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Growth and persistence of a recent invader *Carcinus maenas* in estuaries of the northeastern Pacific

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Abstract

During the summer of 1998 a new year class of the invasive European green crab, *Carcinus maenas*, appeared in Oregon and Washington estuaries as well as in northern California, USA, and on Vancouver Island, Canada. This invader was first discovered in San Francisco Bay almost a decade earlier and by 1995 it had spread to northern California. The coast-wide colonization event we studied in 1998 (El Niño cohort) was correlated with unusually strong north flowing coastal currents from September 1997 to April 1998. Larval transport by ocean currents from established populations to the south appeared to be the mechanism for the colonization. Crabs from the 1998-year class grew faster than counterparts from Maine and Europe, averaging 14 mm in carapace width in June, and 46 mm by September 1998. By the end of their second summer, males ranged from 52 to 80 mm in carapace width, and by fall of 2000 some males attained a carapace width of over 90 mm. The life span for *C. maenas* in Oregon, Washington and British Columbia is estimated to be similar as in Europe and Maine: 4–6 years. Even though the initial colonists (98-year class) are dying of senescence, and coastal currents have not been favorable for larval transport from source populations in California, green crabs do persist in Oregon and Washington estuaries. It appears that local reproduction and recruitment in some years is high enough to keep this population from going extinct.

Introduction

The European green crab, *Carcinus maenas*, native to Europe and North Africa, has a long history of range expansion. During the last two centuries populations of *C. maenas* were introduced and have established themselves in Australia, including Tasmania, South Africa and on both coasts of North America (Almaça 1962; Le Roux et al. 1990; Cohen et al. 1995; Grosholz and Ruiz 1995). On the east coast of North America, warm winters have been correlated with high green crab abundance and pole-ward range expansions while severe winters, with mass mortality and range contraction (Welch 1968; Berrill 1982).

In 1989, a self-perpetuating population of *C. maenas* was discovered in San Francisco Bay.

The crabs likely arrived much earlier and built up their population 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 marine products such as lobsters and baitworms, and transport of larvae in ballast tanks of ships. From the source population in San Francisco Bay, larvae of *C. maenas* were carried north in ocean currents to Bodega Harbor, California in 1993. Subsequently, *C. maenas* was discovered in Monterey Bay, California (1994), Humboldt Bay, California (1995), Coos Bay, Oregon (1997), Morro Bay, California (1998), Willapa Bay, WA (1998) and Vancouver Island (1999) (Grosholz and Ruiz 1995; Miller 1996; Richmond 1998; Behrens Yamada and Hunt 2000; Figlar-Barnes et al. 2002; Grosholz, unpublished observations, Jamieson, unpublished observations).

The most recent range expansion of *C. maenas* into the Pacific Northwest is correlated with the strong El Niño event of 1997/1998. Seawater temperatures were unusually warm and strong poleward coastal currents of up to 50 km/day existed from September 1997 to April 1998 (Hickey 2001; Huyer et al. 1998). That summer, a strong new year class of *C. maenas* appeared in Oregon and Washington coastal estuaries as well as in northern California and on the west coast of Vancouver Island, British Columbia. Transport of larvae by ocean currents from established populations in the south appeared to be the mechanism for this coast-wide colonization event (Behrens Yamada et al. 2000; Behrens Yamada and Hunt 2000).

Scientists are concerned that *C. maenas,* a hardy generalist and effective predator, could permanently alter marine ecosystems on the west coast of North America. When abundant, these crabs can prevent the establishment of young bivalves, snails, urchins, barnacles and other species (Kitching et al. 1959; Muntz et al. 1965; Menge 1983; Jensen and Jensen 1985; Janke 1990). For example, the range expansion and population increase of *C. maenas* in New England in the 1950s has been linked to a drastic decline in landings of the 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 (Welch 1968). If the distribution and abundance of *C. maenas* on the Pacific Coast of North America increases, its ecological impact on existing native communities and its economic impact on the seafood industry (e.g., *Cancer magister*, flatfish and bivalves) could be substantial (Lafferty and Kuris 1996; Jamieson et al. 1998; Behrens Yamada 2001; Hunt and Behrens Yamada 2003).

