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Introduction, dispersal and potential impacts of the green crab *Carcinus maenas* in San Francisco Bay, California

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Abstract The North Atlantic portunid crab *Carcinus maenas* (Linnaeus, 1758) has invaded the North Pacific Ocean following more than two centuries of global dispersal due to human activities. *C. maenas* was first collected in San Francisco Bay, California, in 1989–1990, where its distribution and prey selectivity were investigated in 1992–1994. It has become abundant in shallow, warm lagoons (which as favorable and retentive microhabitats may have served as invasion incubators) and spread throughout the north, central and south bays. It may have arrived in ballast water, on fouled ships, amongst algae with imported live bait or lobsters, or by intentional release; genetic comparisons of the Bay population with possible source populations may aid in defining the transport mechanism. *C. maenas*' eurytopic nature, its high breeding potential, and its diet and feeding behavior suggest the potential for extensive ecosystem alterations through predator–prey interactions, competition, disturbance, and indirect effects. Although both negative economic impacts through reduction or disruption of fisheries and positive impacts of providing bait and human-food fisheries have been documented in a few regions, the potential economic impacts in San Francisco Bay remain largely unknown.

Introduction

Marine biological invasions continue to be a major global phenomenon at the close of the twentieth century (Carlton

1989, 1992b; Zibrowius 1992; Carlton and Geller 1993). In the 1980s, several species of Japanese dinoflagellates and the Japanese kelp *Undaria pinnatifida* invaded Australia (Hay 1990; Hallagraeff and Bolch 1991), the western Atlantic comb jelly *Mnemiopsis leidyi* invaded the Black and Azov Seas (Vinogradov et al. 1989; Shushkina and Musayeva 1990), the European bryozoan *Membranipora membranacea* and the European nudibranch *Tritonia plebeia* invaded the northwestern Atlantic (Allmon and Sebens 1988; Berman et al. 1992; Lambert et al. 1992), the Venezuelan mussel *Perna perna* became established in Texas (Hicks and Tunnell 1993), the Japanese crab *Hemigrapsus sanguineus* arrived in New Jersey (McDermott 1991), the American spionid *Marenzelleria viridis* appeared in Germany (Essink and Kleef 1993), the tropical green alga *Caulerpa taxifolia* colonized the Mediterranean (Meinesz and Hesse 1991), and several Asian copepods became established on the Pacific coast of the United States (Orsi and Walter 1991; Cordell et al. 1992). Numerous other interoceanic and transoceanic invasions of exotic marine, estuarine and freshwater organisms have been reported, including the spectacular invasion of the Laurentian Great Lakes in the 1980s by the Eurasian zebra mussels *Dreissena polymorpha* and *D. bugensis*, and four other European invertebrates and fish (Mills et al. 1993).

Major routes exist for the dispersal of introduced species into and within the Pacific Ocean (Carlton 1987). Carlton (1979b) listed 97 species of invertebrates introduced into San Francisco Bay, California, and Carlton et al. (1990) in reporting on the invasion of the Asian clam *Potamocorbula amurensis* listed ten additional introduced invertebrates and noted that new species were arriving in the Bay at a rate of about one a year.

Following reports in August 1991 by a local fisherman of an unidentified crab in bait traps in San Francisco Bay (subsequently identified by D. Chivers as *Carcinus maenas*), combined with A. Cohen's simultaneous discovery of a molt on the East Bay shore, we undertook field investigations to establish the extent of the crab's colonization. We report on its early dispersal in San Francisco Bay and investigate its diet and feeding behavior as an indication

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of its potential trophic impact. Grosholz and Ruiz (1995) report the subsequent appearance of *C. maenas* in four nearby estuaries (Bollinas Lagoon, Drake's Estero, Tomales Bay and Bodega Harbor). We use the common name "green crab" following Williams et al. (1989).

Materials and methods

Distribution

We visited sites in San Francisco Bay from the South Bay north to Martinez. At each site, one or two people searched for one to several hours in rock riprap, shore debris and marsh vegetation for live crabs, carcasses and molts. At several sites, baited traps were set for 3 to 12 h. We interviewed anglers and bait collectors at these sites, describing or showing them pictures or specimens of the green crab, *Carcinus maenas*. We contacted regional biologists and shoreline park personnel for possible records and specimens, circulated a "Green Crab Wanted" poster to park authorities, marinas, bait stores, bait trappers and shrimpers, and published requests for information in the newsletters of environmental organizations and coastal resource agencies.

All specimens of *Carcinus maenas* obtained were sexed and measured. Representative specimens of *C. maenas* have been deposited at the California Academy of Sciences, San Francisco (CAS).

Feeding experiments

Feeding tests were conducted to determine *Carcinus maenas*' prey selectivity between common bivalves in San Francisco Bay. Ten female *C. maenas*, 55 to 60 mm in carapace width, were collected from Redwood Shores Lagoon, California, and placed individually into 25 × 25 × 29 cm tanks in a closed, circulating seawater system at 15°C with a 12 h light:12 h dark cycle. All crabs were nonovigerous and in anecysis. They were maintained on anchovies and starved for 48 h prior to each run to ensure a similar hunger level (Jubb et al. 1983; Abbas 1985).

Prey items collected from the Bay were offered to the same ten crabs in all pair-wise combinations of prey, with 15 of each species offered per run. All prey items were 10 to 20 mm in shell length, within the size range of bivalves preferentially selected by *Carcinus maenas* (Elner and Hughes 1978; Juanes 1992). Prey species offered were: the shallow infaunal Asian clam *Venerupis philippinarum* (= *Tapes japonica*); the shallow infaunal/epifaunal Asian clam *Potamocorbula amurensis*, which has a thinner shell than *V. philippinarum*; and an epifaunal mussel (hereafter called *Mytilus* sp.) belonging to either of two species or their hybrids that can be distinguished only through genetic analysis, the native *M. trossulus* and the Mediterranean *M. galloprovincialis* (McDonald and Koehn 1988).

