (*Asterias amurensis*) and the European green crab.

The rate of these species introductions has accelerated over the past two centuries because of faster and more frequent sea and air travel (Cohen and Carlton 1995). In the days of wooden sailing ships, marine invaders typically arrived as fouling organisms on the hulls of wooden ships or along with ballast rock inside the ship's hold. Since wooden ships were leaky, the ballast holds were always damp. Thus, green crab could survive ocean voyages from Europe to eastern North America or to Australia on either side of the ship's hull.

While hull fouling has become less of a problem with the adoption of steel hulls and antifouling paint, the new vector for species transport is ballast water. Large cargo vessels use water inside special tanks for stability during voyages when they are carrying less than a full load. Typically, millions of gallons of water are pumped into these tanks in one port and discharged in another. All types of species, including their larval and resting stages, have been found in ballast water (Carlton and Geller 1993). It is estimated that on any day, as many as 3,000 species of aquatic organisms are traveling in the ballast tanks of ships in the world oceans (Carlton 2000). Some of these species will survive and reproduce and establish populations in the new port. Progress has been made within the past 20 years to recognize this important vector and to minimize its role in species introductions. The United Nations International Maritime Organization and the Unites States government recommend that ships exchange their ballast water at sea. This practice reduces the chances of coastal organisms from one port establishing themselves in another. Government, industry, and resource managers need to cooperate to develop new ballast management technologies. Possible candidates are onboard and port-side treatment of ballast water with heat, UV radiation, ozonation, biocides, clyclonic separation, and filtration (Cangeloshi 2000). Although green crab larvae could survive in ballast tanks, it is not known whether ballast water has acted as a vehicle for introductions of green crabs.

Mariculture operations have been responsible for many introductions (Carlton 1992). When the Atlantic oyster (*Crassostera virginica*) and the Pacific oyster (*Crassostrea gigas*) were carried to the west coast of North America, they brought with them associated species. Thus, the eastern oyster drill (*Urosalpinx cinerea*) and mud snail (*Ilyanassa obsoleta*) arrived from the Atlantic and the Japanese oyster drill (*Ocenebra japonica*) and mud snail (*Batillaria attramentaria*) arrived from Japan (Carl and Guiguet 1957). With the development of local shellfish hatcheries and with the use of cultchless seed, this vector is less of a problem today. However, the practice of shellfish growers' moving stock and gear from bay to bay could have accelerated the range expansions of the green crab in Tasmania and in eastern North America (Ron Thresher and Brian Beal, personal communication)

The air transport of Atlantic lobsters, bait worms, and marine specimens around the world is another very important vector for dispersing marine species. Typically, these products are wrapped in the seaweed *Ascophyllum*. It is thus quite common for small snails and young green crabs to hitch rides on this seaweed (Gregory Jensen, personal communication). Likewise, it is common for seafood restaurant workers and fishers in San Francisco to simply toss *Ascophyllum* into the bay. A small colony of the viviparous Atlantic snail, *Littorina saxatilis*, recently established itself in San Francisco Bay. The fact that this colony is close to a favorite fishing site suggests that the vector may have been *Ascophyllum* used for shipping bait worms (Carlton and Cohen 1998).

Although it is not possible to stop all marine introductions, efforts should be made to slow the accelerating process. The first step is to identify the most important vectors. The second is to decide on the most effective plan of action to affect a change. In some cases this could be as simple as using nonliving packing material for shipping seafood, bait worms, and biological specimens. It might also be possible to soak

Ascophyllum in fresh water long enough for attached biota to die or fall off. A minimal investment in educating shippers of marine products, workers in seafood restaurants, educators, scientist, and anglers of the possibility of introducing nonnative species could yield great benefits.

Managing Introductions

Once a nonnative species is introduced to a new geographic region, it may be possible to prevent or slow down further spread. For those species that lack a planktonic dispersal stage, eradication of the pest is possible if the infestation is detected early and a persistent and cooperative effort is made to remove the pest and its resource. This was done for the small sabellid tube worm *Terebrasabella heterouncinata*, which arrived on a California abalone farm in 1987 along with a shipment of South African abalone. When a sabellid attaches to the abalone shell, the abalone produces more shell material in an attempt to overgrow the sabellid. This reaction results in slow growth and shell deformation in the abalone. The sabellid reproduces by brooding its embryos inside the tube. The miniature worms crawl out and find new molluskan hosts to infect. Once the sabellid population was discovered, every effort was made to prevent its spread. Infected abalones were removed and the population of potential hosts was reduced. These hosts included uninfected abalones as well as alternative species such as turban snails. Thus, any remaining young sabellids had difficulty finding new hosts and died. This eradication was successful because mariculturists, agencies, and pest control scientists acted rapidly and persisted in their control efforts well after the sabellid was no longer found (Culver and Kuris 2000).

Eradication of an invader can be very costly, even when the species is sessile and the invasion is still well contained. The Central American brackish water black-striped mussel (*Mytilopsis* sp.) was discovered around three marinas in Darwin Harbor, Australia. This relative of the zebra mussel was eradicated by closing the floodgates to the harbor and poisoning all biota around the three infected marinas with bleach and copper sulfate. The short-term costs of this operation were over a million dollars and the annihilation of existing biota. The long-term benefit is that no efforts will be needed in the future to control this pest in the Darwin area as long as care is taken not to reintroduce it (Myers et al. 2000).

While eradication of a marine invader was possible in the above examples, it should be noted that both invading species were sessile, both invasions were still well contained, and the sabellid lacks a planktonic dispersal stage. Eradication does not appear to be an option for introduced green crabs because they are highly mobile as adults and possess planktonic larvae. By the time green crabs are first discovered, they are typically not confined to a single site: adults have been observed to travel up to 15 km (Gomes 1991). Once a species with planktonic larvae has spread and established satellite populations, removal of adults in one site will have no lasting effect, as new colonists from adjacent populations will keep arriving. In such a case, the best solution is to control the density of the invader to a level at which it does minimal damage. Various methods have been tried to control green crab densities. They include poisoning crabs with bait and trapping them. Biological control is a new tool in the marine environment that is being considered for controlling green crabs in the future.

Poisoned bait to control green crabs was tested by Hanks (1961). He soaked fish bait in the pesticide lindane and created a band of bait 30 feet wide across the mouth of a small creek in Maine. Poisoned bait was renewed every two weeks over the summer and crab abundance was monitored by setting six traps at 100, 400, and 800 meters on either side of the barrier. Average daily catches of green crabs closest to the barrier were between 15 and 20 crabs/day while at 800 meters they were 30 and 40 crabs/day on the inside and outside of the barrier, respectively. While catches of green crabs were slightly higher outside than inside the barrier, crabs inside the barrier remained abundant all summer. It thus appears that the use of poisoned bait is not effective in controlling green crabs. Furthermore, some shellfish growers are opposed to this method, as other species, including birds of prey and household pets, could become victims.

While fishing is a potential method for controlling green crabs, there is very little evidence that this method is effective in substantially reducing numbers. A green crab fishery has existed in Venice Lagoon, Italy, for centuries. Years of poor catches are correlated with high catches of gobies, a predator on newly molted green crabs (Varagnolo 1968). This natural predator appears to be more of a factor in affecting green crab abundance in Venice Lagoon than fishing. A traditional green crab fishery also exists in the Ria de Aveiro Lagoon in Portugal. An average of 1,200 tons (2.6 million lbs) are harvested annually from the estuary and shipped to Spain (Gomes 1991). Despite these high landings, there is no evidence that green crabs are decreasing in abundance in Portuguese estuaries. Landings primarily reflect market conditions in Spain (Armand Kuris, personal communication).

Green crabs in Maine and Massachusetts are so abundant that various methods have been tried to reduce their numbers. Some communities offer a 30¢ bounty per crab, while others require clam diggers to collect green crabs before they are issued a harvesting permit. Municipalities on Martha's Vineyard, Massachusetts, conduct trapping programs. The goal is to allow planted clams (*Mercenaria mercenaria*) to reach harvestable size by reducing predation. Walton (2000) assessed the effectiveness of this practice by continually trapping and removing green crabs from a confined embayment. Daily catches remained between 10 and 35 crabs per trap from the end of May to early October. It thus appears that trapping had little or no effect on green crab abundance.

In searching for a biological control agent for introduced populations of the green crab, one looks for natural enemies in both its native and newly adopted habitats. The benefit of an effective biological control agent is that it could provide a permanent solution to the pest problem. Of all the green crab enemies listed in the previous chapter, the parasitic castrators *Sacculina carcini* and *Portunion meanadis* and the egg predators *Carcinonemertes* and nicothoid copepods hold promise as potential control agents (Armand Kuris, personal communication). Before a nonnative biological control agent is released, however, many factors need to be considered and many laboratory tests carried out (Lafferty and Kuris 1996). A potential control agent should infect proportionately more hosts at high than at low green crab densities. The agent must also survive over most of the host's range and not affect other species.

Thresher (1996) explored the possibility of using the parasitic barnacle *Sacculina carcini* to control green crabs in Tasmania. He found that the parasite could be cultured in the lab and that the parasite and host overlapped in their temperature and salinity requirements. Hoeg et al. (1997) tested the susceptibility of various Scandinavian and Australian crab species to *Sacculina carcini* by exposing them to the parasite. As expected, both the Scandinavian and Australian *C. maenas* developed infections after exposure. Although a genetic probe detected the presence of *Sacculina carcini* in the Australian crab *Paragrapsus gaimardii*, the crab did not developed an infection. Recent tests in California show that *Sacculina carcini* readily infects the native crabs *Cancer magister*, *Pachygrapsus crassipes*, *Hemigrapsus nudus*, and *H. oregonensis*. However, *Sacculina carcini* cannot complete its life cycle in these hosts and always dies (Armand Kuris, personal communication). A lot more research is needed before parasites like *Sacculina carcini* can be released as biological control agents of nonnative green crab populations around the world.

A microsporidian disease found in Dungeness *(Cancer magister)* and red rock *(C. productus)* crabs on the west coast of the Untied States held promise as a natural biological control agent for green crabs. Needles disease caused by *Nadelspora canceri* is found primarily in young Dungeness crabs, in which it destroys skeletal muscles. The disease develops over a period of months but eventually is lethal to all infected individuals. Crabs in the terminal stage of infection are sluggish and lack the strength to effectively use their claws in feeding and defense. The parasite is spread via the oral route, and in one Oregon estuary the infection rate was as high as 41% in young crabs (Childers et al. 1996). Laboratory trials have shown that green crabs are not susceptible to needles disease (Christopher Hunt, unpublished data). If green crabs are not infected by this parasite, they could have a competitive advantage over native Dungeness crabs in those estuarine habitats where the two species overlap.

Another approach to biological control is to enhance the habitat for a native natural enemy. On the west coast of North America, it may be possible to increase the abundance of native shore crabs in the high intertidal zone of mudflats where green crab larvae settle out from the plankton. This could be accomplished by adding shelters such as rocks, stepping stones, plywood sheets, and oyster shells. Both shore crabs *Hemigrapsus oregonensis* and *H. nudus* have been shown to colonize such newly created shelters (Dumbauld et al. 2000; Ison 1998). Larger crabs typically displace smaller crabs from shelters and often prey on them, regardless of species. Lohrer (2000) found that green crabs smaller than 35 mm were disappearing from New England rocky shores with the arrival of the Asian shore crab, *Hemigrapsus sanguineus*. This new invader was feeding on green crab recruits. Jensen et al. (2000) showed that the shore crab *H. oregonensis* is a better competitor for shelter than green crabs of similar size. It is thus conceivable that adding shelter could give the native shore crabs a competitive advantage over green crabs of smaller or equal size. Predation of green crab recruits by the two *Hemigrapsus* species could also occur. The outcome of such shelter addition on green crab abundance would need to be investigated.

Finding an effective way to control green crabs will take a major international effort. Most likely, a combination of control agents will provide the best possible control of green crabs. These methods need to be developed now so that they can be implemented when green crab populations build up.

Limiting Impact

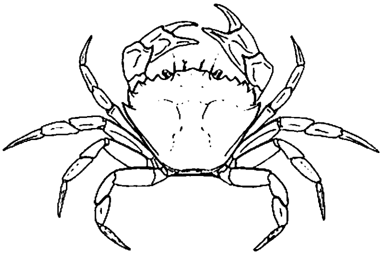
Various methods have been tried to limit the impact of green crabs. Smith (1954) experimented with fences for protecting clams from green crab and horseshoe crab predation. He found that a circular 36 cm-high fence constructed of 2.5 cm chicken wire mesh with a flange on the top worked reasonably well. The circular shape reduced eddies and the flange discouraged green crabs from crawling inside. He planted 17 mm clam seed (*Mya arenaria*) inside and outside the enclosure and found good survival inside but no survival outside the enclosure. Underwater observations revealed green crabs feeding on the small clams. Fences with flanges are successfully used in France to discourage crab predators (Cathy Sanford, personal communication). Although fences can work as effective crab barriers, the drawback is that they are costly to build and maintain and there is no incentive to protect noneconomically important native species (Smith 1954).