Managers and researchers routinely use life history patterns to predict the future status of sport, commercial, and pest species (Figure 1). The study of growth and recruitment strength of *C. maenas* can give us clues about the future of

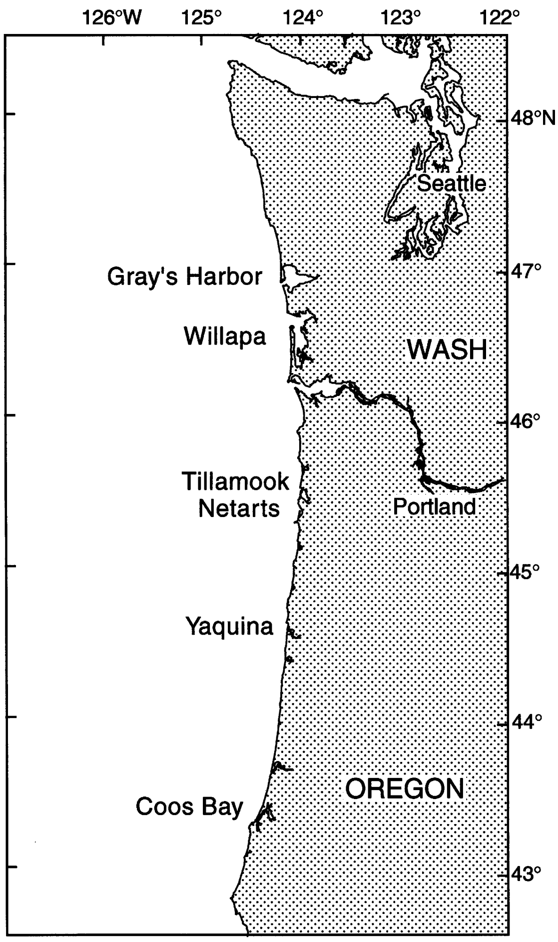

Figure 1. Map showing study sites in Oregon and Washington.

this invader in its new environment. The goals of this study were:

(1) to present growth data for the 1998-year class of *C. maenas* in Oregon and Washington,
(2) to compare growth and other life history features of the green crab in Oregon and Washington with those in Maine and Europe,
(3) to evaluate the relative recruitment strengths of the 1998–2003 year classes in Oregon and Washington, and
(4) to make predictions on the future of green crab populations in northeastern Pacific estuaries.

Methods

Growth and recruitment strength

By following the size frequency distributions of *C. maenas* in Oregon and Washington estuaries over time, we gained information on growth for the strong 1998-year class and the relative abundance of young-of-the-year crabs ('recruits') in subsequent years. We sampled for these 'recruits' at the end of the growing season in September and October. Because *C. maenas* larvae settle high on the shore (Zeng et al. 1999), and crabs move into deeper water as they age (Crothers 1968), we trapped throughout the intertidal zone to sample all life stages. Pitfall and minnow traps were deployed in the high intertidal to sample primarily young-of-the-year crabs, while minnow and collapsible Fukui fish traps were set at the mid and low intertidal zones to target larger crabs.

Pitfall traps are 20-l buckets filled with seawater and embedded in the substrate such that the rim is flush with the mudflat. Thus any actively foraging crab has a chance of falling into these un-baited buckets. In Yaquina Bay, we placed these traps in the high intertidal zone at the intersection of marsh vegetation (e.g., *Scirpus* sp.) and the upper mudflat. In Willapa Bay where the Atlantic cordgrass (*Spartina alterniflora*) has invaded this intertidal zone, traps were placed directly amongst the *Spartina* plants. In these high intertidal locations, pitfall traps are a successful method for sampling young crabs less than 45 mm. We employed this method with 10 traps over 6 days in Yaquina Bay in early fall of 1999 and on a monthly basis in Willapa Bay from 1998 to 2003. Each month 20 traps were monitored for three consecutive days. While we sampled five stations throughout Willapa Bay, we only report the 'recruitment' data for our main study site near the estuary mouth (Stackpole).

We used bait to attract crabs to the other types of traps. Fish (either salmon backbones with attached flesh or mackerel) were cut into sections and placed into egg-shaped commercial bait containers (15×8 cm). Holes (1 cm) were drilled into the plastic sides and lid to allow bait odors to diffuse. Minnow traps (21×31 cm), deployed throughout the intertidal zone in Yaquina Bay and Willapa Bay, were effective for trapping crabs from 30 to 70 mm. Collapsible Fukui fish traps ($63 \times 46 \times 23$ cm) were successful in trapping crabs over 40 mm. Yearly sampling effort for Yaqina Bay ranged from 150 to over 1000 trap-days and from 500 to over 2000 trap-days for Willapa Bay. Other Oregon estuaries and Grays Harbor, Washington received a trapping efforts ranging from 44 to 200 trap-days per year.