In the first set of tests, prey items were scattered randomly on the bare floor of the aquaria. In a second set of tests under conditions that more closely resembled natural conditions, prey were offered in aquaria containing 6 cm of sandy mud (heat-sterilized and sieved through 1 mm mesh) from San Francisco Bay. When the two clam species were tested together they were allowed to bury themselves; when *Potamocorbula amurensis* was tested against *Mytilus* sp., the clams were pressed to their natural depth just under the surface of the sediment, and the mussels were allowed to clump and then placed on the surface of the sediment.

Each run was conducted twice. The number of prey consumed was calculated by subtracting the number of unbroken prey items remaining after 2 h from the number offered. The results were analyzed using a paired-design *t*-test (Sokal and Rohlf 1981). For each run, crabs that did not eat were excluded from the analysis.

Results

Identification

A complex taxonomic history accompanies the uncertain recognition of two species of *Carcinus* in Europe and North Africa: *C. maenas* and *C. mediterraneus* Czerniavsky, 1884 [= *C. aestuarii* (Nardo, 1847)]. Many years of work have resulted in a host of inconclusive and sometimes inconsistent characteristics reported in the literature as distinguishing between these two species or subspecies. It is likely that for many centuries both forms have been carried about Europe by shipping, thereby obfuscating distributional patterns and contributing to the difficulties of identifying material from regions within the range of one taxon or the other. Although the distinctions between *C. maenas* and *C. mediterraneus* remain in large part to be resolved, we tentatively identify the San Francisco Bay crabs as *C. maenas* based upon characteristics provided by Demeusy and Veillet (1953), Demeusy (1953, 1958), Almaça (1961, 1963), Zariquiey Alvarez (1968) and Rice and Ingle (1975). These characteristics include: male pleopods curved outwards; carapace texture slightly granulated, not hairy; females with sparse or no hair on rostrum, males with no hair; rostrum not notably protuberant; no hair on antero-external border of carpus; fifth antero-lateral tooth of carapace directed forwards.

Distribution

Carcinus maenas was first seen in California in May 1989 when a large (85 mm carapace width) male was caught in a gill net in Estero Americano, 70 km north of San Francisco in Sonoma County (J. Roth personal communication 1989). We examined this specimen and deposited it at CAS. No other *C. maenas* have been reported from the Estero Americano, nor did we find any when we set bait traps there and interviewed local crab fishermen in December 1992. An earlier report of *C. maenas* on the Pacific Coast in Willapa Bay, Washington, in 1961 (Hedgpeth 1968) cannot now be verified (J. Hedgpeth personal communication 1991).

The green crab was next collected in the summer of 1989 or 1990 by bait trappers in Redwood Shores Lagoon, Redwood City, on the western side of south San Francisco Bay. This artificial, 76-acre enclosed lagoon averages 1 to 2 m in depth, and is connected to the Bay by tide gates and pumps. By August 1991 the crabs had reached sufficient densities, described as "hundreds per trap" in an overnight set, to come to the attention of local biologists.

The known distribution of *Carcinus maenas* in San Francisco Bay as of July 1994 is shown in Table 1 and Fig. 1, as compiled from our observations and collections and those of individuals listed in the "Acknowledgements". Only records of living specimens, not molts or carcasses, are shown. *C. maenas* has been collected in the main channel south of the Dumbarton Bridge, on the west shore of the South Bay from Redwood Creek to Coyote Point, along

Table 1 *Carcinus maenas*. Living specimens reported in San Francisco Bay; compiled from observations and collections of the present authors and of the individuals listed in the "Acknowledgements"

Location	Date of first collection	Comments
1 Redwood Shores Lagoon, San Mateo County	Summer 1989 or 1990	First crabs seen in Bay; caught in bait traps with "hundreds" per overnight set by 1991; brought to attention of researchers in August 1991; many males: 39–76 mm; fewer females: 40–64 mm, some gravid
2 Belmont Slough, San Mateo County	Feb. 1992	Caught in otter trawl and bait traps; several: 49–72 mm; gravid females common
3 Hayward shore, Alameda County	Mar. 1992	Caught in seine and by hand in marsh channels and on mudflats; males: 41–74 mm; females: 57–64 mm
4 Foster City Lagoon, San Mateo County	Mar. 1992	Caught in bait traps; male: 67 mm; females: 58, 66 mm
5 Crab Cove, Crown Beach and east shore of Bay Farm Island, Alameda County	May 1992	In outlet channels of lagoons and among rocks; also caught in pit traps in cordgrass marsh; males: 20–82 mm; females: 29–54 mm, several gravid
6 Coyote Point, San Mateo County	June 1992	Two crabs, under rocks in intertidal zone
7 Cargill Ponds, Alameda County	July 1992	Reported as abundant in salt ponds
8 Aquatic Park, Alameda County	July 1992	On mud in lagoon; males: 76, 80 mm
9 Loch Lomond Harbor, Marin County	Summer 1992	Many caught in bait traps; males: 46–83 mm; females: 36–64 mm, one gravid
10 Redwood Creek, San Mateo County	Fall 92	A few caught in bait traps and seine net; one gravid
11 South Bay, south of Dumbarton Bridge	Dec. 1992	Shrimp trawler reported several caught in main channel, mainly gravid females
12 San Pablo Bay, main channels	Jan. 1993	Caught by shrimp trawler; male: 45 mm; females: 40–52 mm, one gravid
13 Richardson Bay, Marin County	Mar. 1993	One male: 53 mm
14 China Camp, Marin County	Mar. 1993	One gravid female: 52 mm
15 Point Pinole, Contra Costa County	July 1993	Caught in baited ring nets; few males: 37–53 mm; several females: 38–76 mm ^a
16 Black Point, Marin County	Sep. 1993	Caught in baited ring nets; females: 59, 60 mm ^a
17 Berkeley Marina, Alameda County	Feb. 1994	Caught in bait traps; males: 50, 58 mm
18 Bay Farm Island Lagoon, Alameda County	June 1994	Caught in bait traps; dozens per 30 minute set