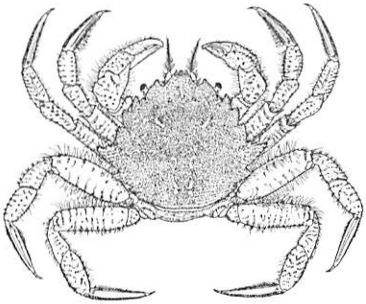
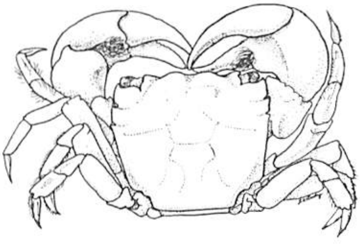
Shellfish growers can adjust their growing practices to reduce green crab damage, much as they have done for other predators. So far, green crabs are not a problem in Tasmania where shellfish growers culture their stocks off the sea bed by using raft or tray culture (Procter 1997b). Growers can also choose species that are less vulnerable to crab predators. For example, whereas green crabs readily feed on Pacific oysters (*Crassostrea gigas*), they avoid the New Zealand oysters (*Tiostrea lutaria*). Their flat oval shape makes them very difficult for crabs to manipulate (Richardson et al. 1993). The practice of growing bivalves under mesh covers or inside mesh bags appears to be very effective in discouraging predators from preying on them. Walne and Davies (1977) planted various sizes of Pacific oysters (*Crassostrea gigas*) on a sea bed in Wales. The treatments included controls with no cover and with 12 mm mesh and 36 mm mesh covers. After 30 days, the smallest oysters experienced 50% mortality if unprotected but only 11% mortality when covered with 12 mm mesh. Survival of the largest oysters was over 80% in all the treatments. The authors attributed most of the mortalities of unprotected oysters to green crabs. A similar study with mussels (*Mytilus edulis*), also in Wales, yielded the same pattern. During the first year, unprotected mussels experienced significantly higher mortalities (70–85%) than those inside crab-proof cages (22–57%) (Dare and Edwards 1976). Once the settlement pattern of young green crabs is known for an area, growers can adjust the time of planting their seed stocks. The goal is to get the seed oysters to a large enough size that they are not vulnerable to young crabs that might settle from the plankton or to plant the seed after the green crabs are too large to enter mesh bags.

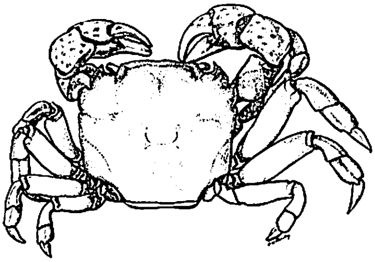
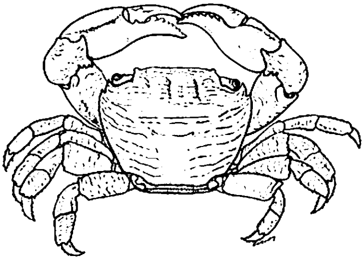
While we should carefully evaluate the feasibility and effectiveness of any potential control measure, we should also be prepared for the possibility that we will not be able to control green crab abundance. So far, green crabs have not been successfully eradicated or controlled anywhere in the world, and the new tools of biological control using parasites and egg predators are still in the exploratory phase. While we are awaiting future developments, we should identify critical habitats and species that we want to protect in the event that green crabs increase their abundance and geographic range. For example, preventing green crabs from eliminating some of the unique biota in Port Davey in southwestern Tasmania, keeping green crabs out of nature preserves such as Langebaan Lagoon in South Africa, preventing the local extinction of vulnerable prey species with direct development, and keeping green crabs out of Hood Canal, Washington, are worthy goals. These small-scale goals could be achieved if we focus our efforts.

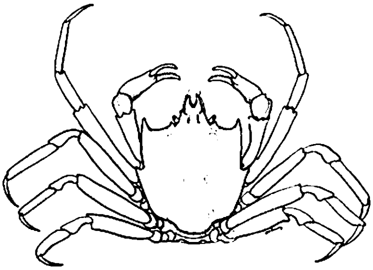
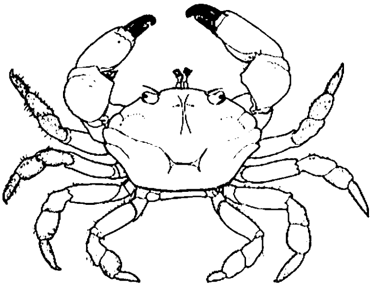
Appendix A

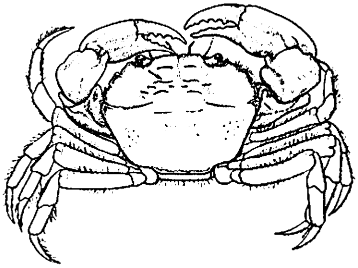
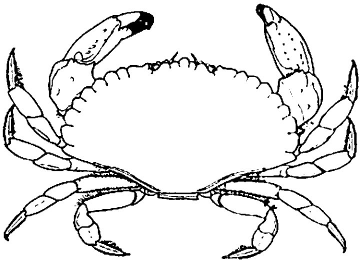
The following table lists the distinguishing characteristics of *Carcinus maenas* and other Pacific Northwest crabs. Descriptions were compiled from Morris Abbott and Haderlie 1980, Hart 1982, Rudy and Rudy 1983, and Jensen 1995.

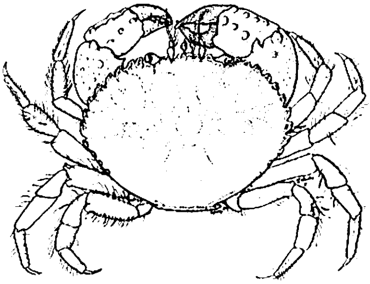
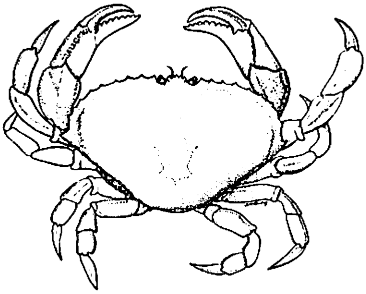
Species	Distinguishing Features	Biology
European green crab *Carcinus maenas* 	Five spines, or teeth, on each side of the fan-shaped shell (carapace). Three rounded lobes between eyes (frontal area). Last pair of legs somewhat flattened.	Mottled, dark green with yellow patches on back; underside green, orange, or red. **Size:** up to 96 mm (3.7") across the shell (carapace). Carapace broader than long. **Native Range:** Iceland and northern Norway to Mauritania. **Habitat:** intertidal and shallow subtidal of estuaries. Often associated with cordgrass *(Spartina)*, eelgrasses, and soft sediments.

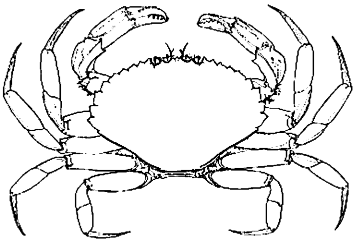
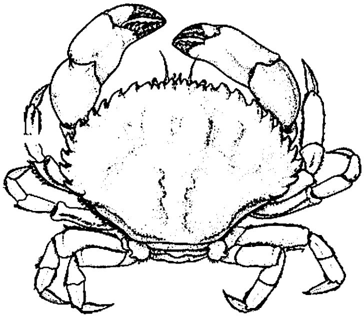
Species	Distinguishing Features	Biology
Helmet or horse crab *Telmessus cheiragonus* 	Six unequal, jagged spines on each side of carapace. Widest at fourth spine. Frontal area protrudes in front of eyes. Entire body covered with stiff, bristly hairs. Long, bristly antennae. Spiny, short front claws.	Predominantly yellow green. **Size:** up to 102 mm (4"). **Range:** Alaska to California, rare south of Puget Sound. **Habitat:** intertidal to 110 m (360'). Prefers subtidal areas on sandy or muddy tideflats, among eelgrass or algae. In early spring sometimes found among algae-covered rocks.
Hairy Oregon shore crab *Hemigrapsus oregonensis* 	Three spines on each side of rectangular carapace. Two lobes on frontal area. Hairy legs, no spots on claws.	Color varies from dull brownish green to mottled gray, grayish green, or muddy yellow. **Size:** maximum up to 49.5 mm (1.9") but typically up to 33 mm (1.3"). **Range:** Baja California to Alaska. **Habitat:** intertidal, under rocks on sheltered mud or gravel beaches; burrows into mud banks of estuaries.

Species	Distinguishing Features	Biology
Purple shore crab *Hemigrapsus nudus* 	Three spines on each side of rectangular carapace. Frontal area slightly rounded, without prominent lobes. Smooth, hairless legs. Claws with spots.	Dark purple, reddish brown, or solid olive green. **Size:** up to 56 mm (2.2") but typically up to 35 mm (1.4"). **Range:** Baja California to Alaska. **Habitat:** mid to high intertidal, under large rocks on beaches that are partly wave-exposed to protected. Found in burrows of marsh banks but not in soft muddy sediments.
Lined shore crab *Pachygrapsus crassipes* 	Two spines just behind eyes. Smooth frontal area. Broad, compressed legs with bristles. Transverse lines across carapace.	Dark green carapace, with dark red or blue transverse lines. **Size:** up to 48 mm (1.9") but typically 30 mm (1.2"). **Range:** Oregon to Gulf of California. **Habitat:** mid to high intertidal. Crevices and crannies between rocks and boulders, jetties, and also inside burrows in marsh banks.

Species	**Distinguishing Features**	**Biology**
Kelp crab *Pugettia producta* 	Surface smooth, carapace longer than wide with three spines. Last two most prominent. Widest at third spine. Frontal area composed of two small preorbital spines and prominent two-forked rostrum protruding beyond eyes. Serrated claws, slender, cylindrical walking legs.	Dark brown or olive green, sometimes red or orange, underside yellow or scarlet. **Size:** up to 93 mm (3.6"). **Range:** Alaska to Baja California. **Habitat:** intertidal to subtidal. Lives on eelgrass, kelp, and seaweed on pilings and tidepools. Does not tolerate low salinity.
Black-clawed crab *Lophopanopeus bellus* 	Smooth, oval-shaped carapace with three lobelike spines on either side. Frontal area straight. Smooth, stout claws, unequal in size with black fingers, large spine at base of movable finger. Velvetlike hairs on walking legs.	Brown, orange, violet, purple, gray, white. **Size:** up to 40.5 mm (1.6") but typically up to 30 mm (1.4"). **Range:** Alaska to California. **Habitat:** subtidal to low intertidal, in bays. Burrow in sand and mud under large rocks. Also found in kelp holdfasts.

Species	Distinguishing Features	Biology
White-fingered mud crab *Rhithropanopeus harrisi* 	Oval carapace with prominent horizontal ridges. Frontal area straight with a triangular median notch. Five lateral spines; last three point forward, last one smaller. Claws unequal in size. Fingers whiter than palm. Long, slender, hairy legs.	Dull green, white underside. **Size:** up to 19 mm (0.7"). **Range:** native to eastern North America, established in west coast estuaries. **Habitat:** brackish water sloughs, under rocks or oyster shells or in soft sediment.
Red rock crab *Cancer productus* 	Fan-shaped carapace with 10 spines becoming more acute posteriorly. Widest at ninth spine. Frontal area protrudes beyond eyes, with five spines. Large claws with black tips Tip of walking legs fringed with hairs.	Adults generally uniform brick red; juveniles are extremely variable in coloring patterns. **Size:** maximum 200 mm (7.8") but typically up to 160 mm (6.3"). Carapace much wider than long. **Range:** Alaska to Baja California. **Habitat:** midintertidal to subtidal. Most common on gently sloping gravel and boulder beaches. Does not tolerate low salinity.

Species	Distinguishing Features	Biology
Pygmy *Cancer* crab *Cancer oregonensis* 	Carapace oval with knobs and grooves. Widest at seventh or eighth spine. Frontal area with five spines. Outer spines are more prominent. Stout claws with black fingers. Hairy, light-colored walking legs.	Carapace dark red or brown above, lighter below. **Size:** up to 53 mm (2"). **Range:** Alaska to California. **Habitat:** subtidal to low intertidal, under rocks, wedged into crevices, and in kelp holdfasts.
Dungeness crab *Cancer magister* 	Broadly oval carapace with 10 spines. Last spine is very sharp. Carapace widest at 10th spine. Narrow frontal area with five unequal spines. Serrations on upper margin of claws. Lightly colored leg tips.	Generally light reddish brown, often light orange below; sometimes gray purple. **Size:** maximum 230 mm (9") or larger but generally up to about 190 mm (7.5"). **Range:** Alaska to California. **Habitat:** Low intertidal to 230 m (750 ft). Prefers mud or sand substrate, eelgrass beds. Burrows into the sediment during low tide.