Typically, one bait container with fresh bait was placed in a trap for one high tide cycle (6–24 h depending on tidal height) before the trap was checked. All trapped crabs were identified to species and sex. The carapace widths (CW) of green crabs were measured with vernier calipers between the tips of their fifth anterio-lateral spines to the nearest lowest mm.

Researchers from Fisheries and Oceans Canada kindly provided us with their 10 green crab sightings. These crabs were discovered, primarily by shellfish growers, in remote locations on the west coast of Vancouver Island.

Growth comparisons with Maine and Europe

Absolute growth in crabs is a function of molt increment, the increase in size after a molt, and molt frequency. Rearing crabs in the lab until they molted yielded molt increment (Behrens Yamada et al. 2000). The results from this study were compared to similar studies done in Belgium with gravid females (d'Udekem d'Acoz 1993) and both sexes in Maine (Berrill 1982).

To measure the growth of crabs in the field, determine molt frequency, and provide a reference for interpreting our size frequency distribution data, we instituted a mark-recapture program. Numbered Floy Tags with molting cones (floytag @halcyon.com) were injected into the suture line between the posterior upper and lower carapaces. Because this is the first suture to open up during molting, the tag is retained. Thirty-six *C. maenas*, ranging in carapace width between 36 and 60 mm were trapped and tagged between December 4 and 10, 1998. In the process of retrieving marked crabs, another 200 were tagged over the next two years. Results from this study were compared to a similar study carried out in the Ria de Aveiro estuary Portugal (Gomes 1991).

Results

Growth of C. maenas in Oregon and Washington

Because no strong year-class immediately preceded or followed the strong 1998-year class of *C. maenas*, we were able to track its growth over time (Figure 2). Growth patterns for crab in all of the Oregon and Washington estuaries were similar (Behrens Yamada et al. 2000). Crabs reached a mean CW of 14 mm by the end of June, 32 mm by the end of July, and 42 mm by the end of August 1998. We estimate that most of the crabs settled between January and April of 1998.

By September 1998, the 1998-year class in both Yaquina Bay and Willapa Bay ranged in size from 32 to 60 mm and averaged around 46 mm in carapace width (Figure 2, Table 2). During the first summer we observed no difference in the number and size of males and females that entered baited traps in Yaquina Bay, Oregon, but in Willapa Bay, Washington the number of males outnumbered females 2 : 1. Very few females were trapped in their second and subsequent summers. Females that did enter traps and those that were turned in by clam harvesters and shellfish growers were typically one molt smaller than males of the same year class.

Mark-recapture data support the view that many crabs molted twice in the summer of 1999 (see next section). By late summer 1999, crabs ranged from 52 to 80 mm CW (Figure 2). During their third summer, crabs molted only once. In early fall 2000, males ranged in size from 70 to 92 mm and females from 61 to 80 mm. Growth slowed in subsequent years, with some crabs not molting in over a year (Appendix 1). After 2001 it became more difficult to distinguish the slow-growing individuals from 98-year class from fast-growing individuals of subsequent year classes.