^a Data from San Francisco Bay Study of Interagency Ecological Study Program

the east shore of the Bay from Hayward to Point Pinole, and on the Marin County shore from Richardson Bay to Black Point. It is sometimes common to abundant at Redwood Shores Lagoon, Foster City Lagoon, Bay Farm Island Lagoon, Aquatic Park in Berkeley, and Loch Lomond Harbor. Like Redwood Shores Lagoon, the Foster City Lagoon, Bay Farm Island Lagoon and Aquatic Park are artificial lagoons connected to the Bay by tidegates, pumps or culverts. The furthest upstream record of *C. maenas* (toward the Sacramento and San Joaquin Rivers, the main sources of freshwater for the estuary) consists of a few individuals collected in February and March of 1993 in the main channel of San Pablo Bay near the mouth of Carqui-

nez Strait. In October 1994, the Interagency Ecological Study Program caught *Carcinus maenas* in baited ring nets further upstream at Crockett and Benicia in Carquinez Strait (K. Hieb personal communication).

Feeding experiments

When offered prey in tanks without sediment, *Carcinus maenas* did not select between *Potamocorbula amurensis* and *Mytilus* sp., but did select *P. amurensis* and *Mytilus* sp. over *Venerupis philippinarum* (Table 2). When offered prey in sediment, *C. maenas* selected *P. amurensis* over

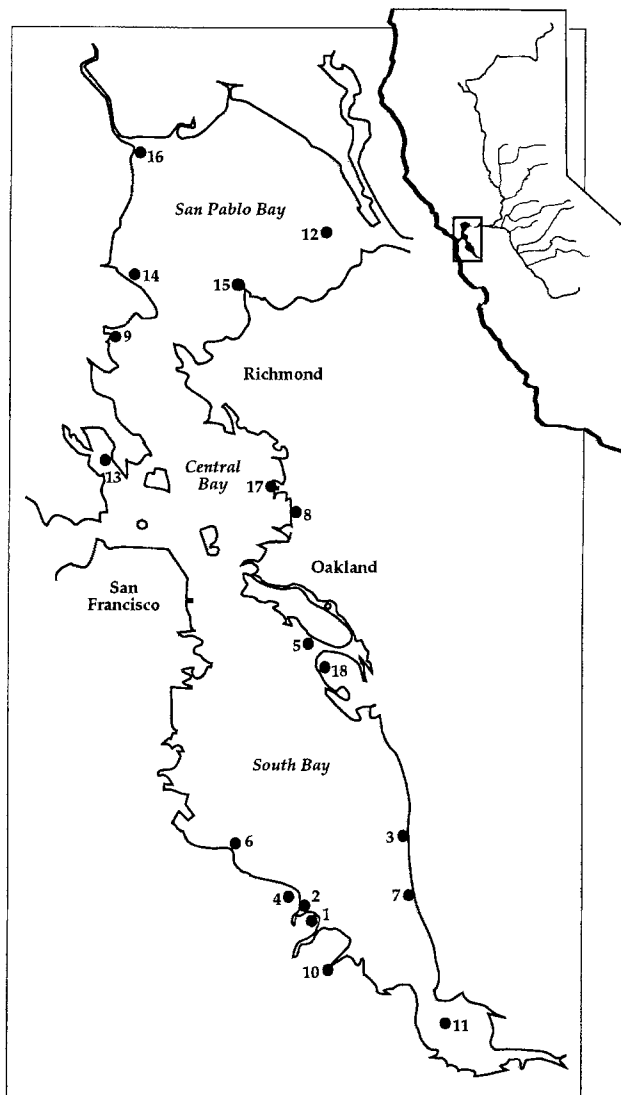


Fig. 1 *Carcinus maenas*. Records of living specimens in San Francisco Bay. Locations numbered as in Table 1

V. philippinarum, and selected buried *P. amurensis* over *Mytilus* sp. clustered on the surface.

Discussion

Mechanisms of introduction and establishment

Carcinus maenas is native to Europe and perhaps to north-west Africa. It was reported in the western Atlantic in 1817 and has become established south to New Jersey, with occasional records further south, and north to Nova Scotia (Say 1817; Williams 1984). In the spring of 1900, Fulton and Grant (1900) recorded *C. maenas* as "plentifully distributed" in the region of Port Phillip, Victoria, Australia, and it has since spread north into New South Wales and

west into South Australia (Zeidler 1978, 1988; Rosenzweig 1984). In 1983 the green crab was collected at the Table Bay Docks in Capetown, South Africa, where it has become well established (Le Roux et al. 1990; Carlton and Cohen 1995 regarding *C. maenas*' global spread).

There are no records of *Carcinus maenas* found at sea on floating algae or logs. In the laboratory *C. maenas*' planktonic larval stage ranges from 17 d at 25°C to 80 d at 12°C (Williams 1968; Dawirs 1985). This is too short a time to enable transport of larvae from Europe to North America by ocean currents, as this would entail passage through 1000s of kilometers of oligotrophic, tropical water to the Caribbean region followed by transport north to coastal waters that are within *C. maenas*' temperature range (Carlton and Cohen 1995). Natural planktonic transport to other localities where *C. maenas* has been reported is similarly impossible, given the direction and temperature of currents and the time that would be required for such dispersal. Instead, *C. maenas*' global dispersal in the 19th century appears to be linked to the movement of fouled and bored ships. The potential for such vessels to transport mobile organisms has been discussed by Carlton (1985, 1987, 1992a) and considered relative to crab dispersal by Fulton and Grant (1902), Chilton (1910) and Boschma (1972).