Species	Distinguishing Features	Biology
Graceful crab *Cancer gracilis* 	Smooth, convex carapace, widest at ninth spine. Margins of spine are outlined in cream. Frontal area with five spines. Central spine is smaller. No serration on upper margin of white-tipped claws. Slender, purple or reddish walking legs.	Light purple or reddish-brown with cream-colored granules. **Size:** up to 115 mm (4.5"). **Range:** Alaska to Mexico. **Habitat:** Subtidal to low intertidal on high saline mudflats.
Pacific rock crab *Cancer antennarius* 	Fan-shaped carapace, widest at ninth spine. Frontal area with five spines. Central spine is smaller. Large, smooth, black-tipped claws. Red spots on claw and underside. See Appendix B, plate 17. Hairy legs.	Reddish brown. **Size:** up to 178 mm (7") but typically up to 130 mm (5.1"). **Range:** Queen Charlotte Sound, British Columbia to Baja California. **Habitat:** outer coast, subtidal to low intertidal; buried in sand under large rocks and in kelp beds.

Appendix B: Plates

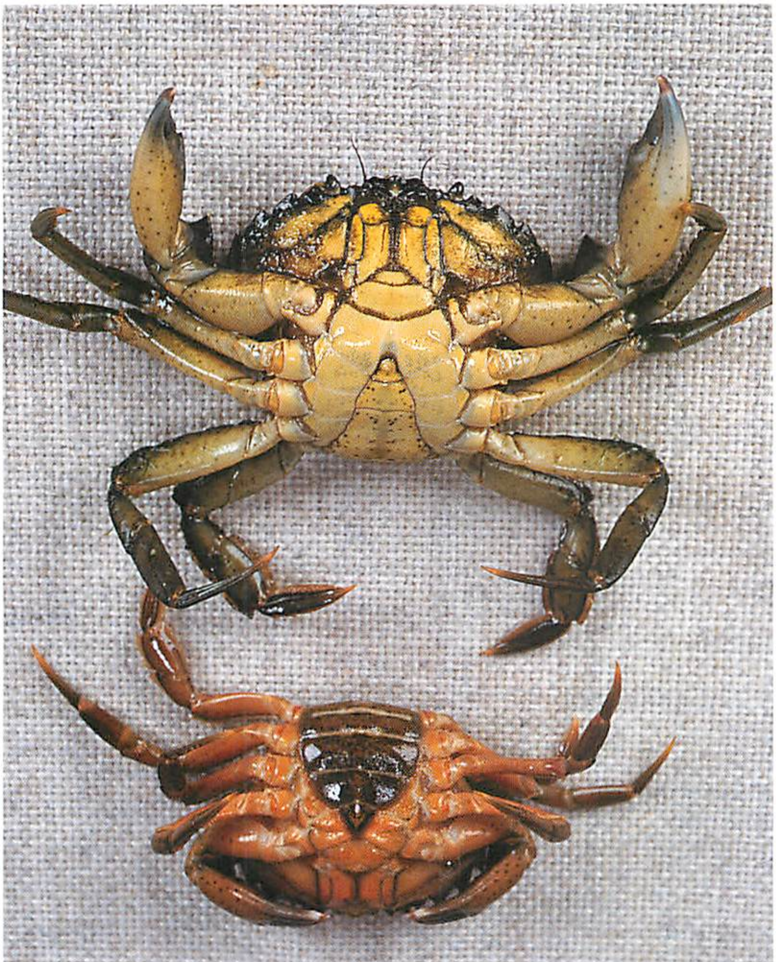


Plate 1. European green crab, *Carcinus maenas*, underside.

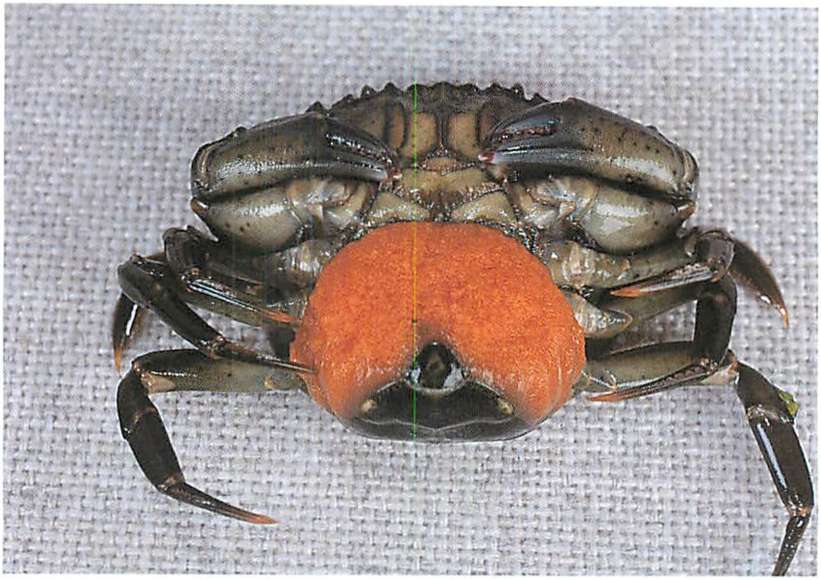


Plate 2A. European green crab, *Carcinus maenas*, female with eggs. Underside.

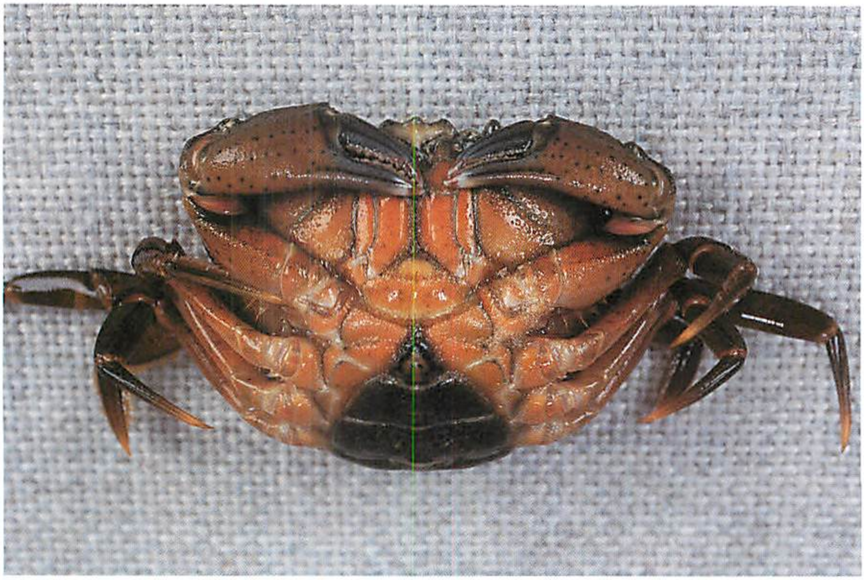


Plate 2B. European green crab, *Carcinus maenas*, female. Underside.

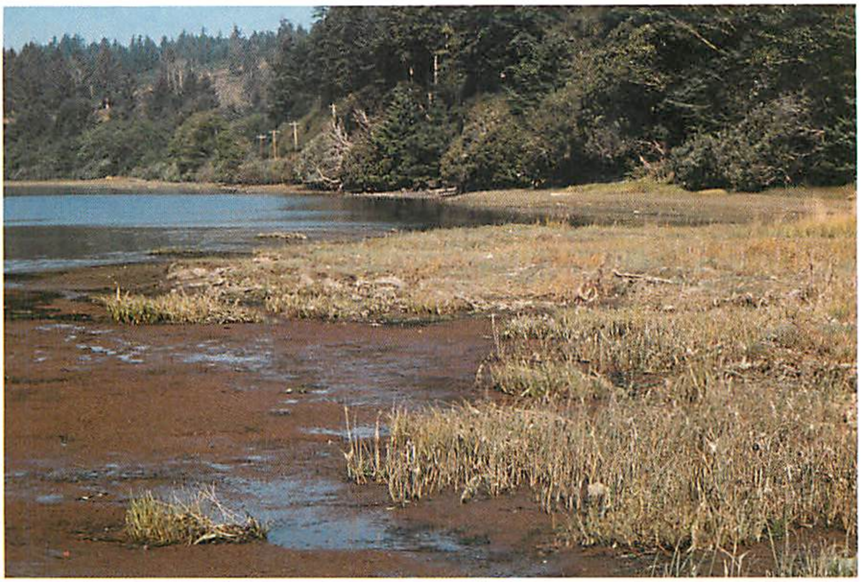


Plate 3. Typical habitat.

Plate 4. European green crab, *Carcinus maenas*.

Plate 5. Helmet crab, *Telmessus cheiragonus.*

Plate 6. Hairy Oregon shore crab, *Hemigrapsus oregonensis.*

Plate 7. Purple shore crab, *Hemigrapsus nudus.*

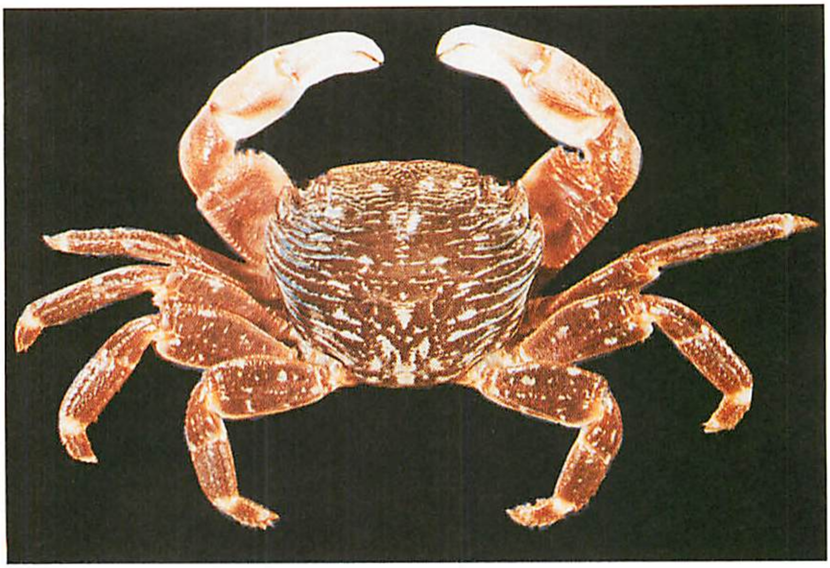


Plate 8. Lined shore crab, *Pachygrapsus crassipes.* Reprinted with permission of Stanford University Press.

Plate 9. Kelp crab, *Pugettia producta.*

Plate 10. Black-clawed crab, *Lophopanopeus bellus.*

Plate 11. White-fingered mud crab, *Rhithropanopeus harrisi*

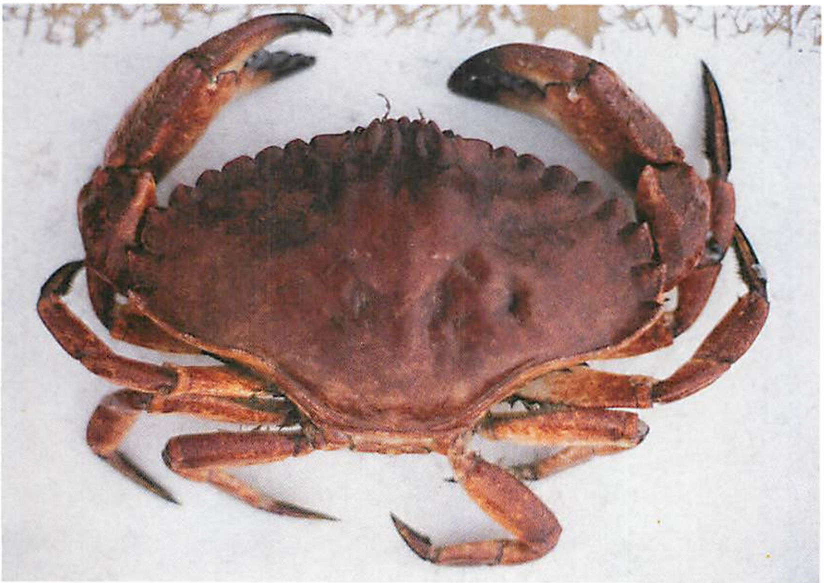


Plate 12. Red rock crab, *Cancer productus.*

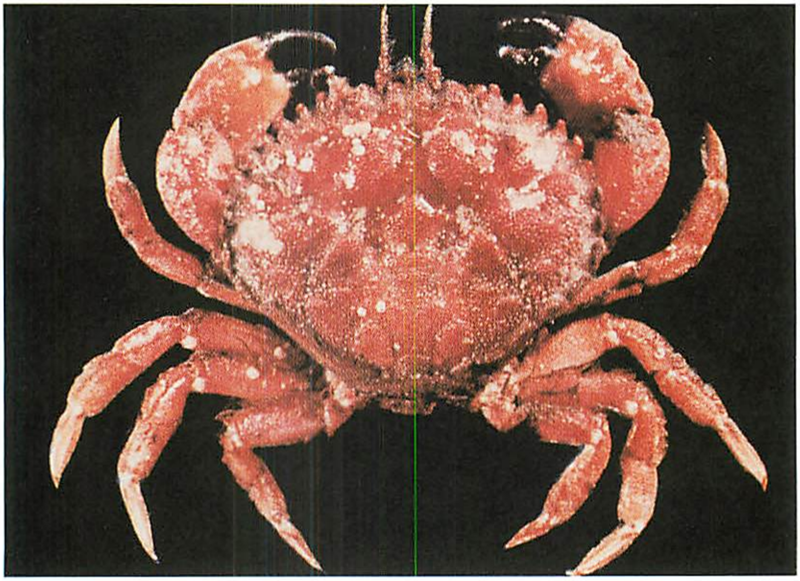


Plate 13. Pygmy *Cancer* crab, *Cancer oregonensis.* Reprinted with permission of Stanford University Press.