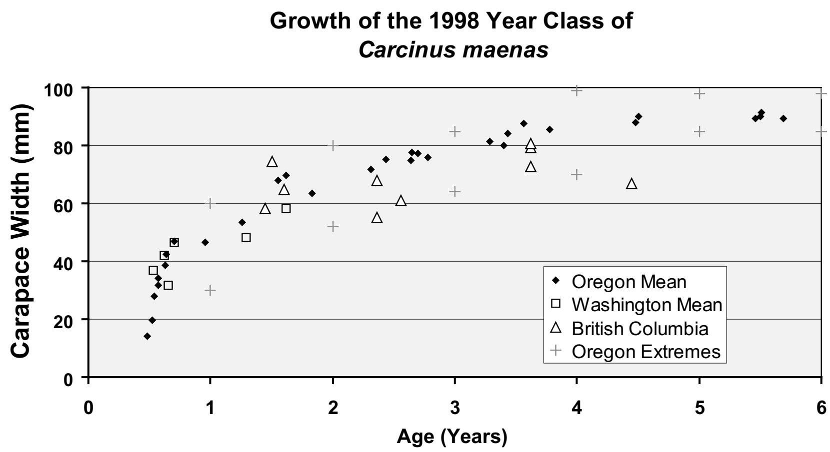

Figure 2. Growth of the 1998-year class of *Carcinus maenas* in northeastern Pacific estuaries. Data points represent means of 3–374 specimens collected from various sampling sites in Figure 1. Crosses indicate the range of values observed for Oregon at the end of each growing season. Year 0 = 1998; Year 5 = 2003. Note that the lower limits for the last two years are high estimates because we wanted to exclude fast growing individuals from subsequent year classes. Individual *C. maenas* sightings from the west coast of Vancouver Island, British Columbia were kindly supplied by Fisheries and Oceans Canada. The last crab from British Columbia was collected in June of 2002 and reared under favorable conditions in the lab. It never molted and died of senescence in November 2003.

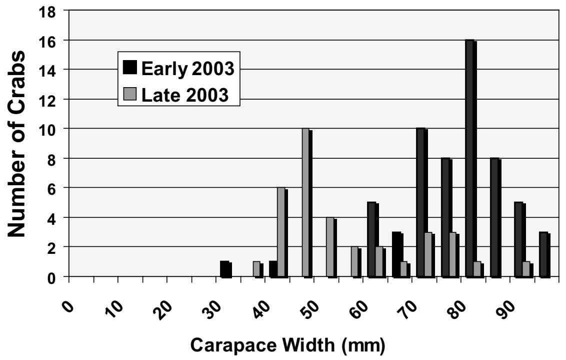

Figure 3. Size distribution of *Carcinus maeans* retrieved from Oregon estuaries in 2003. Note that crabs $\geq$ 85 mm were still present from April to July but dropped out of the population between August to October when a new year class (with a mean of just under 50 mm) entered the population.

Consequently, our estimates for the lower size ranges for these older crabs may be high (Figure 2). It is interesting to note that the 9/10 green crab sightings for British Columbia fall within the size ranges observed for the 98-year class from Oregon (Figure 2). This observation supports the view that strong northward currents during the 1997/98 El Niño resulted in a coast-wide seeding of estuaries. While we still recovered individuals from the 98-year class in the spring and early summer of 2003, these older crabs were noticeably absent by early October 2003 (Figure 3).

Growth comparisons with Maine and Europe

Molt increment comparison

Crabs from Oregon, Maine, Belgium and Portugal add a similar percentage to their CW when they molt (Table 1). While the growth increments for Oregon crabs were slightly higher than the rest, these differences, were not statistically significant.

Mark-recapture study

Nine of 36 crabs tagged in Yaquina Bay, Oregon in early December 1998 were recaptured the following spring and summer. Molt increments varied from 23% to 31% for one molt and 56–63% for two molts (Figure 3, Appendix 1). By July 1999, three smaller crabs (initial CW 39–42 mm) had molted twice, while three larger crabs (CW 50–61 mm) had molted only once. Molting frequency decreased after August and crabs did not molt between October and the beginning of April. Data from other recovered crabs indicate that adult *C. maenas* typically molt once in their third summer. One exception was an 82 mm male, which did not molt between April 2000 and April 2001 (Figure 4, Appendix 1).

Tagged crabs recovered by fishermen in the Ria de Aveiro estuary in Portugal exhibited similar molt increments (Table 1) but lower molt frequencies than *C. maenas* from Oregon. Only 22/490 (4%) of the marked crabs recovered by Portuguese fishermen had molted once and one crab did not molt in two years (Gomes 1991). With an average of 3 months between release and recovery, it appears that crabs in the Ria de Aveiro estuary molt less frequently than those in Oregon.

'Recruitment' of C. maenas *in Oregon and Washington*

By late summer and early fall 1999, a new cohort of *C. maenas* entered traps in both Yaquina and

Table 1. Comparison of molt increments of *C. maenas* from various parts of the world.