With the decline in wooden ships, *Carcinus maenas*' recent transport to Pacific North America was probably not by hull fouling, but by one of the following vectors:

(1) *C. maenas* larvae or juveniles may be carried in ballast water (Carlton 1985). Ballast water commonly contains crab larvae (Carlton and Geller 1993), and a juvenile crab was recovered from mud at the bottom of a ballast water tank (Hutchings et al. 1989). Adult crabs are not as likely to be transported by ballast water due to the small mesh size of ballast intake screens.

(2) *C. maenas* may be transported in fouled seawater pipe systems of ocean-going vessels, a modern-day counterpart to the hull crevices and fouled hulls of earlier wooden vessels (Carlton 1985). Little is known of this mechanism.

(3) *C. maenas* may reach California in shipments of commercial fisheries' products. Juvenile *C. maenas* are common in the New England rockweed *Fucus* spp. and the kelp *Ascophyllum nodosum* (Carlton 1992a; J. Carlton personal observations) which are used to pack live bait worms shipped to bait shops and live Atlantic lobsters (*Homarus americanus*) shipped to restaurants on the west coast (Miller 1969). The continued presence of fresh drift *A. nodosum* in San Francisco Bay, where there is no reproducing population, indicates that these seaweeds are regularly discarded in the Bay (M. Josselyn personal communication 1991). *C. maenas* adults can also arrive with lobster shipments. In 1988, J. Carlton observed a large adult *C. maenas* in an Atlantic lobster holding tank in a Coos Bay, Oregon, restaurant (Carlton 1989).

(4) *C. maenas* may be accidentally or intentionally released from school or research aquaria, as has apparently happened with several other invertebrates. For example,

Table 2 *Carcinus maenas*. Average number of prey items eaten when crabs offered a mixture of two prey species. Experiments were conducted in order of presentation. Analysis of results is based on number of crabs that consumed some prey in each run (*n*) (*t*, paired-design *t*-test)

Experiment	(<i>n</i>)	<i>Potamocorbula amurensis</i>	<i>Venerupis philippinarum</i>	<i>Mytilus</i> sp.	<i>t</i>	<i>p</i>
Without sediment						
<i>P. amurensis</i> vs <i>Mytilus</i> sp.						
Run 1	(10)	3.8 ± 0.96	—	6.0 ± 1.04	−1.53	<0.1599
Run 2	(10)	7.6 ± 1.59	—	6.3 ± 1.14	0.99	<0.3464
<i>P. amurensis</i> vs <i>V. philippinarum</i>						
Run 1	(9)	7.33 ± 1.22	1.44 ± 0.53	—	6.51	<0.0002
Run 2	(9)	9.78 ± 1.53	2.33 ± 1.26	—	4.99	<0.002
<i>Mytilus</i> sp. vs <i>V. philippinarum</i>						
Run 1	(9)	—	0.44 ± 0.24	6.44 ± 0.96	6.27	<0.0002
Run 2	(9)	—	0.44 ± 0.34	6.11 ± 0.84	7.42	<0.0001
With sediment						
<i>P. amurensis</i> vs <i>V. philippinarum</i>						
Run 1	(9)	11.33 ± 0.73	1.78 ± 0.72	—	17.20	<0.0001
Run 2	(8)	11.88 ± 0.93	1.75 ± 0.65	—	11.31	<0.0001
<i>P. amurensis</i> vs <i>Mytilus</i> sp.						
Run 1	(8)	10.12 ± 1.52	—	2.88 ± 1.53	4.47	<0.0029
Run 2	(7)	11.29 ± 0.97	—	1.71 ± 1.13	6.95	<0.0004

young Atlantic lobsters (*H. americanus*) were found in tidepools near the Bodega Marine Laboratory in California (Carlton 1992b), and the New England Aquarium's public displays include a large California spiny lobster (*Panulirus interruptus*) that was trapped offshore of the Marine Science Center at Nahant, Massachusetts. Experiments on the respective non-native lobsters were in progress at each laboratory. Living *C. maenas* can be readily ordered and air-shipped in large quantities from a number of Atlantic coast biological supply houses (such as the Marine Biological Laboratory, Woods Hole, Massachusetts).

(5) *C. maenas* may be imported and released by private parties as a potential food resource. Blue crabs (*Callinectes sapidus*) from the Atlantic have been so released to Pacific coastal waters on several occasions in recent years (D. Chivers personal communication).

If the established *Carcinus maenas* populations of Europe, Atlantic North America, Australia, and South Africa are genetically distinct (due to founder effect, genetic drift, or natural selection), it should be possible through molecular genetic techniques to determine which is the source of the northeastern Pacific population (currently being investigated by M. Fountain). In turn, this information would aid in assessing which is the likeliest transport mechanism.

Carlton (1979a, 1985) posited a sequence of steps in the introduction of nonindigenous species via ship fouling and ballast water. These steps act as filters, selectively reducing the number of taxa which make it past each step. Following the release (inoculation) of individuals of a species

into the environment, a given species may or may not become established, depending in part upon synergisms between the physiological and ecological requirements of the species and the novel environment in which it now finds itself. An initial step in successful establishment consists of achieving a reproducing population large enough to make continuing survival probable, what Moller (1995) has termed the "minimum viable beachhead population", as an analogue to the concept of minimum viable population size developed by conservation biologists.

We here suggest that for the green crab (and perhaps for other invaders of systems like San Francisco Bay) microhabitats within the estuary may act as "incubators" for the establishment of beachhead populations, providing an initially depauperate but environmentally favorable habitat in which the invader is able to successfully pass the colonization step. *Carcinus maenas* was first observed in the Bay in Redwood Shores Lagoon, where it achieved its greatest reported densities, and from which it appears to have dispersed progressively throughout the Bay (Fig. 1). In winter the water level of this lagoon and other artificial lagoons around the Bay is lowered; the lagoons then receive a substantial volume of freshwater runoff. The reduction in water level kills many sessile organisms, which along with the decreased winter salinities apparently contributes to an observed winter decline in the abundance of organisms.