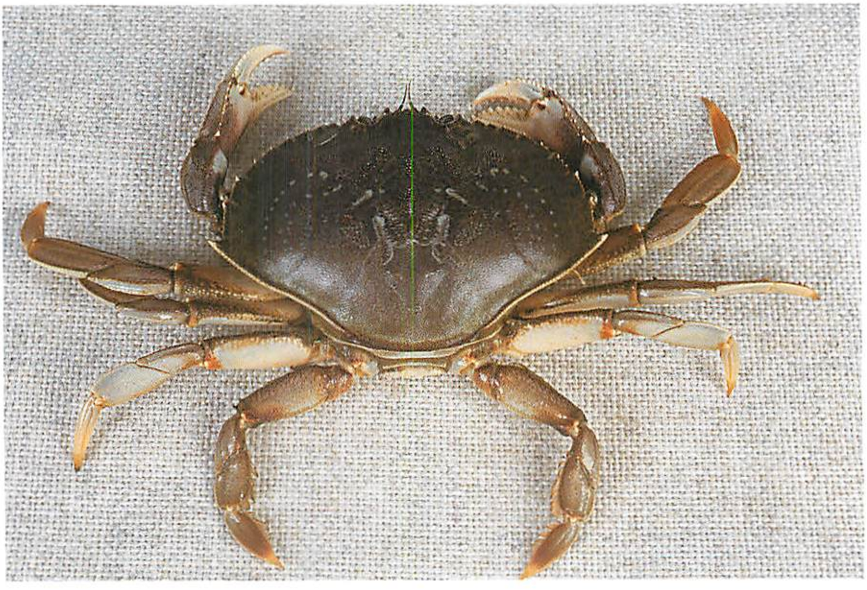


Plate 14. Dungeness crab, *Cancer magister.*

Plate 15. Graceful crab, *Cancer gracilis.*

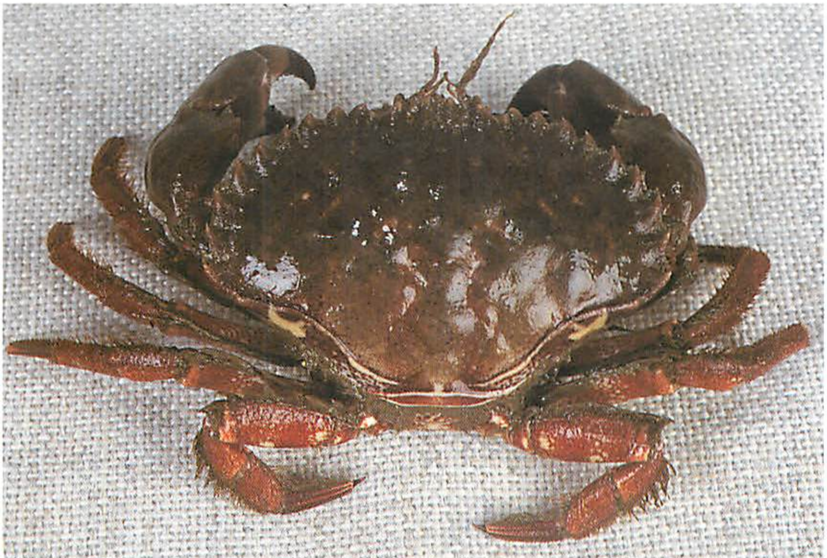


Plate 16. Pacific rock crab, *Cancer antennarius.* Top.

Plate 17. Pacific rock crab, *Cancer antennarius.* Underside.

Glossary

acanthocephalan—parasitic, spiny-headed worm that lives in the gut of its host.

amphipod—shrimplike crustacean with flat sides; includes sand fleas, beach hoppers, and skeleton shrimps.

annelid—group of segmented worms including marine worms (polychaetes), earthworms and leeches.

anterio-lateral—region of a crab's body bordered by the eyes and the widest part of the carapace.

benthic—aquatic bottom dwelling.

bivalve—mollusk bearing two (bi) shells (valves), such as clams, mussels, scallops, and oysters.

bryozoans—moss animals; small, colonial animals that sit in calcareous "houses" and capture food particles on their tentacles.

carapace—the shell of a crab covering the fused head and thorax.

chitin—tough, yet flexible polysaccharide compound found in the arthropod exoskeletons.

chromatophore—pigment cell capable of dispersing and concentrating pigment in response to stimuli.

circatidal—an event that occurs around the tidal cycle, or every 12.4 hours.

columella—central supporting axis of snail shells.

conspecific—organisms of the same species.

copepod—a small, shrimplike animal of the plankton.

copepodite—juvenile copepod.

cultchless seed—young oysters that are reared from larvae without attaching to a shell substrate. These seed oysters are typically reared in trays or racks off the sea bottom.

denticle—small, toothlike serrations on the cutting edge of crab claws.

deposit feeder—an animal that ingests substrate, such as sand or mud, along with organic material, detritus, and bacteria.

detritus (adjective: **detrital**)—particles of decomposing organic matter, often rich in bacteria.

dorsal—back of an animal.

eelgrass—marine vascular plant with long blades, roots, and flowers.

El Niño—coastwide oceanographic event during which water temperatures are higher and seasonal poleward currents are stronger than usual.

endogenous—produced from within.

foraminiferans—protozoans protected by a calcareous "skin."

gonopore—external opening of male and female reproductive systems.

hydroids—colony of small anemone-like animals arranged on branches.

infauna—animals larger than sand grains living within soft sediment; includes tube-building worms and amphipods, burrowing worms, clams, and shrimps.

infaunal—living within soft sediment.

intermolt—between molts.

intertidal—part of the shore between the low and high tide mark.

isopod—small, flat crustaceans, including pill bugs, which can roll up into a ball.

maxillae—paired anterior appendages used in feeding.

maxillipeds—appendages between the claws and maxillae.

mechanical advantage (MA) of a crab claw's lever system—defined by the ration of two length measurements of the movable finger. The shorter the movable fingers and higher the claw, the greater is the MA and the strength of the claw.

megalopa—final larval stage of crabs; makes the transition from the planktonic to the sedentary life style; can swim with pleopods or crawl with walking legs.

metacercaria—final larval stage of parasitic flukes.

mother shell—empty oyster shell to which young oysters are attached.

nauplius—free-swimming, first larval stage of many marine crustaceans, characterized by three pairs of appendages and a single eye.

nematoda—round worm, found in sediments and in guts of animals. They are pointed at both ends and characterized by thrashing movements.

nemertean—ribbon worm; a nonsegmented, highly elastic predatory worm.

neuroendocrine—hormones (bloodborne chemical messengers) secreted by the nervous system.

nicothoid copepod—family of small crustaceans, some of which feed on crab eggs.

occlusal—"cutting" surface of claws that come together when the two fingers close.

osmoregulation—the ability to control the salt concentration of body fluids.

ostracod—small crustacean resembling a clam shell with jointed appendages.

ovigerous—carrying eggs.

pheromone—airborne or waterborne chemical messenger produced by a "sender" that elicits a behavioral change in the "receiver."

phoronid—small, wormlike tube dweller with a protruding crown of tentacles used in food gathering and respiration.

phytoplankton—small plant cells drifting in the water column.

plankton—small, aquatic organisms drifting in the water column.

planktonic—living suspended in the water column.

pleopods—or "swimmerettes"—paired abdominal appendages of crustaceans used for swimming, for carrying the eggs in the female, and for copulation in the male.

polychaete—segmented marine worms related to earthworms.

protozoea—first larval stage of decapod crustaceans, followed by the zoea.

sabellid—tube-building marine worm, also called "feather duster worm" because it extends its feathery gills out of the tube to catch food particles and to respire.

sarcomeres—microscopic contractile unit of muscles, made up of sliding interdigitating protein fibers.

setae—bristlelike projections of crustacean and polychaete bodies; aid in swimming or crawling.

spermathecae—paired pouches for storing sperm inside the female reproductive tract.

subtidal—below the low tide mark and thus not exposed to air during the tidal cycle.

suture—a seamlike line between the plates of an exoskeleton that splits open in the molting process.

symbiont—organism intimately associated with another organism of a different species.

telson—or tail—last abdominal segment in crustaceans; lacks appendages.

terminal instar—the last life stage of a crab. Because it can molt no more, it will eventually die of old age.

trophic level—feeding level such as herbivore, predator, or scavenger.

tunicate—or sea squirt—common colonial or solitary fouling organisms on floats and natural hard substrates whose water-filled bodies have two openings, encased in a cellulose-like covering. Tunicates pump water through their body and strain food particles on their sticky gill slits or basket.

umbone—or beak—raised area near the hinge of bivalves that denotes the point where growth began.
valves—the paired shells of bivalves (clams, mussels, oysters, scallops).
ventral—"belly" side of an animal.
zoea—crustacean larval stage bearing big compound eyes, prominent dorsal spine, and segmented abdomen. *Carcinus maenas* goes through four zoea stages, followed by the megalopa stage.
zooplankton—small animals suspended in the water column.

References

Publications marked by an asterisk have not been seen in the original.

Aagaard, A., C.G. Warman, and M.H. Depledge. 1995. Tidal and seasonal changes in the temporal and spatial distribution of foraging *Carcinus maenas* in the weakly tidal littoral zone of Kerteminde Fjord, Denmark. *Marine Ecology Progress Series* 122:165–72.

Abby-Kalio, N.J., and G.F. Warner. 1984. Effects of two different feeding regimes on the chela closer muscles of the shore crab *Carcinus maenas* (L.). *Marine Behavior and Physiology* 11:209–18.

Abello, P., C.C. Warman, D.G. Reid, and E. Naylor. 1994. Chela loss in the shore crab *Carcinus maenas* (Crustacea: Brachyura) and its effect on mating success. *Marine Biology* 121:247–52.

Adelung, D. 1971. Untersuchungen zur Häutungsphysiologie der dekapoden Krebse am Beispiel der Strandkrabbe *Carcinus maenas*. *Helgoländer wissenschaftliche. Meeresuntersuchungen* 22:66–199.

Alexander, R.McN. 1968. *Animal mechanics*. London: Segewick and Jackson.

Almaça, C. 1962. Sur la distribution geographique du genre *Carcinus* Leach. (Crust. Dec. Brach.) Revista da Faculdade de Ciências da Universidade de Lisboa, Série 2, C. *Ciências Naturai* 10:109–13.

Ameyaw-Akumfi, C., and E. Naylor 1987. Spontaneous and induced components of salinity preference behaviour in *Carcinus maenas*. *Marine Ecology Progress Series* 37:153–58.

Ameyaw-Akumfi, C., and R.N. Hughes. 1987. Behaviour of *Carcinus maenas* feeding on large *Mytilus edulis*. How do they assess the optimum diet? *Marine Ecology Progress Series* 38:213–16.

Anger, K., E. Spivak, and T. Luppi. 1998. Effects of reduced salinities on development and bioenergetics of early larval shore crab, *Carcinus maenas*. *Journal of Experimental Marine Biology and Ecology* 220:287–304.

ap. Rheinallt, T. 1986. Size selection by the crab *Liocarinus puber* feeding on mussels *Mytilus edulis* and on shore crabs *Carcinus maenas*: the importance of mechanical factors. *Marine Ecology Progress Series* 29:45–53.

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

Atkinson, R.J.A., and A.J. Parsons. 1973. Seasonal patterns of migration and locomotion rhythmicity in populations of *Carcinus*. *Netherlands Journal of Sea Research* 7:81–93.

Atwood, H.L. 1973. An attempt to account for the diversity of crustacean muscles. *American Zoologist* 13:357–78.

Auster, P.J., and L.R. Crockett. 1984. Foraging tactics of several crustacean species for infaunal prey. *Journal of Shellfish Research* 4:139–43.

Bagley, M.J., and J.B. Geller. 2000. Microsatellite DNA analysis of native and invading populations of European green crabs. In *Marine bioinvasions: proceedings of the first national conference*, ed. Judith Pederson, 241–43. Cambridge, MA: Massachusetts Institute of Technology Sea Grant College Program.

Baker, P., N. Richmond, and N. Terwilliger. 2000. Reestablishment of a native oyster, following a natural local extinction. In *Marine bioinvasions: proceedings of the first national conference*, ed. Judith Pederson, 221–31. Cambridge, MA: Massachusetts Institute of Technology Sea Grant College Program.

