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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 (Vinogradev 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 (Bolinas 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 $25 \times 25 \times 29$ 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 anecdysis. 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 Carquinez 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

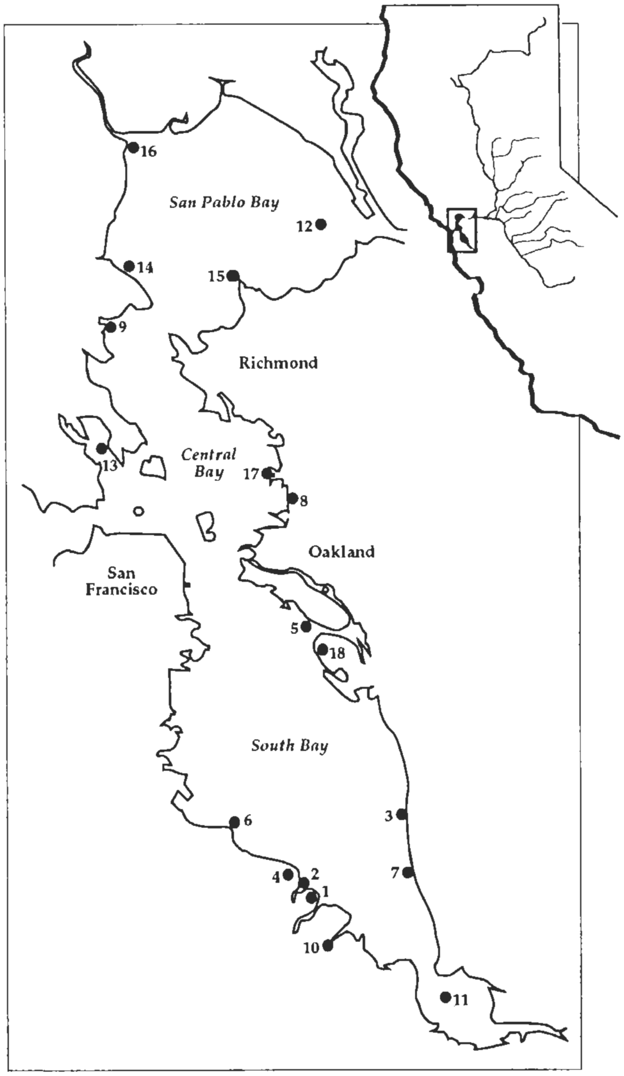

Fig. 1 *Carcinus maenas*. Records of living specimens in San Francisco Bay. Locations numbered as in Table 1

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 northwest 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	(n)	*Potamocorbula amurensis*	*Venerupis philippinarum*	*Mytilus* sp.	t	p
Without sediment						
P. amurensis vs *Mytilus* 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
P. amurensis vs *V. philippinarum*						
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
Mytilus sp. vs *V. philippinarum*						
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						
P. amurensis vs *V. philippinarum*						
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
P. amurensis vs *Mytilus* 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 nonindigenous species. The shallow lagoons are typically a