During the remainder of the year, however, the water level in these lagoons is more stable than in the Bay, creating conditions that may nurture new inoculations of non-indigenous species. The shallow lagoons are typically a

few degrees warmer than the Bay in the spring to fall months, when they are characterized by high primary productivity. Most of the lagoons are free of potentially disruptive high-energy waves and boat wakes. The lagoons are also retentive environments, which may be crucial to maintaining the critical densities of adult organisms needed for sexual reproduction.

The conditions in Redwood Shores Lagoon may thus have provided a safe beachhead for the subsequent invasion of San Francisco Bay by *Carcinus maenas*. This is suggested by the relatively greater abundance of *C. maenas* in other artificial lagoons than in the open waters of the Bay, and its early appearance and greater abundance in such lagoons in South Africa (LeRoux et al. 1990).

Whether San Francisco Bay's artificial lagoons have served as incubators for previous invasions may bear examination. For example, the Australian serpulid polychaete *Ficopomatus enigmaticus* (= *Mercierella enigmatica*) was first noted in San Francisco Bay in large, coral-like colonies in Lake Merritt, a lagoonal environment (Carlton 1979a, b). From the lake, this tubeworm has spread to a number of localities within the Bay, both to other lagoons and to more open environments.

Potential distribution and abundance

Carcinus maenas is common to abundant in protected marine and estuarine habitats (Crothers 1970; Berrill and Berrill 1981); it is scarce in high-energy, outer-coast environments. It is found on mud, sand and rock substrates, among *Zostera marina* beds and in cordgrass marshes. It is common subtidally to 6 m depth and has been reported to at least 60 m (Crothers 1968). Some populations remain wholly subtidal, while others commonly migrate shoreward to feed with the rising tide, sometimes concentrating at low tide in tide pools on rocky shores, or in sloughs or under rocks and other debris on sand and mud flats (Edwards 1958; Crothers 1968; Klein Breteler 1976a; Dare and Edwards 1981). Small crabs often inhabit burrows in *Spartina* banks (Crothers 1968; Ropes 1968).

Carcinus maenas is euryhaline, with adults residing in water from 34 to 4‰ S, and in intertidal zones flooded by 1.4‰ S water (Broekhuysen 1936; Crothers 1967; Muus 1967; Perkins et al. 1969). Populations breed successfully down to at least 13‰ S (Dries and Adelung 1982), although Rasmussen (1973) reports that larvae require at least 17 to 19‰ S to metamorphose and settle.

Carcinus maenas' range in both native and invaded regions falls within equatorial limits of average summer surface-temperatures around 22°C, and polar limits of average winter ocean-temperatures of -1 to 0°C, and thus its potential range in the northeastern Pacific is from Baja California to southern Alaska (Sverdrup et al. 1947; Carlton and Cohen 1995). This is consistent with a reported upper temperature breeding barrier of 18 to 26°C (Naylor 1965), and with reports of the death of adult crabs, especially larger crabs, during severe winters with sustained water temperatures of 0°C or below (Patterson 1912; Dexter

1947; Glude 1955; MacPhail et al. 1955; Crisp 1964; Welch 1968).

When water temperatures drop in the winter the crabs, especially berried females and sacculinized crabs, move to deeper water (Broekhuysen 1936; Crothers 1967; Muus 1967; Rasmussen 1973; Dries and Adelung 1982). In some areas, berried females and sacculinized crabs are found a few meters deeper than other crabs at other times of the year as well (Thorson 1946; Rasmussen 1959, 1973; Crothers 1968). Since Broekhuysen has shown that at colder temperatures *Carcinus maenas* eggs are less tolerant of low salinities, this may be an adaptation for keeping developing eggs in the more saline and sometimes warmer water found at depth (Broekhuysen 1936; Crothers 1967), although this hypothesis has not been tested. In the laboratory, adult *C. maenas* prefer salinities in the range of 22 to 41‰ (Thomas et al. 1981; Ameyaw-Akumfi and Naylor 1987; McGraw and Naylor 1992), and tolerate and successfully carry and hatch eggs at salinities up to 53–54‰, which is considerably more saline than the green crab's normal environment (Broekhuysen 1936; Eriksson et al. 1975a).

Within San Francisco Bay, these habitat tolerances would allow *Carcinus maenas* to establish breeding populations from the South Bay through San Pablo Bay (Conomos et al. 1985). Populations could also be maintained in fresher waters, such as Suisun Bay, through immigration, as occurs in Danish waters (Muus 1967). *C. maenas* has enormous breeding potential in favorable habitats, with mature females producing 185 000 to 200 000 eggs per year (Broekhuysen 1936). In Europe, population densities have been estimated at 0.1 to 20 adult crabs per square meter and 10 to 2 000 0-group crabs per square meter in suitable habitats during the summer (Hancock and Urquhart 1965; Crothers 1968; Klein Breteler 1976a, b; Scherer and Reise 1981; Jensen and Jensen 1985; Janke 1990). In Passamaquoddy Bay, Nova Scotia, 15 000 crabs were taken in two traps over 24 d, with no decline in daily catch (MacPhail et al. 1955). Similar numbers of green crabs were taken in traps in Maine and Connecticut, with peak catches of over 1000 crabs per trap-day (Marshall 1960).

Trophic biology

Carcinus maenas has been shown to consume an enormous variety of prey items, including organisms from at least 104 families and 158 genera in 5 plant and protist and 14 animal phyla (Table 3). We review here the trophic biology of *C. maenas* to provide a foundation for understanding its potential impact.

