

Invasive green crab, *Carcinus maenas*, on the Atlantic coast and in the Bras d'Or Lakes of Nova Scotia, Canada: larval supply and recruitment

Beth Cameron* and Anna Metaxas

Department of Oceanography, Dalhousie University, Halifax, Nova Scotia, Canada, B3H 4J1.

*Corresponding author, e-mail: beth.cameron@ns.sympatico.ca

Patterns in larval supply and recruitment of the invasive European green crab, *Carcinus maenas*, were examined at two sites in Nova Scotia, Canada: a typical Atlantic coastal site with high salinity (~33) and strong tidal signal (Terence Bay); and a microtidal site in the Bras d'Or Lakes, where surface salinity fluctuated from 0 to 23 (Benacadie Pond). Abundance of all life history stages (zoeae, megalopae, juveniles and ovigerous females) was sampled approximately biweekly at each site from June 2001 to June 2002. The reproductive season, based on the presence of ovigerous females, is ~5 months (June to October) at both sites. Zoeae-I were collected from June to July 2001 and in June 2002 at Terence Bay, and from June to August 2001 at Benacadie Pond. We did not collect later zoeal stages at either site. Megalopae were collected from September to October 2001 at Terence Bay, and from August to September 2001 at Benacadie Pond. Juveniles 1–6 mm carapace width (CW) were present throughout the summer at Terence Bay, and only in autumn at Benacadie. Juveniles 6–12 and 12–27 mm CW were present throughout the summer and autumn at both sites. At Terence Bay, densities of 1–6 and 12–27 mm CW juveniles did not vary among intertidal zones. In contrast, the 6–12 mm CW size-class appeared to move higher in the intertidal through the season, possibly due to effects of predation.

INTRODUCTION

Non-indigenous species can have drastic ecological effects on the environments they invade, frequently with serious economic implications. Marine biological invasions are particularly difficult to manage or predict if the invading species are tolerant of a wide range of environmental conditions. The green crab, *Carcinus maenas* (Linnaeus), is native to Europe, where it is found from Norway to Mauritania (Clark, 1986). This species has become established in many parts of the world, including both coasts of North America (Ropes, 1967; Cohen et al., 1995).

The green crab has significant impacts on populations of mussels (*Mytilus edulis* (Linnaeus)), dogwhelks (*Nucella lapillus* (Linnaeus)), and cockles (*Cerastoderma edule* (Linnaeus)) in its native range (Sanchez-Salazar et al., 1987), and is capable of preying on small oysters and scallops (Ropes, 1967). An efficient burrower, *C. maenas* is also capable of feeding on infaunal species, and preys on quahogs (*Mercenaria mercenaria* (Linnaeus)) and softshell clams (*Mya arenaria* (Linnaeus)) in eastern North America (Ropes, 1967). It is held responsible for the near demise of the soft-shell clam (*Mya arenaria*) fishery in the New England states in the 1950s (Ropes, 1967). In Bodega Bay, California, the green crab caused 5- to 10-fold declines in the abundances of two clam species (*Nutricula tantilla* (Gould) and *N. confusa* (Gray)) and the native shore crab (*Hemigrapsis oregonensis* (Dana)), within three years of its arrival (Grosholz et al., 2000). Understandably, there are grave concerns about the potential impact

of the green crab on commercially important bivalve aquaculture operations in Nova Scotia, on the Atlantic coast of Canada.

Carcinus maenas was first reported on the eastern coast of the United States in 1817 (Cohen et al., 1995) and has been spreading episodically northward ever since. In the Gulf of Maine, USA, pulses of northward expansion have been coincident with periods of warmer surface temperatures in the 1930s, 1950s and 1970s (Berrill, 1982). *Carcinus maenas* was first found in Nova Scotia, Canada, in 1953, in Pereau River on the Minas Basin and at Sandy Point in St Mary Bay (MacPhail et al., 1955). During the last decade, *C. maenas* has become extremely abundant on most coasts of the Province, and has invaded the Bras d'Or Lakes in Cape Breton. Also, it has been expanding northward rapidly, and *C. maenas* was found in Prince Edward Island in 1998 (Gillis et al., 2000), and the Gulf of St Lawrence coast of New Brunswick in 2002 (A. Locke, personal communication). Interestingly, in the 1980s, this species was not considered able to tolerate lower water temperatures than those found on the central coast of Maine, USA (Berrill, 1982), and northern expansion was not considered likely.