Data set	Range of x (mm)	Mean molt increment (%)	N	Regressions	R^2
Maine[a]	12–72	21	49	$y = ? + 1.17\,x$	0.988
Oregon	22–53	30	58	$y = 3.74 + 1.88\,x$	0.987
Belgium/females[b]	20–47	21	40	$y = 5.82 + 1.05\,x$	0.971
Oregon/females	22–51	28	26	$y = 4.74 + 1.15\,x$	0.969
Portugal[c]	36–59	22	22	$y = 10.06 + 1.02\,x$	0.977
Oregon	39–69	27	12	$y = 9.49 + 1.08\,x$	0.957

Regression equations give new carapace width (mm) as a function of old carapace width (mm). While mean growth increments for Oregon crabs appear larger, none of the pair-wise comparisons for slope and adjusted y values were statistically significant at $\alpha = 0.05$. Comparisons were based on Berrill 1982[a], d'Udekem d'Acoz 1993[b] and Gomes 1991[c]. Because we had to switch axes for the Maine data, we were not able to estimate the y intercept. The last comparison was done in the field with marked and recaptured crabs.

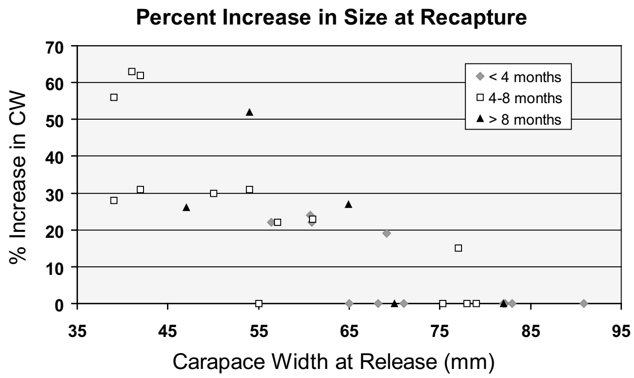

Figure 4. Percent increase in carapace width of marked and recaptured *Carcinus maenas* from Yaquina Bay, Oregon as a function of size at release and time interval. Note that growth increments under 35% represent one molt while those over 50%, two molts.

Willapa Bay (Table 2). At the end of their first growing season, these new 'recruits' ranged in size from 30 to 47 mm CW (Table 2) and were easily distinguishable from the 1998–year class ranging from 52 to 80 mm CW.

We observed much weaker 'recruitment' of young *C. maenas* from 1999 to 2003 compared to 1998 (Table 2). Average catches at the monthly monitoring site in Willapa Bay were one order of magnitude lower. The lowest recruitment rates

Table 2. Relative abundance (CPUE) and size of young-of-the-year *Carcinus maenas* at the end of their first growing season in the Coos, Yaquina, Netarts, and Tillamook estuaries, Oregon and in Willapa Bay, Washington.

Year class	Estuary	# Months <10 °C	Mean winter temperature (°C)	N	CPUE pitfall traps	CPUE minnow traps	Mean carapace width (mm)	SD	Range
2002	Coos		na	0		0			
2003	Coos		na	1		0.01	59.4		
1998	Yaquina	0	10.9	201		5.0	46.9	5.0	32–60
1999	Yaquina	4	9.0	13	0.20		38.0	5.0	30–47
2000	Yaquina	3	9.5	14		0.31	37.5	5.0	30–45
2001	Yaquina	3	9.5	1		0.0*	55		
2002	Yaquina	4	9.2	1		0.01	38.9		
2003	Yaquina	0	10.5	9		0.07	44.9	5.5	41–59
2004	Yaquina	3	9.9	4		0.07	35.3	5.1	32–43
2002	Netarts		na	0		0.0			
2003	Netarts		na	6		0.15	49.4	3.7	45–55
2002	Tillamook		na	0		0			
2003	Tillamook		na	5		0.17	50.0	3.1	46–55
2004	Tillamook		na	2		0.10	41.0		37–45
1998	Willapa	3	8.9	47	0.778	0.743	45.9	4.0	37–55
1999	Willapa	4	7.6	3	0.023	0	38.2	7.5	32–47
2000	Willapa	4	8.0	9	0.046	0.033	43.4	12.0	19–58
2001	Willapa	5	8.0	7	0.046	0.017	51.3	2.7	48–56
2002	Willapa	4	7.6	0	0.0	0.0	–		
2003	Willapa	3	9.0	10	0.133	0.0	48.3	5.1	43–59