Bambler, S.D., and E. Naylor. 1997. Sites of release of putative sex pheromones and sexual behaviour in female *Carcinus maenas* (Crustaces: Decapoda). *Estuarine and Shelf Science* 44:195–202.

*Bang, F.B. 1971. Transmissible disease, probably viral in origin, affecting the amebocytes of the European shore crab, *Carcinus maenas*. *Infection and Immunity* 3:617–23.

Barth, J.A., and R.L. Smith. 1998. The coastal ocean off Oregon and northern California during the 1997 El Niño, part 3: Lagrangian view. *Transactions of the American Geophysical Union* 79(45):F485.

Bassett, Z. 2000. The impact of the introduced green crab, *Caracinus maenas*, on selected bivalves and meiofaunal communities. Master's thesis, Portland State University.

Beal, B.F. 1998. Commercial impacts and management efforts in controlling green crab populations in northern New England. Presentation at Green crab: potential impacts in the Pacific Northwest, a workshop sponsored by Oregon and Washington Sea Grant, February 9–10, Vancouver, WA.

Behrens Yamada S., and C. Hunt 2000. The arrival and spread of the European green crab, *Carcinus maenas* in the Pacific Northwest. *Dreissena!* 11(2):1-7.

Behrens Yamada, S., and E.G. Boulding. 1998. Claw morphology, prey size selection and foraging efficiency in generalist and specialist shell-breaking crabs. *Journal of Experimental Marine Biology and Ecology* 220:191–211.

Behrens Yamada, S., and G. Allison. 1998. The European green crab in Oregon. For student reports, see: http://www.ucs.orst.edu/~yamadas.

Behrens Yamada, S., C. Hunt, and N. Richmond. 2000. The arrival of the European green crab, *Carcinus maenas*, in Oregon estuaries. In *Marine bioinvasions: proceedings of the first national conference*, ed. Judith Pederson, 94–99. Cambridge, MA: Massachusetts Institute of Technology Sea Grant College Program.

Behrens Yamada, S., and L. Hauck. In press. Field identification of the European green crab species: *Carcinus maenas* (L.) and *Carcinus aestuarii* (Nardo). *Journal of Shellfish Research.*

Bergham. R. 1987. Effects of tidal migration on growth of 0-group plaice (*Pleuronectes platessa* L.) in the North Frisian Wadden Sea. *Meeresforschung: Reports on Marine Research* 31(3–4):209–26.

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

Berrill, M., and M. Arsenault. 1982. Mating behavior of the green shore crab *Carcinus maenas*. *Bulletin of Marine Science* 32:632–38.

Beukema, J.J. 1991. The abundance of shore crabs *Carcinus maenas* (L.) on a tidal flat in the Wadden Sea after cold and mild winters. *Journal of Experimental Marine Biology and Ecology* 153:97–113.

*Bonami, J.R. 1976. Viruses from crustaceans and annelids: our state of knowledge. *Proceedings of the International Colloquium on Invertebrate Pathology* 1:20–23.

*Bonami, J.R., and R. Pappalardo. 1980. Rickettsial infection in marine crustacean. *Experientia* 36:180–81.

Boulding, E.G., and K. Van Alstyne. 1993. Mechanisms resulting in differential survival and growth of two species of *Littorina* on wave-exposed and on protected shores. *Journal of Experimental Marine Biology and Ecology* 169:139–66.

Brenchley, G.A. 1982. Predation on encapsulated larvae by adults: effects on introduced species on the gastropod *Ilyanassa obsoleta*. *Marine Ecology Progress Series* 9:255–62.

Brock, J.A., and D.V. Lightner. 1990. Diseases of Crustacea: diseases caused by microorganisms. In *Diseases of marine animals*, ed. O. Kinne. Vol. 3, 245–349. Hamburg: Biologische Anstalt Helgoland.

Broekhuysen, G.J. 1936. On development, growth, and distribution of *Carcinus maenas* (L.). *Archives Neerlandaises de Zoologie* 2:257–339.

Bückmann, D., and D. Adelung. 1964. Der Enfluß der Umweltfaktoren auf das Wachstum und den Häutungsrhythmus der Strandkrabbe *Carcinus maenas. Helgoländer wissenschaftliche Meeresuntersuchungen* 10:91–103.

Buhr, K-J. 1981. Auswirkungen des kalten Winters 1978/79 auf das Makrobenthos der *Lance-* Siedlung im Weser-Ästuar. Veröff. *Institut für Meeresforshung Bremerhaven* 19:1150131.

Cals, P. 1983. Diversite des capacities migratoires des larvaes de crustaces et evolution historique des oceans. *Oceanis. Serie de Documents Oceanographiques* 9 (Cycles de Vie et Biogeographie):335–87.

Cangelosi, A. 2000. Ballast water management: developments in policy and technology. In *Marine bioinvasions: proceedings of the first national conference,* ed. Judith Pederson, 273–77. Cambridge, MA: Massachusetts Institute of Technology Sea Grant College Program.

Carl, G.C., and C.J. Guiguet. 1972. *Alien animals in British Columbia.* Handbook no. 14. Victoria, B.C.: British Columbia Provincial Museum.

Carlton, J.T. 1985. Transoceanic and interoceanic dispersal of coastal marine organisms: the biology of ballast water. *Oceanography and Marine Biology Annual Review* 23:313–71.

_______. 1992. Dispersal of living organisms into aquatic ecosystems as mediated by aquaculture and fisheries activities. In *Dispersal of living organisms into aquatic ecosystems,* ed. A. Rosenfield and R. Mann, 13–46. College Park, MD: Maryland Sea Grant College.

_______. 2000. *Quo Vadimus Exotica Oceanica?* Marine bioinvasion ecology in the twenty-first century. In *Marine bioinvasions: proceedings of the first national conference,* ed. Judith Pederson, 6–23. Cambridge, MA: Massachusetts Institute of Technology Sea Grant College Program.

Carlton, J.T., and A.N. Cohen. 1998. Perwinkle's progress: the Atlantic snail *Littorina saxatilis* (Mollusca: Gastropoda) established a colony on a Pacific shore. *Veliger* 41(4):333–38.

Carlton, J.T., and J.B. Gelller. 1993. Ecological roulette: the global transport of nonindigenous marine organisms. *Science* 261:78–82.

Childers, R.K., P.W. Reno, and R.E. Olson. 1996. Prevalence and geographic range *of Nadelspora canceri* (Microspora) in Dungeness crab *Cancer magister. Diseases of Aquatic Organisms* 24:135–42.

Ching, H.L. 1965. Systematic notes on some North American Microphallid trematodes. *Proceedings of the Helminthological Society of Washington* 32:140–48.

_______. 1989. *Profilicollis botulus* (Van Cleave, 1916) from diving ducks and shore crabs of British Columbia. *Journal of Parasitology* 75:33–37.

_______. 1991. List of larval worms from marine invertebrates of the Pacific coast of North America. *Journal of the Helminthological Society of Washington* 58:57–68.

Christiansen, M.E. 1969. Crustacea Decopoda Brachyura. *Marine invertebrates of Scandinavia.* Oslo: Universitetsforlage.

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. *Journal of Crustacean Biology* 21(1):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.* Groton, CT: Connecticut Sea Grant.

_______. 1998. Accelerating invasion rate in a highly invaded estuary. *Science* 279:555–58.

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. *Marine Biology* 122:225–37.

CRIMP. 2000a. Marine pest information sheets: European shore crab (*Carcinus maenas*). http://www.marine.csiro.au/CRIMP/Marine%20pest%20infosheets.html

_______. 2000b Marine biological invasions of Port Phillip Bay, Victoria. Executive summary. http://www.marine.csiro.au/CRIMP/ppbesum.html

Crisp, D.J. 1964. Mortalities in marine life in North Wales during the winter of 1962–63. In *The effect of the severe winter of 1962–63 on marine life in Britain*, ed. D.J. Crisp, 190–97. *Journal of Animal Ecology* 33.

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

_______. 1968. The biology of the shore crab *Carcinus maenas* (L). 2. The life of the adult crab. *Field Studies* 2:597–614.

_______. 1970. The distribution of crabs on rocky shores around the Dale Peninsula. *Field Studies* 3:263–74.

Culver, C.S., and A.M. Kuris. 2000. The apparent eradication of a locally established introduced marine pest. *Biological Invasions* 2(3):245–53.

Cunningham, P.N., and R.N. Hughes. 1984. Learning of predaceous skills by shorecrabs *Carcinus maenas* feeding on mussels and dogwhelks. *Marine Ecology Progress Series* 16:21–26.

Currey, J.D., and R.N. Hughes. 1982. The strength of the dogwhelk *Nucella lapillus* and the winkle *Littorina littorea* from different habitats. *Journal of Animal Ecology* 51:47–56.

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. *Cahiers de Biologie Marine* 35:1–13.

Dare, P.J., and D.B. Edwards. 1976. Experiments on the survival, growth and yield of relaid seed mussels (*Mytilus edulis* L.) in the Menai Strait, North

Wales. *Journal Du Conseil International pour l' Exploration de la Mer* 37:16–28.

Dare, P.J., G. Davies, and E.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, U.K., Fisheries Research Technical Report No. 73.

Data on average monthly anomalies of sea level from 1975–2000. 2000. ftp://ilikai.soest.hawaii.edu/islp/islpp.anomalies

Davis, R.C., F.T. Short, and D.M. Burdick. 1998. Quantifying the effect of green crab damage to eelgrass transplants. *Restoration Ecology* 6:297–302.

Dawirs, R.R. 1985. Temperature and larval development of *Carcinus maenas* (Decopoda) in the laboratory, predictions of larval dynamics in the sea. *Marine Ecology Progress Series* 24:297–302.

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. *Journal of Marine Biology and Ecology* 100:47–74.

Demeusy, N., and M.A. Veillet. 1953. Sur l'existence de deux populations de *Carcinus maenas* Pennant et sur les charactères morphologiques qui les distinguent. *Comptes Rendus Hebdomadaires Des Séances De L' Academie Des Sciences* 236:1088–90.

Dernedde, T. 1993. Vergleichende Untersuchungen zur Nahrungszusammensetzung von Silbermöve (*Larus argentatus*), Sturmmöve *(L. canus)* ·und Lachmöve (*L. ridibundus*) im Königshafen/Sylt. *Corax* 15:222–40.

Dries, M., and D. Adelung. 1982. Die Schlei, ein Modell für die Verbreitung der Strandkrabbe *Carcinus maenas. Helgoländer Meeresuntersuchungen* 35:65–77.

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). *Journal of Experimental Marine Biology and Ecology* 169:89–101.

Dumbauld, B.R., E.P. Visser, D.A. Armstrong, L. Cole-Warner, K.L. Feldman, and B.E. Kauffman. 2000. Use of oyster shell to create habitat for juvenile Dungeness crab in Washington coastal estuaries: status and prospects. *Journal of Shellfish Research* 19(1):379–86.

Dunstone, N., and J.D.S. Birks. 1987. The feeding of mink (*Mustela vision*) in coastal habitats. *Journal of Zoology* 212:69–83.

*Elner, R.W. 1977. The predatory behaviour of the shore crab *Carcinus maenas* (L.). Ph.D. diss., University College of North Wales, Bangor, Wales.

_______. 1978. The mechanics of predation by the shore crab, *Carcinus maenas* (L) on the edible mussel, *Mytilus edulis* (L). *Oecologia* 36:333–44.

_______. 1981. Diet of green crab *Carcinus maenas* (L.) from Port Herbert, southwestern Nova Scotia. *Journal of Shellfish Research* 1(1):89–94.

Elner, R.W., and D.G. Raffaelli. 1980. Interactions between two marine snails, *Littorina rudis* Maton and *Littorina nigrolineata* Gray, a predator, *Carcinus maenas* (L.), and a parasite, *Microphallus similis* Jägerskiold. *Journal of Experimental Marine Biology and Ecology* 43:151–60.

Elner, R.W., and R.N. Hughes. 1978. Energy maximization in the diet of the shore crab, *Carcinus maenas*. *Journal of Animal Ecology* 47:103–16.

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. *Journal of Experimental Marine Biology and Ecology* 30:233–48.

Eriksson, S., S. Evans, and B. Tallmark. 1975. On the coexistence of scavengers on shallow sandy bottoms in Gullmar Fjord (Sweden). *Zoon* 3:65–70.

Factor, J.R., and B.L. Dexter. 1993. Suspension feeding in larval crabs (*Carcinus maenas*). *Journal of the Biological Association of the United Kingdom* 73:207–11.

Figlar-Barnes, R., B. Dumbauld, and A. Randall. 2001. Monitoring and control of European green crab (*Carcinus maenas*) populations in the coastal estuaries of Washington State 1998–2000. Progress Report, Washington Department of Fish and Wildlife.

Finger, J. 1998. Concerns for the molluscan shellfish industry. Abstract of talk presented at the Oregon/Washington Sea Grant Workshop: The exotic green crab. February 9–10, 1998, Vancouver, Washington.

First impressions count: males behaving badly. 1998. *Marine Biological Association News* 20:1.