Although some workers describe *Carcinus maenas* as opportunistically feeding on whatever is available (Elner 1977, 1981; Abbas 1985; Le Calvez 1987), many experiments have shown it to be selective with regard to prey species (Elner and Raffaelli 1980; Scherer and Reise 1981; Jensen and Jensen 1985; Rangeley and Thomas 1987) and prey size (Walne and Dean 1972; Elner and Hughes 1978; Hughes and Elner 1979; Scherer and Reise 1981; Sanchez-

Table 3 *Carcinus maenas*. Number of species (minimum) reported as food [Sources: Blegvad 1914; Lebour 1928; Smidt 1951; MacPhail et al. 1955; Spear 1955 (cited in Ropes 1968); Dearborn 1957; Buchsbaum and Milne 1960; Yonge 1960; Muntz et al. 1965; Kitching et al. 1966; Perkins 1967; Crothers 1968; Ropes 1968; Williams 1968; Parsons 1974; Heller 1976; Elner 1977; Stenzler and Atema 1977; Rivest 1978; Elner 1981; Scherer and Reise 1981; Zanette et al. 1981; Behbani and Croker 1982; Dawirs 1982; Le Calvez 1984, 1987; Abbas 1985; Brandwood 1985; Gee et al. 1985; Jensen and Jensen 1985; Lake et al. 1987; Rangeley and Thomas 1987; Harms and Seeger 1989; Raffaelli et al. 1989; Ropes 1989; Janke 1990; Le Roux et al. 1990; Pohle et al. 1991; Grosholz and Ruiz 1995; present paper – includes aquarium feeding (MCF), stomach contents (ANC and JTC, from San Francisco Bay), and field observations (JTC, in Massachusetts)]

Prey taxon	Eaten by larvae in aquaria	Eaten by 0-group crabs	Eaten by adults:	
			in aquaria or enclosures	from stomach contents or field observations
Algae		1		
Phytoplankton	5			1
Chlorophyta				4
Phaeophyta			2	2
Rhodophyta				1
Spermatophyta		1	1	4
Protista				
Foraminifera		1		1
Rotifera	1			
Animalia				
Hydrozoa			1	1
Nemertea				1
Nematoda		1		1
Turbellaria		1		
Oligochaeta		1	2	1
Polychaeta		2	13	26
Chelicerata				2
Anostraca	1			
Ostracoda		1		
Copepoda		1	2	1
Cirripedia			2	2
Mysidacea				1
Isopoda			2	5
Amphipoda			2	1
Natantia			3	1
Astacura			1	
Anomura			2	2
Brachyura		1	5	4
Insecta				1
Cephalopoda				1
Polyplacophora				3
Gastropoda		1	19	19
Bivalvia	1	1	18	23
Bryozoa				1
Phoronida			1	
Asteroidea			1	1
Echinoidea			1	1
Urochordata				1
Fish			6	6

Salazar et al. 1987a; Juanes 1992). In these experiments the selection of prey size and sometimes prey species varied with the size of the crab (Elner and Hughes 1978; Elner 1980; Abbas 1985; Rangeley and Thomas 1987; Sanchez-Salazar et al. 1987a), with its color (Kaiser et al.

1990), and sometimes with its sex (Elner 1980; Scherer and Reise 1981), although sometimes not (Dearborn 1957). Differences in prey selection between crabs of different color may result from differences in chela strength (Kaiser et al. 1990), while sexual differences in prey selection may be explained by differences in chela shape (Scherer and Reise 1981) or chela size (Elner 1980).

Wide variation in predominant prey has been observed in the stomachs of *Carcinus maenas* from different locations. The major prey items reported are bivalves in Plum Island Sound, Massachusetts, Hampton Harbor, New Hampshire, Port Herbert, Nova Scotia, and Gareloch, Scotland; bivalves and gastropods for larger crabs, and gastropods and polychaetes for smaller crabs, in Burry Inlet, South Wales; crustaceans, algae and bivalves for larger crabs, and crustaceans and algae for smaller crabs, in Menai Straits, North Wales and Pettamquamscutt River, Rhode Island; barnacles, bivalves and gastropods in Ythan Estuary, Scotland; bivalves and gastropods in "Danish waters", and decapods in the Danish Wadden Sea; gastropods, isopods and polychaetes at Bloubergstrand, South Africa; and polychaetes and algae in the Rance Estuary in France (Blegvad 1914; Smidt 1951; Ropes 1968, 1989; Perkins and Penfound 1969; Elner 1977, 1981; Le Calvez 1984, 1987; Abbas 1985; Raffaelli et al. 1989; Le Roux et al. 1990). These geographic differences in diet result partly from differences in prey availability [e.g. the relatively high proportion of isopods in the diet at Bloubergstrand is due to the presence there of the large, slow-moving isopod *Paridotea unguolata* (LeRoux et al. 1990)], and partly from geographic differences in prey preference. For example, Perkins (1967) noted that *C. maenas* at Solway Firth readily took and ate *Mytilus edulis*¹, but that *C. maenas* at Gareloch ignored *M. edulis* even though they were plentiful. Stomach contents have also shown differences in prey composition between juvenile and adult *C. maenas* (Ropes 1968, 1989; Elner 1977; Abbas 1985) and between seasons (Elner 1981; Le Calvez 1984, 1987; Abbas 1985).