Crabs were typically caught in September and October. Catch per unit effort (CPUE) is reported as number of crabs per trap per day. N = number of young crabs sampled; SD = Standard Deviation; na = temperature data not available. Asterisk indicates that only 7 minnow traps were deployed and that the one young crab entered a collapsible Fukui fish trap. Surface water temperatures for December-March for the Hatfield Marine Science Center Dock in Yaquina Bay were provided by David Specht of the Newport EPA, those for Willapa Bay, by Jan Newton of the DOE. Note that large mean size in 1998 and 2003 may be linked to warm water temperatures during the previous winter.

observed were in 2002 with only one recruit in Oregon and none in Washington. The end of the 2003-growing season, however, produced higher recruitment than in 2002 in all five of the estuaries sampled (Table 2, Figure 3). This higher 'recruitment' and larger mean size of 'recruits' (45–48 mm CW) appears to be linked to warmer water temperatures during the previous winter (Table 2).

Discussion

Life history

Since the life history patterns of *C. maenas* in northeastern Pacific estuaries have only been studied for a few years, we summarize our observations and compare them to studies carried out elsewhere in the world (Table 3).

Colonization pattern

When *C. maenas* colonized estuaries in California in 1993 and in Oregon and Washington in 1998, scientists were able to follow the growth of these two strong cohorts. In both cases, young crabs appeared simultaneously in a number of adjacent estuaries in late spring. This dispersal is attributed to unusually strong coastal currents that carried the larvae north from well-established populations to the south (Grosholz and Ruiz 1995; Behrens Yamada and Hunt 2000; Behrens Yamada 2001). Similar patterns of northward range expansions following strong El Niños have been documented for marine fishes and invertebrates (Schoener and Fluharty 1985; Hart 1982).

Settlement time

We estimated the settlement time of *C. maenas* larvae from the plankton using observed size distributions and from growth rates of young crabs measured in other parts of the world. In Bodega Harbor, California, crabs averaged 18 mm CW in June and by September of 1993 attained 47 mm. The corresponding values for Oregon and Washington estuaries in 1998 were 14, and 46 mm respectively. Rearing studies indicate that newly settled green crabs can molt as frequently as once a week and that it takes 133 days for a newly settled crab to reach 25 mm at 15 °C (Klein Breteler 1975b; Mohammedeen and Hartnoll 1989). Furota et al. (1999) followed the growth of a single *Carcinus aestuarii* megalopa under natural conditions in Tokyo Bay. It settled from the plankton in late March and by early June had attained a carapace width of 18.6 mm. In April of 1998, Heath Hampel, a shellfish grower in Coos Bay, Oregon observed "thousands" of small crabs (<10 mm) sheltering under oyster shells. We thus estimate that most of the 1998-year class of *C. maenas* settled in Oregon and Washington estuaries during the first 4 months of 1998.

Growth rates

Populations of *C. maenas* on the west coast of North America exhibit faster growth rates than populations in other parts of the world (Table 3). In Oregon and Washington, *C. maenas* from the 1998-year class reached a CW of 32–60 mm after their first summer and 52–80 mm after their second summer. By contrast, researchers studying *C. maenas* in the southern North Sea documented carapace widths ranging from 5 to 30 mm after their first growing season, and 35–50 mm after their second growing season (Broekhuysen 1936; Klein Breteler 1976a,b). In central Maine, crabs attain only 3–10 mm after their first summer and 13–28 mm after their second summer (Berrill 1982).

Various factors, including food availability and temperature affect molt increment and molt frequency. Molt increment can be affected by severe food limitation (Klein Breteler 1975b). Adelung (1971) found that growth increment ranged from 30% to 31% when *C. maenas* were raised under favorable conditions in the lab, and from 20% to 23% under marginal conditions. In their first summer, green crabs in Oregon exhibited growth increments ranging from 20% to 40% and averaged 30% (Behrens Yamada et al. 2000), indicating that they experienced close to ideal growing conditions.

Most of the rapid growth of crabs from Oregon can be attributed to a higher molting frequency than in their native habitat and in Maine. Crabs molt more frequently at higher temperatures (Mohamedeen and Hartnoll (1989) and Klein Breteler (1975b) (Table 3). Water temperature also sets the length of the growing season.

Table 3. Comparison of length of growing season and life history features of *Carcinus maenas* in various parts of the world.