Food and Agriculture Organization (FAO). 1999. *Yearbook, fishery statistics, capture production for the year 1997.* Rome: Food and Agricultural Organization of the United Nations. Vol. 86.

Fulton, S.W., and F.E. Grant. 1900. Note on the occurrence of the European green crab, *Carcinus maenas* Leach, in Port Phillip. *Victorian Naturalist* 17:147–48.

Furota, T., S. Watanabe, T. Watanabe, S. Akiyama, and K. Kinashita. 1999. Life history of the Mediterranean green crab, *Carcinus aestuarii* Nardo, in Tokyo Bay, Japan. *Crustacean Research* 28:5–15.

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. *Estuarine, Coastal and Shelf Science* 21:429–48.

Geller, J.M, W.C. Walton, E.D. Grosholz, and G.M. Ruiz. 1997. Cryptic invasions of the crab *Carcinus* detected by molecular phylogeography. *Molecular Ecology* 6:901–6.

Geller, J.M., and M.J. Bagley. 1997. Genetic and systematic studies of *Carcinus maenas*. In *Proceedings of the first international workshop on the demography, impact and management of introduced populations of the European crab* Carcinus maenas, ed. R. Thresher. Center for Research on Introduced Marine Pests.

CSIRO Marine Laboratory, Hobart, Tasmania. Technical Report 11:19–20.

Gilbert, W., and B. Wyatt. 1969. *Surface temperature and salinity observations at Pacific Northwest shore station for 1968.* Data Report No. 37 for Office of Naval Research. Corvallis: School of Oceanography, Oregon State University.

Gillis, D.J., J.N. Mac Pherson, and T.T. Rattray. 2000. *The status of the green crab* (Carcinus maenas) *in Prince Edward Island in 1999.* Technical Report 225. Charlottetown, Prince Edward Island: Prince Edward Island Department of Fisheries and Tourism, Fisheries and Aquaculture Division.

Glenner, H., and M. Werner. 1998. Increased susceptibility of recently moulted *Carcinus maenas* (L.) to attack by the parasitic barnacle *Sacculina carcini* Thompson 1836. *Journal of Experimental Marine Biology and Ecology* 118:29–33.

Glude, J.B. 1955. The effect of temperature and predators on the abundance of the soft-shell clam, *Mya arenaria*, in New England. *Transactions of the American Fishery Society* 84:13–26.

Gomes, V. 1991. First results of tagging experiments on crab *Carcinus maenas* (L.) in the Ria de Aveiro Lagoon, Portugal. *Ciência Biológica Ecology and Systematics* (Portugal) 11(1/2):21–29.

Griffiths, C.L., P.A.R. Hockey, C. van Erkom Schurink, and P.J. Le Roux. 1992. Marine invasive aliens on south African shores: implications for community structure and trophic function. *South African Journal of Marine Science* 12:713–22.

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

_______. 1996. Predicting the impact of introduced marine species: lessons from the multiple invasions of the European green crab. *Biological Conservation* 78:59–66.

Grosholz, E.D., G.M. Ruiz, C.A. Dean, K.A. Shirley, J.L. Maron, and P.G. Connors. 2000. The implications of a nonindigenous marine predator in a California bay. *Ecology* 81:1206–24.

Gross Custard, J.D., R.E. Jones, and P.E. Newbery. 1977. The ecology of the Wash. I. Distribution and diet of wading birds (Charadrii). *Journal of Applied Ecology* 14: 681–700.

Gunderson, D.R., D.A. Armstrong, Y-B. Shi, and R.A. McConnaughey. 1990. Patterns of estuarine use by juvenile English sole (*Parophrys vetulus*) and Dungeness Crab (*Cancer magister*). *Estuaries* 13:59–71.

Günter, C.-P. 1996. Development of small *Mytilus* beds and its effect on resident intertidal macrofauna. *Marine Ecology* 17:117–30.

Hadlock, R.P. 1980. Alarm response of the intertidal snail *Littorina littorea* (L.) to predation by the crab *Carcinus maenas* (L.). *Biological Bulletin* 159:269–79.

Hanks, R.W. 1961. Chemical control of the green crab, *Carcinus maenas* (L.). *Proceedings of the National Shellfisheries Association* 52:75–84.

Hart, J.F.L. 1982. *Crabs and their relatives of British Columbia.* British Columbia Provincial Museum Handbook, no. 40. Victoria, B.C.: Ministry of Provincial Secretary and Government Services.

Harvell, C.D. 1990. The ecology and evolution of inducible defenses. *Quarterly Review of Biology* 65:323–40.

Hauck, L. 2000. Use of tethered prey for estimating the impact of the invasive European green crab. Senior thesis, Oregon State University.

Hauck, L., S. Behrens Yamada, and S. Mahaffy. 2000. Where does the green crab fit into the hierarchy of native crab predators? Abstract in *Journal of Shellfish Research.*

Hedvall, O., P.-O. Moksnes, and L. Pihl. 1998. Active habitat selection by megalopae and juvenile shore crabs *Carcinus maenas:* a laboratory study in an annular flume. *Hydrobiologia* 375/376:89–100.

Hoeg, J., M. Werner, and H. Glenner. 1997. The parasitic *Sacculina carcini* as a possible biological control agent of *Carcinus maenas:* background and results of preliminary work. In *Proceedings of the first international workshop on the demography, impacts and management of introduced populations of the European green crab,* Carcinus maenas, ed. R. Thresher. CRIMP Technical Report. Hobart, Tasmania: Centre for Research on Introduced Marine Pests, CSIRO.

Hopkins, T.S. 1985. Physics of the Sea. In *Western Mediterranean*, ed. R. Margalef. Oxford: Pergamon Press.

Hughes, R.N., and R.W. Elner. 1979. Tactics of a predator, *Carcinus maenas*, and morphological responses of the prey, *Nucella lapillus. Journal of Animal Ecology* 48:65–78.

Hughes, R.N., and R. Seed. 1995. Behavioural mechanisms of prey selection in crabs. *Journal of Experimental Marine Biology and Ecology* 193:225–38.

Hunt, C. 2000. Potential limitations of the European green crab, *Carcinus maenas*, in habitat suitable for the native red rock crab, *Cancer productus.* Abstract in *Journals of Shellfish Research* 9(1) 686–87.

_______. 2001. The role of predation by the red rock crab, *Cancer productus*, on the invasive European green crab, *Carcinus Maenas*, in Yaquina Bay, Oregon. Master's thesis, Oregon State University.

Huyer, A., J.A. Barth, J. Fleischbein, P.M. Kosro, and R.L. Smith. 1998. The coastal ocean off Oregon and northern California during the 1997/1998 El Niño, part 1: temperature, salinity and geostropic velocity fields. *Transactions of the American Geophysical Union* 79(45):F485.

Isaksson, I., L. Pihl, and J. van Montfrans. 1994. Eutrophication-related changes in macrovegetation and foraging of young cod (*Gadus marhua* L.): a mesocosm experiment. *Journal of Experimental Marine Biolgoy and Ecology* 177:203–17.

Ison, T. 1998. Using artificial cover as a sampling method of shore crab density. http://osu.orst.edu/~yamadas/crab/ch6.htm

Jamieson, G.S., E.D. Grosholz, D.A. Armstrong, and R.W. Elner. 1998. Potential ecological implications for the introduction of the European green crab, *Carcinus maenas* (Linneaus), to British Columbia, Canada, and Washington, USA. *Journal of Natural History* 32:1587–98.

Janke, K. 1990. Biological interactions and their role in community structure in the rocky intertidal of Helgoland (German Bight, North Sea). *Helgoländer Meeresuntersuchungen* 44:219–63.

Jensen, G.C. 1995. *Pacific coast crabs and shrimps.* Monterey, CA: Sea Challengers.

Jensen, G.C., P.S. McDonald, and D.A. Armstrong. 2000. East meets west: competitive interactions between green crab, *Carcinus maenas* and *Hemigrapsus* spp. Abstract in *Journal of Shellfish Research* 19 (1):632.

Jensen, K.T., and J.N. Jensen. 1985. The importance of some epibenthic predators on the density of juvenile benthic macrofauna in the Danish Wadden Sea. *Journal of Experimental Marine Biology and Ecology* 89:157–74.

Johannesson, B. 1986. Shell morphology of *Littorina saxatilis* Olivi: the relative importance of physical factors and predation. *Journal of Experimental Marine Biology and Ecology* 102:183–95.

Johnson, M.W. 1957. The copepod *Choniophaera cancrorum* parasitizing a new host, the green crab *Carcinus maenas*. *Journal of Parasitology* 43:470–73.

Juanes, F. 1992. Why do decapod crustaceans prefer small-sized molluscan prey? *Marine Ecology Progress Series* 87:239–49.

Juanes, F., and E.B. Hartwick. 1990. Prey size selection in Dungeness crabs: the effect of claw damage. *Ecology* 77:744–758.

Jubb, C.A., R.N. Hughes, and T. ap Rheinallt. 1983. Behavioural mechanisms of size selection by crabs, *Carcinus maenas* (L.) feeding on mussels, *Mytilus edulis* (L.). *Journal of Experimental Marine Biology and Ecology* 66:81–87.

Kaiser, M.J., R.N. Hughes, and D.G. Reid. 1990. Chelal morphometry, prey-size selection and aggressive competition in green and red forms of *Carcinus maenas* (L.). *Journal of Experimental Marine Biology and Ecology* 140:121–34.

Kitching, J.A., J.F. Sloane, and F.J. Ebling. 1959. The ecology of Louch Ine. VIII. Mussels and their predators. *Journal of Animal Ecology* 28:331–41.

Klein Breteler, W.C.M. 1975a. Growth and moulting of juvenile shore crabs, *Carcinus maenas* in a natural population. *Netherlands Journal of Sea Research* 9:86–99.

_______. 1975b. Laboratory experiments on the influence of environmental factors on the frequency of moulting and the increase in size at moulting of juvenile shore crabs, *Carcinus maenas*. *Netherlands Journal of Sea Research* 9:100–20.

_______. 1975c. Food consumption, growth and energy metabolism of juvenile shore crabs, *Carcinus maenas. Netherlands Journal of Sea Research* 9:255–72.

_______. 1976. Settlement, growth and production of the shore crab, *Carcinus maenas*, on tidal flats in the Dutch Wadden Sea. *Netherlands Journal of Sea Research* 10(3):354–76.

_______. 1983. The shore crab *Carcinus maenas*. In *Ecology of the Wadden Sea*, ed. J.W. Wolff. Rotterdam: A.A. Balkema 1:119–21.

Kumulu, M., and D.A. Jones. 1997. Digestive protease activity in planktonic crustaceans feeding at different trophic levels. *Journal of the Biological Association of the United Kingdom* 77:159–65.

Kuris, A.M. 1975. Biology of decapod crustacea. In *Light's manual: intertidal invertebrates of the central California coast.* 3rd ed. Ed. by R.I. Smith and J.T. Carlton, 378–84. Berkeley: University of California Press.

_______. 1991. A review of patterns and causes of crustacean brood mortality. *Crustacean Issues* 7:117–41.

Lafferty, K., and A. Kuris. 1996. Biological control of marine pests. *Ecology* 77:1989–2000.

Lake, N.C.H., M.B. Jones, and J.D. Paul. 1987. Crab predation on scallop *(Pecten maximus)* and its implication for scallop cultivation. *Journal of the Marine Biological Association of the U.K.* 67:55–64.

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). *Investigacion Pesquera* 51:431–42.

Le Roux, P.J., B.M. Branch, and P.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. *South African Journal of Marine Science* 9:85–93.

Legeay, A., and J.-C. Massabuau. 2000. The ability to feed in hypoxia follows a seasonally dependent pattern in shore crab, *Carcinus maenas. Journal of Experimental Marine Biology and Ecology* 247:113–29.

Leonard, G.H., P.J. Ewanchuk, and M.D. Bertness. 1999a. How recruitment, intraspecific interactions, and predation control species borders in a tidal estuary. *Oecologia* 118:492–502.

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

Lohrer, A.W. 2000. Mechanisms and consequences of an exotic crab species invasion. Ph.D. diss., University of Connecticut.

Luetzen, J. 1981. Field studies on regeneration in *Sacculina carcini* Thompson (Crustacea: Rhizocephala) in the Isefjord, Denmark. *Journal of Experimental Marine Biology and Ecology* 53:241–239.

Lutz, P.E. 1985. *Invertebrate zoology*. Reading, MA: Addison-Wesley Publishing Company.

McDonald, P.S., G.C. Jensen, and D.A. Armstrong. 1998. Green crabs and native predators: possible limitations on the west coast invasion. Abstract in *Journal of Shellfish Research* 17:1283.

_______. 2001. The competitive and predatory impacts of the nonindigenous crab *Carcinus maenas* (L) on early benthic phase Dungeness crab *Cancer magister* Dana. *Journal of Experimental Marine Biology and Ecology* 258(1):39–54.

McGaw, I.J., and E. Naylor 1992. The effect of shelter on salinity preference behaviour of the shore crab *Carcinus maenas. Marine Behavior and Physiology* 21:145–52.