Carcinus maenas is thought to be a tactile (Elner and Hughes 1978; Scherer and Reise 1981; Abbas 1985; Sanchez-Salazar et al. 1987a) and chemosensory (Patterson 1912; Crothers 1968; Ropes 1968; Elner and Hughes 1978; Hadlock 1980) rather than visual hunter. *C. maenas* feeds on algae and on sessile and mobile epifauna, and readily detects and captures shallowly buried infauna. Adults generally feed in the top few centimeters of sediment (LeCalvez 1987), although they have been observed digging pits up to 15 cm deep to extract large clams (Smith and Chin 1951; also see Muus 1967). 0-group crabs feed in the top half-centimeter (Scherer and Reise 1981). Fish have been found in *C. maenas*' stomach including "small Gobiidae swallowed almost entire" (Le Calvez 1987). Blegvad

¹ In recent years, many molecular genetics studies have revealed that *M. edulis* actually comprises three species, *M. edulis*, *M. galloprovincialis*, and *M. trossulus*. Given current knowledge of the distribution of these species, it is likely that at least some of the studies summarized in this paragraph that recorded *M. edulis* in fact encountered one of the other species or hybrids of two of the species.

(1914) watched *C. maenas* capture and feed on fish in aquaria, and Ropes (1968) observed *C. maenas* feeding on herring that had been stunned or killed by gulls.

In the laboratory, *Carcinus maenas* opens and consumes the soft-shell clam *Mya arenaria* and the mussel *Mytilus edulis* at lengths up to and greater than its carapace width (Dearborn 1957; Elner 1978); and eats the cockle *Cerastoderma edule* and the snail *Nucella lapillus* at lengths over half of its carapace width (Ebling et al. 1964; Sanchez-Salazar et al. 1987a). Summarizing the results from many feeding experiments (sources given in Table 3), we find that adult *Carcinus maenas* (with carapace widths generally between 30 and 70 mm) mainly select *Mytilus* sp. of 10 to 25 mm length, *Mya arenaria* of <20 mm length, other clams (*Cerastoderma edule*, *Mercenaria mercenaria*, and *Macoma balthica*) of <15 mm length, and gastropods of <20 mm length. In three studies of stomach contents where smaller crabs (<20 mm carapace width) were analyzed separately, bivalves were a major prey item of the larger but not the smaller crabs. Similarly, Ropes (1968) found that crabs of <30 mm carapace width ate fewer mollusks and more *Spartina* (unidentified as to species) than did larger crabs.

Carcinus maenas eats more in warm water than in cold (Walne and Dean 1972; Wallace 1973; Sanchez-Salazar et al. 1987a; but see Elner 1980), although its dominant prey size does not vary with temperature (Elner 1980; Sanchez-Salazar et al. 1987a). Feeding activity has been reported as normal down to 6–7°C, depressed below this, and ceasing somewhere between 2 and 7°C (Hancock and Urquhart 1965 reporting on the experiments of B. W. Jones; Ropes 1968; Walne and Dean 1972; Eriksson and Edlund 1977).

Potential ecological and economic impacts

If *Carcinus maenas* becomes widely abundant in California, it may significantly affect other organisms by predation, by being preyed upon, by competing for food or space, by digging and disturbing the sediments with its feeding activities, and by indirect effects. Many of these effects have been observed in other localities.

Predation by *Carcinus maenas* is thought to be the cause of dramatic declines in the numbers of soft-shell clams *Mya arenaria* in northern New England and southeastern Canada (Smith and Chin 1951; Glude 1955; MacPhail et al. 1955), and a major control on populations of the cockle *Cerastoderma edule* in Europe (Hancock and Urquhart 1965; Jensen and Jensen 1985; Sanchez-Salazar et al. 1987a, b). *Carcinus maenas* is reported to control the local distribution of mussels, sea urchins, dog whelks and periwinkles (Ebling et al. 1964; Muntz et al. 1965; Dare and Edwards 1976; Janke 1990), and to prevent the establishment of bivalve beds by preying on spat (Jensen and Jensen 1985). Heavy predation by *C. maenas* on snails in some areas may have selected for thicker and differently shaped shells (Hughes and Elner 1979; Elner and Raffaelli 1980; Vermeij 1982; Johannesson 1986), and for alarm re-

sponses (Atema and Stenzler 1977; Ashkenas and Atema 1978; Hadlock 1980).

Since introduced species make up more than 90% of the benthic biomass in all but the deepest parts of San Francisco Bay (Nichols and Pamatmat 1988; Nichols et al. 1990), it is expected that here *Carcinus maenas* will feed mainly on a variety of introduced species, some of which it has encountered in the Atlantic and many of which will be new to it. The Asian clam *Potamocorbula amurensis*, first collected in the Bay in 1986, is now the most abundant subtidal macrobenthic organism in Suisun Bay and is locally abundant intertidally (Nichols et al. 1990; J. Thompson personal communication 1993). It is a soft-shelled, shallow-infaunal or epifaunal clam whose maximum length lies within the size range of bivalves mainly eaten by *C. maenas* in laboratory experiments (as reviewed in previous subsection), and in our experiments it was readily consumed by *C. maenas*. We expect *P. amurensis* will be a major prey item for subtidally feeding and possibly intertidally feeding *C. maenas*. Such predation could lead to an increase in benthic diversity in those areas now wholly dominated by *P. amurensis*.

The most common and appropriately-sized potential prey species on San Francisco Bay mudflats and sloughs include the western Atlantic mud snail *Ilyanassa obsoleta*, the native shore crab *Hemigrapsus oregonensis*, the western Atlantic gem clam *Gemma gemma*, the Japanese mussel *Musculista senhousia*, the smaller individuals of the Asian littleneck clam *Venerupis philippinarum*, and the smaller individuals of the western Atlantic soft-shell clam *Mya arenaria*. In cordgrass banks, which *Carcinus maenas* has densely colonized on both sides of the Atlantic (Crothers 1968; Ropes 1968), likely prey include the New Zealand isopod *Sphaeroma quoyanum*, various introduced gammarid amphipods, small *H. oregonensis*, possibly the smaller sizes of the western Atlantic ribbed mussel *Geukensia demissa*, and pieces of the cordgrass itself (including the increasingly common Atlantic cordgrass *Spartina alterniflora*). On rocky substrate and pilings, various barnacles (both native and introduced species) and two nearly indistinguishable mussels, the native *Mytilus trossulus* and the Mediterranean *M. galloprovincialis*, along with algae such as *Ulva lactuca* are the likeliest prey.