Location	Ref.	Length of Growing Season, number of months water temperature is above 10 °C	Peak* and range of settlement	CW by first winter (mm)	CW by second winter (mm)	CW of mature female (mm)	Age at first mating (years)	Maximum carapace width (mm) males	Maximum carapace width (mm) females	Maximum life span (years)	Generation time (years)
Central Maine	1	5	September* Late Aug–September	3–10	13–28	34	2–3	82	70	5–6	3–4
Baltic/Germany	2	6	September*	7.5	25–45	30	2	75	60	4+	3
Kattegat/ Denmark	3	6	Aug–September*	7–13	30–45	30	2	92		4+	3
Western Sweden	4	6	July–August* late June–late September	5–20	25–35	30 estimate	2	100		4+ estimate	2–3
Southern North Sea	5	7	July* June–November	5–30	35–50	30	1–2	86	70	3–4	1–2
Oregon/Washington 1998 El Niño year class	6	8–12	Winter to Spring, estimate	32–60	52–80	32	<1	99.6	79	4–6	1
Portugal	7	12	Late April–June* April–October	5–30	30–40 estimate	21	<1	71.5		4 estimate	1

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-Olav Moksnes unpublished observations; 5 = Broekhuysen (1936), Klein Breteler (1975a, 1976a,b); d'Udekem d'Acoz (1993); 6 = Behrens Yamada and Hunt (2000), Figlar-Barnes et al. (2002), Behrens Yamada, unpublished data; 7 = Almaça (1982), Gomes (1991), Queiroga (1989), Henrique Queiroga, unpublished data. Green crabs can molt (grow) when water temperatures are above 10 °C. CW = carapace width.

When water temperatures drop below 10 °C in winter, crabs stop molting. When temperature drops below 7 °C, crabs stop feeding and start looking for shelter in deep crevices or in the sediment (Ropes 1968). Thus, in areas like Maine, the German Baltic, eastern Denmark, and western Sweden, where water temperatures drop below 10 °C for at least half the year, crabs undergo fewer molts per year and thus grow considerably slower than those in Oregon and Washington (Table 3).

Water temperature, however, cannot explain the observation that *C. maenas* appear to molt more frequently in Oregon than in Portugal. Tagged adult *C. maenas* below 80 mm molted at least once a year in Yaquina Bay, Oregon while crabs from the Ria de Aveiro, Portugal molted less frequently. In Oregon and Washington, seawater temperatures typically drop below 10 °C for 3–4 months during most years. Our tagged crabs ceased molting between the end of September and the beginning of April. In Portugal, however, temperatures rarely fall below 10 °C and crabs molted between August and September and between January and February (Gomes 1991). Even though the growing season is typically longer in Portugal, crabs molt less frequently. The reasons for this discrepancy are difficult to determine. Contributing factors could be food limitation, cannibalism and high incidence of parasitism at high crab densities in their native habitat (Bückmann and Adelung 1964; Torchin et al. 2001).

Age of sexual maturity

On the West Coast of North America, *C. maenas* reach sexual maturity at a similar size as in northern Europe and Central Maine, however, they do so at an age of less than one year (Table 3). Sexual maturity in green crab females from the Isle of Man, UK occurs around the 11th or 12th molt stage at a carapace width of 32–34 mm (Mohamedeen and Hartnoll 1989). In Belgium, d'Udekem d'Acoz (1993) found that all of the mature females in June were above 31 mm but that a small proportion of females in late summer and fall were between 26 and 30 mm. Thus, in a typical year, most females in the southern North Sea do not attain sexual maturity until their second summer, at the age of over 1 year. In central Maine the smallest mature female reported was 34 mm at age 2–3 (Berrill 1982). In Oregon, a 25-mm female was in its pre-puberty molt while the smallest mature female was 32-mm.

Maximum size and longevity

While the size distribution of crabs in a population varies from area to area (Torchin et al. 2001), the maximum size reached by *C. maenas* appears to remain fairly constant: over 70 mm carapace width for females and over 90 mm for males (Table 3). Females are generally smaller than males after they reach sexual maturity and start brooding eggs. The largest male *C. maenas* on record was 100 mm in CW and was recovered off the west coast of Sweden in 2000 (Moksnes, unpublished data). One male crab from Yaquina Bay approached that size in October 2001 with a carapace width of 99.6 mm. While there is no indication of a terminal instar in *C. maenas*, the rate of growth decreases with age and crabs that have not molted for a long time appear to die of senescence. From observing the death of captive green crabs of known age and from observing the disappearance of the 98-year class in 2003, we conclude that longevity of *C. maenas* in Oregon and Washington is around 4–6 years, similar to that reported for Europe and Maine (Table 3).