MacGinitie, G.E., and N. MacGinitie. 1968. *Natural history of marine animals*. Second Edition. New York: McGraw-Hill.

MacKinnon, C. 1997. Preliminary evaluation of impacts of *Carcinus maenas* on bivalve populations in Tasmania. *Proceedings of the first international workshop on the demography, impacts and management of introduced populations of the European crab*, Carcinus maenas. Centre for Research on Introduced Marine Pests, Technical Report 11.

MacPhail, J.S., E.I. Lord, and L.M. Dickie. 1955. The green crab—a new clam enemy. Fisheries Research Board of Canada, Progress Report of the Atlantic Biological Station 63:3–11.

*Mari, J., and J.R. Bonami. 1986. Les infections virales du crabe *Carcinus mediterraneus* Czerniavski, 1884. In *Pathology in marine aquaculture (pathologie en aquaculture marine)*, ed. C.P. Vivars, J.R. Bonami, and E. Jaspers, 283–93. Special publication no. 9. Bredene, Belgium: European Aquaculture Society.

*_______. 1988. PC84, a parvo-like virus from the crab, *Carcinus mediterraneus*: pathological aspects, ultrastructure of the agent, and first biochemical characterization. *Journal of Invertebrate Pathology* 51:145–56.

Mathieson, S., and A.J. Berry. 1997. Spatial, temporal and tidal variation in crab populations in the Forth Estuary, Scotland. *Journal of the Biological Association of the U.K.* 77:167–83.

Menge, B.A. 1983. Components of predation intensity in the low zone of New England rocky intertidal region. *Oecologia* (Berlin) 58:141–55.

Miller, T.W. 1996. First record of the green crab, *Carcinus maenas* in Humboldt Bay, California. *California Fish and Game* 82(2):93–96.

Mohamedeen, H., and R.G. Hartnoll. 1989. Larval and postlarval growth of individually reared specimens of the common shore crab *Carcinus maenas* (L.). *Journal of Experimental Marine Biology and Ecology* 134:1–24.

Moksnes, P-O., L. Pihl, and J. van Montfrancs. 1998. Predation on postlarvae and juveniles of the shore crab *Carcinus maenas*: importance of shelter, size and cannibalism. *Marine Ecology Progress Series* 166:211–25.

Moksnes, P-O. 1999. Recruitment regulation in juvenile shore crabs *Carcinus maenas*: importance of intraspecific interactions in space limited refuge habitats. Doctoral dissertation, Göteborg University.

Moreira, F. 1999. On the use by birds of intertidal areas of the Tagus estuary: implications for management. *Aquatic Ecology* 33:301–309.

Morris, R.H., D.P. Abbott, and E.C. Haderlie. 1980. *Intertidal invertebrates of California*. Stanford, California: Stanford University Press.

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

Muntz, L., F.J. Ebling, and J.A. Kitching. 1965. The ecology of Lough Ine XIV. Predatory activity of large crabs. *Journal of Animal Ecology* 34:315–29.

Myers, J.H., D. Simberloff, A.M. Kuris, and J.R. Carey. 2000. Eradication revisited: dealing with exotic species. *Trends in Ecology and Evolution* 15 (8):316–20.

Nagabhushanam, A.K. 1964. On the biology of the whiting, *Cadus merlangus*, in Manx waters. *Journal of the Marine Biological Association of the U.K.* 44:177–202.

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

Palacios, K.C., and S.P. Ferraro. 2001. Food preference of the introduced green crab, *Carcinus maenas*, for the native Yaquina oyster, *Ostrea lurida*, compared to other local bivalves. Report prepared for the National Network for Environmental Management Studies. Abstract in *Journal of Shellfish Research* 19 (1):633.

*Pappalardo, R., J. Mari, and J.R. Bonami. 1986. Tau virus infection of *Carcinus mediterraneus:* histology, cytology and experimental transmission of the disease. *Journal of Invertebrate Pathology* 47(3): 361–68.

*Pappalardo, R., and N. Boemare. 1982. An intracellular *Streptococcus*, causative agent of a slowly developing disease in the Mediterranean crab, *Carcinus mediterraneus*. *Aquaculture* 28:283–92.

Payen, G.G., M. Hubert, Y. Turquier, C. Rubiliani, and C. Chassard-Bouchaud. 1981. Infestations expérimentales de crabes juvéniles par la sacculine. Ultrastructure des racines parasitaires en croissance et relations avec la masse ganglionnaire ventrale de l'hôte. *Canadian Journal of Zoology* 59:1818–826.

Pihl, L., and R. Rosenberg. 1982. Production, abundance, and biomass of mobile epibenthic marine fauna in shallow waters, western Sweden. *Journal of Experimental Marine Biology and Ecology* 57:273–301.

_______. 1984. Food selection and consumption of the shrimp *Crangon crangon* in some shallow marine areas in western Sweden. *Marine Ecology Progress Series* 15:159–68.

Powell, B.L. 1962. The response of the chromatophores of *Carcinus maenas* (L.1758) to light and temperature. *Crustaceana* 4:93–102.

Preston, S.J., I.C. Revie, J.F. Orr, and D. Roberts. 1996. A comparison of the strength of gastropod shells with forces generated by potential crab predators. *Journal of Zoology* 238(1):181–193.

Proctor, C. 1997a. Spatial correlations between *Carcinus maenas* and abundance and elements of the Tasmanian marine benthic community. *Proceedings of the first international workshop on the demography, impacts and management of introduced populations of the European crab,* Carcinus maenas. Technical Report 11. Hobart, Tasmania: Centre for Research on Introduced Marine Pests.

_______. 1997b. Possible Impacts of *Carcinus maenas* on Tasmanian mariculture and fisheries. *Proceedings of the first international workshop on the demography, impacts and management of introduced populations of the European crab,* Carcinus maenas. Technical Report 11. Hobart, Tasmania: Centre for Research on Introduced Marine Pests.

Proctor, C., and R. Thresher. 1997. The invasive history, distribution and abundance of *C. maenas* in Australia. *Proceedings of the first international workshop on the demography, impacts and management of introduced populations of the European crab,* Carcinus maenas. Technical Report 11. Hobart, Tasmania: Centre for Research on Introduced Marine Pests.

PSMFC. 1998 *Annual reports of the Pacific States Marine Fisheries Commission.* http://www.psmfc.org/ann_rpt/index.html http://www.psmfc.org/ann_rpt/1998/Section3.html

_______. 2000. Report 307. Pacific States Marine Fisheries Commission. http://www.psmfc.org/pacfin/data/r307.woc99

Queiroga, H., J.D. Costlow, and M.A. Moreira. 1994. Larval abundance patterns of *Carcinus maenas* (Decapoda, Brachyura) in Canal de Mira (Ria de Aveiro, Portugal). *Marine Ecology Progress Series* 111:63–72.

_______. 1997. Vertical migration of the crab *Carcinus maenas* first zoea in an estuary: implications for tidal stream transport. *Marine Ecology Progress Series* 149:121–32.

Rangeley, R.W., and M.L.H. Thomas. 1987. Predatory behaviour of juvenile shore crab *Carcinus maenas* (L.). *Journal of Experimental Marine Biology and Ecology* 108:191–97.

Rasmussen, E. 1973. Systematics and ecology of the Isefjord marine fauna (Denmark) with a survey of the eelgrass (*Zostera*) vegetation and its communities. *Ophelia* 11:1–507.

Reise, K. 1977. Predator exclusion experiments in an intertidal mud flat. *Helgoländer wissenschaftliche Meeresuntersuchungen* 30:263–71.

_______. 1978. Experiments on epibenthic predation in the Wadden Sea. *Helgoländer wissenschaftliche Meeresuntersuchungen* 31:55–101.

Reise, K., and A. Schubert. 1987. Macrobenthic turnover in the subtidal Wadden Sea: the Norderaue revisited after 60 years. *Helgoländer wissenschaftliche Meeresuntersuchungen* 41:69–82.

Rice, A.L., and R.W. Ingle. 1975. The larval development of *Carcinus maenas* (L) and *C. mediterraneus* Czerniavsky (Crustacea, Brachyura, Portunidae) reared in the laboratory. *Bulletin of the British Museum of Natural History* (Zoology) 28(3):103–19.

Richards, M.G., M. Huxham, and A. Bryant. 1999. Predation: a causal mechanism for variability in intertidal bivalve populations. *Journal of Experimental Marine Biology and Ecology* 241:159–77.

Richardson, C., R. Seed, E. Al-Roumaihi, and L. McDonald. 1993. Distribution, shell growth and predation of the New Zealand oyster, *Tiostrea (=Ostrea) lutaria* Hutton, in the Menai Strait, North Wales. *Journal of Shellfish Research* 12:207–14.

Rodriguez, L.1997. Effect of *Carcinus maenas* on the mud whelk *Batillaria australis. Proceedings of the first international workshop on the demography, impacts and management of introduced populations of the European crab,* Carcinus maenas. Technical Report 11. Hobart, Tasmania: Centre for Research on Introduced Marine Pests.

Ropes, J.W. 1968. The feeding habits of the green crab, *Carcinus maenas* (L). *Fishery Bulletin* 67(2):183–203.

_______. 1988. The food habits of five crab species at Pettaquamscutt River, Rhode Island. *Fishery Bulletin* 87:197–204.

Rubiliani, C., M. Rubiliani Durozoi, and G.G. Payen. 1980. Effects de la sacculine sur les gonades, les glandes androgenes et le systeme nerveux central des crabes *Carcinus maenas* (L.) et *C. mediterraneaus* Czerniavsky. *Bulletin De La Société Zoologogiques De France* 105:95–100.

Rudy, P., and L.H. Rudy. 1983. *Oregon estuarine invertebrates: an illustrated guide to the common and important invertebrate animals.* Fish and Wildlife Service, U.S. Department of the Interior.

Ruiz, G.M., and L. Rodriguez. 1997. Preliminary evaluation and prediction of impacts of *Carcinus maenas* on native crabs in Tasmania. *Proceedings of the first international workshop on the demography, impacts and management of introduced populations of the European crab,* Carcinus maenas. Technical Report 11. Hobart, Tasmania: Centre for Research on Introduced Marine Pests.

Sanchez-Salazar, M.E., C.L. Griffiths, and R. Seed. 1987a. The effect of size and temperature on the predation of cockles *Cerastoderma edule* (L.) by the shore crab *Carcinus maenas* (L.). *Journal of Experimental Marine Biology and Ecology* 111:181–93.

_______. 1987b. The interactive roles of predation and tidal elevation in structuring populations of the edible cockle, *Cerastoderma edule. Estuarine, Coastal and Shelf Science* 25:245–60

Say, T. 1817. An account of the crustacea of the United States. *Journal of the Academy of Natural Sciences of Philadelphia* 1:57–63.

Scherer, B., and K. Reise. 1981. Significant predation on micro- and macrobenthos by the crab *Carcinus maenas* L. in the Wadden Sea. *Kieler Meeresforschungen Sonderheft* 5:490–500.

Schratzberger, M., and R.M. Warwick. 1999. Impact of predation and sediment disturbance by *Carcinus maenas* (L.) on free-living nematode community structure. *Journal of Experimental Marine Biology and Ecology* 235:255–71.

Scripps. 2000. U.S. coastal sea-surface temperature. U.S. West Coast Shore Stations Program. http://www-mlrg.ucsd.edu/shoresta/

Seed, R. 1969. The ecology of *Mytilus edulis* L. (Lamellibranchiata) on exposed rocky shores. II. Growth and mortality. *Oecologia* 3:317–50.

Seed, R., and R.A. Brown. 1975. The influence of reproductive cycle, growth and mortality on the population structure in *Modiolus modiolus, Cerastoderma edule* and *Mytilus edulis.* In *Ninth European marine biology symposium*, ed. H. Barnes, 257–74. Aberdeen, Scotland: Aberdeen University Press.

Seeley, R. 1986. Intense natural selection caused a rapid morphological transition in a living marine snail. *Proceedings of the National Academy of Science of the United States of America* 83:6897–901.

Shen, C.J. 1935. An investigation of the post-larval development of the shore-crab *Carcinus maenas,* with special reference to the external secondary sexual characteristics. *Proceedings of the Zoological Society of London* 1:1–33.

Sinclair, M.A. 1997. Interactions between native grapsid crabs and *Carcinus maenas* in Victoria. *Proceedings of the first international workshop on the demography, impacts and management of introduced populations of the European crab,* Carcinus maenas. Technical Report 11. Hobart, Tasmania: Centre for Research on Introduced Marine Pests.

Singh, R. 1991. Natural diet of, and shelter-use by, the green crab, *Carcinus maenas* (l.) in Nova Scotia. Master's thesis, University of New Brunswick, Canada.

Smith, L.D., and G.C. Trussell. 2000. The influence of water temperature on induced defensive responses by an intertidal snail to an introduced crab predator. In *Marine bioinvasions: proceedings of the first national conference,* ed. Judith Pederson, 411. Cambridge, MA: Massachusetts Institute of Technology Sea Grant College Program.