Carcinus maenas may provide food for a variety of Bay organisms, as indicated by its predators in other waters and by predators of native crabs in the Bay. In the Atlantic, *C. maenas* has been eaten by crabs, shrimp, fish, birds, otters and seals. Many of these are similar to, and in some cases congeneric or conspecific with, organisms in San Francisco Bay, including a crangonid shrimp (Jensen and Jensen 1985), two sculpins, three gobies, various gadids and flatfish, a bass, a ray and a shark (Scott 1902; Hartley 1939; Smidt 1951; Clay 1965; Crothers 1968; Varagnolo 1968), sandpipers, sanderling, curlew, the great blue heron *Ardea herodias*, cormorants, ducks including the mallard *Anas platyrhynchos*, gulls including the herring gull *Larus argentatus* (Witherby et al. 1938–1941; Tinbergen 1953; Naylor 1958; Clay 1965; Harris 1965; Berrill and Berrill 1981; Schneider and Harrington 1981), and the harbor seal

Phoca vitulina (Sergeant 1951). Common predators of native crabs in San Francisco Bay include Dungeness crab *Cancer magister* (Tasto 1983); staghorn sculpin *Leptocottus armatus* (Reilly 1983); Pacific tomcod *Microgadus proximus* (Reilly 1983); starry flounder *Platichthys stellatus*, English sole *Parophrys vetulus* and Pacific sanddab *Citharichthys sordidus* (Reilly 1983); pile perch *Damalichthys vacca*, white surfperch *Phanerodon furcatus* and rubberlip surfperch *Rhacochilus toxotes* (Reilly 1983); striped bass *Morone saxatilis* and white croaker *Genyonemus lineatus* (Thomas 1967; Reilly 1983); white and green sturgeon *Acipenser transmontanus* and *A. medirostris* (McKechnie and Fenner 1971; Reilly 1983); bat ray *Myliobatis californica* and big skate *Raja binoculata* (Reilly 1983); and leopard shark *Triakis semifasciata* and brown smoothhound shark *Mustelus henlei* (Russo 1975; Talent 1982; Reilly 1983).

In Sweden, *Carcinus maenas* was observed to displace shrimp and other crabs from mussel flesh set out as bait (Eriksson et al. 1975b). *C. maenas* grows larger than the common existing shorecrabs in San Francisco Bay, and could compete vigorously for food with the native *Hemigrapsus oregonensis*, *H. nudus* and *Pachygrapsus crassipes*, and with the introduced Atlantic brackish-water crab *Rhithropanopeus harrisii* in the more saline part of *R. harrisii*'s range. Where abundant subtidally, *C. maenas* could compete with several *Cancer* species in the Bay. Competition is also possible with other benthic predators including invertebrates, fish and birds. Competition with *H. oregonensis* and *R. harrisii* for space under rocks on mudflats at low tide seems likely.

As noted above, *Carcinus maenas* digs through the top few centimeters of sediment, and sometimes up to 15 cm deep, searching for prey. Researchers have described changes in infaunal populations due to sediment disturbance by *C. maenas* (Le Calvez 1984, 1987; Gee et al. 1985). Increases in some species' populations have resulted from the reduction of predators or the reduction of competitors for food or space (Le Calvez 1984, 1987; Gee et al. 1985; Janke 1990).

Carcinus maenas' manifold potential for ecologic impacts suggests the possibility of critical economic impacts as well. The arrival of *C. maenas* in central Maine by the 1950s closely correlates with massive losses of softshell clam (*Mya arenaria*) beds on that coast (Smith and Chin 1951; Glude 1955). Control efforts in Maine and Canada included fencing, trapping and poisoning, with varying success (Hanks 1961). Many of the species of bivalves that are cultured and harvested in the northeast Pacific are eaten by *C. maenas* on other coasts, and in the laboratory *C. maenas* has consumed Dungeness crab (*Cancer magister*) up to its own size (Grosholz and Ruiz 1995). Although we have located no estimates of the economic loss in the northwestern Atlantic, substantial impacts on northeastern Pacific commercial and recreational shellfish, through predation on adults or spat, should be anticipated.

In Europe, *Carcinus maenas* has long been used for food, with annual landings from the Gulf of Venice in 1946 to 1965 estimated at 100 to 250 metric tons and a value of

US\$ 500 000 (Varagnolo 1968); and annual landings from the Atlantic by Portugal, Spain, France and England averaging 200 metric tons in 1982 to 1987 (Conseil International pour l'Exploration de la Mer 1982–1987). In the United States, *C. maenas* is occasionally used for bait (Rees 1963; Schmitt 1965).

Carcinus maenas is only the second species of non-native crab to invade American Pacific waters, preceded by the small American Atlantic xanthid crab *Rhithropanopeus harrisii*, which was first collected in Lake Merritt in San Francisco Bay in 1937 (Carlton 1979a). Similarly, only two crab species have invaded American Atlantic waters, *C. maenas* (as noted earlier) and the recently introduced Japanese grapsid *Hemigrapsus sanguineus* (McDermott 1991). Crabs are thus rare invaders in North American estuaries and bays, perhaps because of greater transport difficulties, because the "crab niche" is not as accessible in the face of native crabs as are other guilds (such as bivalve mollusks), or because of other, unknown ecological factors. Despite the paucity of crab invasions, the arrival and establishment of the green crab signals another potentially exceptional level of ecosystem change in San Francisco Bay, on a scale conceivably similar to that caused by the Asian clam *Potamocorbula amurensis* (Nichols et al. 1990; Alpine and Cloern 1992).

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