Growth and persistence

The ideal growing conditions experienced by the 1998 cohort of *C. maenas* in Oregon and Washington during the summer of 1998 could be interpreted, in part, as 'ecological release' experienced by a new invader. Typically an invader enjoys a high growth rate in its new habitat at the leading edge of a biological invasion due to relaxed competition, predation and parasitism (Simberloff et al. 2000; Torchin et al. 2001). Klein Breteler (1975a) observed that *C. maenas* in the first settlement wave in the Dutch Wadden Sea grew larger and survived better than those in subsequent settlement waves. He attributed the slower growth and poorer survival of late recruits to intraspecific competition with and predation by the slightly larger crabs. Ecological release as well as unusually warm weather during the first months of 1998 and early settlement from the plankton all could have contributed to the high growth rate of the 1998-year class. We predict that once a large, viable, self-sustaining population of *C. maenas* is established in Oregon and Washington, growth rates would be lower than those observed for the 1998 cohort.

While *C. maenas* grow and reproduce well in Oregon and Washington estuaries, poor recruitment, at present, is limiting population number. Since larvae rear in the open ocean (Queiroga, personal communication), the dilution factor is great and unfavorable currents could transport them out to sea where they would be lost to the system. Successful recruitment will require a large larval plume, favorable rearing conditions and favorable currents that return larvae to coastal estuaries. Circumstantial evidence indicates that El Niño events provide these favorable conditions (Behrens Yamada and Hunt 2000). Successive years of strong El Niños (as is predicted with global warming) could see range expansions and the build-up of *C. maenas*.

It is difficult to predict whether the satellite population of *C. maenas* in Oregon and Washington estuaries, will persist in the absence of frequent El Niño events. Since northward coastal currents during the winters of 1999–2003 have been much weaker than during 1998 (Hickey 2001; Anonymous 2002; Huyer, personal communication), conditions for larval transport from California have not been favorable. It appears that, at present, local reproduction and recruitment is high enough during some years to keep the Oregon and Washington population of green crabs from going extinct.

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Appendix 1. Carapace width of marked and recovered green crabs in Yaquina Bay, Oregon.

Crab #	Sex	Date released T_1	Date recaptured T_2	Carapace width (mm) at T_1	Carapace width (mm) at T_2	% increase
11	F	12-11-98	5-12-99	39	50	28
13	M	12-11-98	5-12-99	42	55	31
16	M	12-11-98	7-13-99	61	75.3	23
21	M	12-13-98	7-19-99	39	60.7	56*
23	M	12-13-98	7-08-99	54	71	31
25	M	12-13-98	7-09-99	50	67.0	30
40	M	12-14-98	7-21-99	42	68.2	62*
41	M	12-14-98	5-02-00	54	82.0	52*
49	M	12-17-98	7-13-99	41	67.1	63*
58	M	8-03-99	4-30-00	47	59	26
97	M	12-13-99	7-22-01	68.1	89 estimate	molted
157	M	1-19-00	4-30-00	60.7	75.4	24
175	M	4-30-00	8-18-00	56.4	69.2	22
222	M	8-26-00	10-09-00	60.9	74.2	22
221	M	8-26-00	4-10-01	57.1	69.5	22
164	M	1-19-00	4-20-01	64.9	82.3	27
182	M	8-12-00	4-22-01	69.1	82.1	19
288	M	5-28-01	10-20-01	77	89	15
7	M	12-11-98	4-30-99	55	55	0
16	M	7-13-99	12-16-99	75.3	75.3	0
25	M	7-09-99	9-26-99	65	65	0
40	M	7-21-99	8-25-99	68.2	68.2	0
162	M	1-19-00	5-02-00	78	78	0
174	M	4-03-00	4-22-01	82	82	0
180	M	8-11-00	4-10-01	70	70	0
183	M	8-12-00	11-06-00	82.2	82.2	0
184	M	8-12-00	10-19-00	83	83	0
185	M	8-12-00	10-16-00	71	71	0
187	M	8-12-00	9-04-00	82	82	0
214	M	9-17-00	10-07-00	90.9	90.9	0
206	M	10-09-00	4-21-01	79	79	0

Asterisk indicates that crabs with size increments over 50% had molted twice since release. Number 97 was observed by a shrimp harvester and returned to the field. Number 174 did not molt in over a year.

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