Smith, O.S. 1950. Observations on soft clam mortalities in Massachusetts. *Proceedings of the National Shellfisheries Association,* Atlantic City, New Jersey, August 21–24, pp. 31–33.

_______. 1954. Fencing in flats may save some clams from green crabs. *Maine Coast Fisherman* 8(8):20.

Smith, T.E., R.C. Ydenberg, and R.W. Elner. 1999. Foraging behaviour of an excavating predator, the red rock crab (*Cancer productus* Randall) on soft-shell clam (*Mya arenaria* L.). *Journal of Experimental Marine Biology and Ecology* 238:185–97.

Spaargaren, D.H. 1984. On ice formation in sea water and marine animals at subzero temperatures. *Marine Biology Letters* 5:203–16.

_______. 1974. A study on the adaptation of marine organisms to changing salinities with special reference to the shore crab *Carcinus maenas* (L.). *Comparative Biochemistry and Physiology. A Comparative Physiology* 47:499–512.

Strathmann, M.F. 1987. *Reproduction and development of marine invertebrates of the North Pacific coast: data and methods for the study of eggs, embryos and larvae.* Seattle: University of Washington Press.

Stunkhard, H.W. 1956. Studies on parasites of the green crab, *Carcinus maenas. Biological Bulletin* 111:295.

Sverdrup, H.U., M.W. Johnson, and R.H. Fleming. 1942. *The oceans. Their physics, chemistry, and general biology.* New York: Prentice-Hall.

Tettelbach, S.T. 1986. Dynamics of crustacean predation on the northern bay scallop, *Argopecten irradians irriadians.* Ph.D. dissertation, University of Connecticut, Stores.

Theede, H. 1964. Physiologische Unterschiede bei der Strandkrabbe *Carcinus maenas* L. aus der Nord- und Ostsee. *Kieler Meeresuntersuchungen* 20:179–91.

Thiel, M., and T. Dernedde. 1994. Recruitment of shore crabs *Carcinus maenas* on tidal flats: mussel clumps as an important refuge for juveniles. *Helgoländer Meeresuntersuchungen* 48:321–32.

Thresher, R.E. 1996. *Environmental tolerances of larvae of the European parasitic barnacle,* Sacculina carcini *(Rhyzocephala: Sacculinidae): implications for the use as a biological control agent against the introduced European crab,* Carcinus maenas. Technical Report 7. Hobart, Tasmania: Centre for Research on Introduced Marine Pests.

_______. 1997. *Proceedings of the first international workshop on the demography, impacts and management of introduced populations of the European crab,* Carcinus maenas. Technical Report 11. Hobart, Tasmania: Centre for Research on Introduced Marine Pests.

Torchin, M.E., K.D. Lafferty, and A.M. Kuris. 1996. Infestation of an introduced host, the European green crab, *Carcinus maenas,* by a symbiotic nemertean egg predator, *Carcinonemertes epialti. Journal of Parasitology* 82:449–53.

Trussell, G. 1996. Phenotypic plasticity in an intertidal snail: the role of a common crab predator. *Evolution* 50:448–54.

United States Geological Survey. 1999. Water quality of San Francisco Bay. http://sfbay.wr.usgs.gov/access/wqdata/index.html

van der Meeren, G. 1992. Location of spawning shore crabs, *Carcinus maenas* (L. 1758) (Decapoda, Brachyura). *Crustaceana* 63(1):92–94.

van der Veer, H.W., R.J. Feller, A. Weber, and J.I.J. Witte. 1998. Importance of predation by crustaceans upon bivalve spat in the intertidal zone of the Dutch Wadden Sea as revealed by immunological assays of gut contents. *Journal of Experimental Marine Biology and Ecology* 231:139–57.

Varagnolo, S. 1968. Fishery of the green crab (*Carcinus maenas* L.) and soft crab culture in the Lagoon of Venice. Food and Agricultural Organization of the United Nations. General Fisheries Council for the Mediterranean. *Studies and Reviews* 12(37):1–13.

Vermeij, G.J. 1982. Phenotypic evolution in a poorly dispersing snail after the arrival of a predator. *Nature* 299:349–50.

Wahl, M., M.E. Hay, and P. Enderlein. 1997. Effects of epibiosis on consumer-prey interactions. *Hydrobiologia* 355:49–59.

Wallace, J.C. 1973. Feeding, starvation and metabolic rate in the shore crab *Carcinus maenas. Marine Biology* 20:277–81.

Walne, P.R., and G. Davies. 1977. The effect of mesh covers on the survival and growth of *Crassostrea gigas* Thunberg grown on the sea bed. *Aquaculture* 11:313–21.

Walne, P.R., and G.J. Dean. 1972. Experiments on predation by the shore crab, *Carcinus maenas* L., on *Mytilus* and *Mercenaria. Journal du Conseil Conseil International pour l'Exploration de la Mer* 34:190–99.

Walton, W. 1997. Preliminary evaluation of the impact of *Carcinus maenas* upon the native Tasmanian clam, *Katelysia scalarina* fishery. *Proceedings of the first international workshop on the demography, impacts and management of introduced populations of the European crab,* Carcinus maenas. Technical Report 11. Hobart, Tasmania: Centre for Research on Introduced Marine Pests.

Walton, W.C. 2000. Mitigating effects of nonindigenous marine species: evaluation of selective harvest of the European green crab, *Carcinus maenas.* Abstract in *Journal of Shellfish Research* 19(1):634.

Warner, G.F. 1977. *The biology of crabs.* London: Elek Science.

Warner, G.F., D. Chapman, N. Hawkey, and D.G. Waring. 1982. Structure and function of the chelae and chela closer muscles of the shore crab *Carcinus maenas* (Crustacea:Brachyura). *Journal of Zoology*, London 196:431–38.

Weissburg, M.J., and R.K. Zimmer-Faust. 1993. Life and death in moving fluids: hydrodynamic effects on chemosensory-mediated predation. *Ecology* 74:1428–43.

Welch, W.R. 1968. Changes in abundance of the green crab, *Carcinus maenas* (L.), in relation to recent temperature changes. *Fishery Bulletin* 67:337–45.

Whitlow, W.M. 2000. The impact of *Carcinus meanas* on patterns of *Mya arenaria* survivorship. In *Marine bioinvasions: proceedings of the first national* *conference*, ed. Judith Pederson, 410. Cambridge, MA: Massachusetts Institute of Technology Sea Grant College Program.

Zariquiey Alvarez, R. 1968. Crustáceos decápodos ibéricos. *Investigación pesq.* 32:i–xi.

Zeidler, W. 1988. The European shore crab, *Carcinus maenas* in the Coorong—a potential threat to local fisheries. *Transactions of the Royal Society of South Australia* 112:181–82.

_______. 1997. The European shore crab in South Australian waters. *Proceedings of the first international workshop on the demography, impacts and management of introduced populations of the European crab,* Carcinus maenas. Technical Report 11. Hobart, Tasmania: Centre for Research on Introduced Marine Pests.

Zeng, C., and E. Naylor. 1996a. Endogenous tidal rhythms of vertical migration in field collected zoea-1 larvae of the shore crab *Carcinus maenas:* implications for egg tide offshore dispersal. *Marine Ecology Progress Series* 132:71–82.

________. 1996b. Occurrence in coastal water and endogenous tidal swimming rhythms of late megalopae of the shore crab *Carcinus maenas:* implications for onshore recruitment. *Marine Ecology Progress Series* 136:69–79.

_______. 1996c. Synchronization of endogenous tidal vertical migration rhythms in laboratory-hatched larvae of the crab *Carcinus maenas. Journal of Experimental Marine Biology and Ecology* 198:269–89.

_______. 1996d. Heritability of circatidal vertical migration rhythms in zoea larvae of the crab *Carcinus maenas* (L.). *Journal of Experimental Marine Biology and Ecology* 202:239–57.

Zeng, C., P. Abello, and E. Naylor. 1999. Endogenous tidal and semilunar moulting rhythms in early juvenile shore crabs *Carcinus maenas*: implications for adaptations to a high intertidal habitat. *Marine Ecology Progress Series* 191:257–66.

Zeng, C., E. Naylor, and P. Abello. 1997. Endogenous control of timing of metatmorphosis in megalopae of the shore crab *Carcinus maenas. Marine Biology* 128:299–305.

Zimmer-Faust, R.K., C. M. Finelli, N.D. Pentcheff, and D.S. Wethey. 1995. Odor plumes and animal navigation in turbulent water flow: a field study. *Biological Bulletin* 188:111–16.

Zwarts. L. 1981. Habitat selection and competition in wading birds. In *Ecology of the Wadden Sea,* ed. W.J. Wolff, 271–79. Rotterdam: A.A. Balkema.

Illustration Credits

INTRODUCTION: fig. 1 (p. 3), Dave Reinert. **CHAPTER ONE:** fig. 2 (p. 8), fig. 3 (p. 9), and fig. 4 (p. 11), Laura L. Hauck; fig. 5 (p. 15), reprinted with permission from A.L. Rice and R. W. Ingle, 1975, The larval development of *Carcinus maenas* (L) and *C. mediterraneus* Czerniavsky (Crustacea, Brachyura, Portunidae) reared in the laboratory, *Bulletin of the British Museum of Natural History* (Zoology) 28(3), pp. 107, 111, 113, and 114; fig. 6 (p. 24), data courtesy of Todd Miller and Christopher Hunt. **CHAPTER TWO:** fig. 7 (p. 57), Dave Reinert. **APPENDIX A:** *Carcinus maenas* (p. 77), Laura L. Hauck; *Telmessus cheiragonus* (p. 78), Josephine F.L. Hart, reprinted with permission from J.F.L. Hart, 1982, *Crabs and their relatives of British Columbia* (Victoria, B.C.: Ministry of Provincial Secretary and Government Services), p. 205; *Hemigrapsus oregonensis* (p. 78), Paul Rudy and Lynn Hay Rudy, reprinted with permission from P. Rudy and L.H. Rudy, 1983, *Oregon estuarine invertebrates: an illustrated guide to the common and important invertebrate animals* (Fish and Wildlife Service, U.S. Department of Interior), p. 149; *Hemigrapsus nudus* (p. 79), Paul Rudy and Lynn Hay Rudy, p. 147; *Pachygrapsus crassipes* (p. 79), Paul Rudy and Lynn Hay Rudy, p. 151; *Pugettia producta* (p. 80), Paul Rudy and Lynn Hay Rudy, p. 133; *Lophopanopeus bellus* (p. 80), Josephine F.L. Hart, p. 203; *Rhithropanopeus harrisi* (p. 81), Paul Rudy and Lynn Hay Rudy, p. 143; *Cancer productus* (p. 81), Josephine F.L. Hart, p. 207; *Cancer oregonensis* (p. 82), Paul Rudy and Lynn Hay Rudy, p. 141; *Cancer magister* (p. 82), Paul Rudy and Lynn Hay Rudy, p. 137; *Cancer gracilis* (p. 83), Josephine F.L. Hart, p. 215; *Cancer antennarius* (p. 83), Paul Rudy and Lynn Hay Rudy, p. 135. **APPENDIX B: PLATES:** plate 1 (p. 85), Gary Weber; plates 2A and 2B (p. 86), Gary Weber; plate 3 (p. 87), Christopher Hunt; plate 4 (p. 87), Sylvia Yamada; plate 5 (p. 88), Sylvia Yamada; plate 6 (p. 88) and plate 7 (p. 89), Gary Weber; plate 8 (p. 89), reprinted with permission from Robert H. Morris, Donald P. Abbott, and Eugene C. Haderlie, 1980, *Intertidal invertebrates of California* (Stanford, CA: Stanford University Press), plate 25.43a; plate 9 (p. 90), Gary Weber; plate 10 (p. 90), Sylvia Yamada; plates 11 and 12 (p. 91), Gary Weber; plate 13 (p. 92), Robert H. Morris, Donald P. Abbott, and Eugene C. Haderlie, plate 25.21; plate 14 (p. 92), Gary Weber; plate 15 (p. 93), Amy B. Broda; plate 16 (p. 93), and plate 17 (p. 94), Gary Weber.

Index

The European green crab, *Carcinus maenas,* was first discovered on the Pacific coast of the United States in 1989, near San Francisco Bay. By 1998, it was clear that this notorious global invader had reached the Pacific Northwest, and the news was unwelcome to fishers, ecologists, fishery managers, and others who monitored the biological diversity of coastal waters.

The green crab's reputation as a serious threat is well deserved. A voracious predator, able to tolerate air exposure, starvation, and wide ranges in temperature and salinity, the green crab was introduced from Europe to the Atlantic coast of the U.S. nearly 200 years ago and now ranges from Virginia to the southern shores of Prince Edward Island.

In this book, Sylvia Yamada describes the biology and life history of the European green crab, presents five case studies of green crab invasions, and discusses the crab's ecological and economic impact on the Pacific coast of North America.

Sylvia Yamada has done research in fisheries biology, marine ecology, population ecology, predator-prey interactions, the management of invertebrate fisheries, and the role of introduced species in the marine environment. She is a faculty member in the Department of Zoology at Oregon State University.

1-881826-24-4