Surprisingly little data on the larval biology and ecology of this species are available for regions outside of the native range, except Berrill (1982). Thus, little is known about its reproductive biology or the ecology of the early life history stages in Nova Scotia. Although there has only been anecdotal evidence of females bearing eggs in this Province, juvenile and adult crabs are extremely abundant (personal observations), indicating

the high reproductive success of this species. To our knowledge, there have only been two reports mentioning the presence of *C. maenas* zoeae in plankton samples from this Province (Roff et al., 1984, 1986).

The early life history of *Carcinus maenas* has five free swimming larval stages, including four zoeal and one megalopal phase (Rice & Ingle, 1975). The megalopal phase settles onto the substrate and metamorphoses into the first of several juvenile crab stages. Larval development can vary greatly with salinity and temperature (Dawirs, 1985; Nagaraj, 1993) and, while adult *C. maenas* can tolerate practical salinities as low as 5, larvae are not known to complete development to the megalopal stage at salinities below 20 (Nagaraj, 1993; Anger et al., 1998). Survival of zoeae decreases with increasing temperature and decreasing salinity (Nagaraj, 1993; but see Dawirs, 1985). Early zoeal stages (zoeae-I, -II and -III) are more stenohaline than zoeae-IV (Nagaraj, 1993) and megalopae (Lance, 1964). In the Bras d'Or Lakes of Cape Breton Island, summer temperatures are significantly warmer than in coastal waters in Nova Scotia, and salinity ranges from 20 to 26 (Petrie & Bugden, 2002). We have shown that duration of zoeal development is shorter at high (32) than low salinities (20 and 26) in larvae from Benacadie Bras d'Or Lakes (Cameron & Metaxas, unpublished data).

Temperature can have pronounced effects on several life history processes in *C. maenas*. Temperatures in central Maine are similar to those encountered in certain areas in the native range of *C. maenas*, such as parts of Iceland, Denmark, and the German Baltic, resulting in comparable reproductive cycles and rates of growth in these areas (Berrill, 1982; Pihl & Rosenberg, 1982). However, water temperatures are considerably warmer ($\sim 4\text{--}5^\circ\text{C}$) in other parts of the native range (UK, Holland) than in coastal Maine (Berrill, 1982). Consequently, *C. maenas* extrude

eggs, spawn, settle and reach reproductive maturity earlier there (Broekhuysen, 1936; Crothers, 1967; Klein-Breteler, 1975) than in Maine (Berrill, 1982). Temperatures in western Sweden are intermediate between these two ranges, resulting in intermediate timing of settlement and rate of juvenile growth (Dries & Adelung, 1982).

As water temperatures in Nova Scotia are slightly lower than those of the central coast of Maine, the timing of spawning and settlement is likely slightly delayed, and growth rate of juveniles decreased. While the timing and duration of larval development of *C. maenas* in Nova Scotia may differ from other areas where this species occurs, the basic mechanisms affecting recruitment patterns should not.

In this study, we examined patterns of larval release, supply, and recruitment of *Carcinus maenas* on the southern coast and in the inland Bras d'Or Lakes of Nova Scotia. These sites differ in temperature, salinity, and the degree of tidal activity. To determine the temporal patterns of spawning, as well as larval, postlarval and recruit abundance in the water column and on the benthos, each stage was sampled at regular intervals at both sites over the course of one year. Temporal patterns of larval abundance may vary between the Bras d'Or Lakes and Atlantic coast sites because of the effect of temperature on timing of larval release and rates of larval development (Dawirs, 1985), and the salinity threshold for larval survival (Anger et al., 1998). Further, the small size and isolation of the Bras d'Or Lakes from the open ocean may dictate that larval dispersal occurs on a more limited spatial scale than along the coast, affecting the magnitude and temporal extent of total recruitment.

This study was conducted to determine: (1) whether zoeae are present at different times of the year in the Bras d'Or Lakes and on the Atlantic coast; (2) whether settlement occurs over the same period at these sites; and (3) whether the occurrence and/or abundance of newly settled juvenile crabs (recruits) is related to the abundance of larval life history stages (zoeae and megalopae) at these sites.

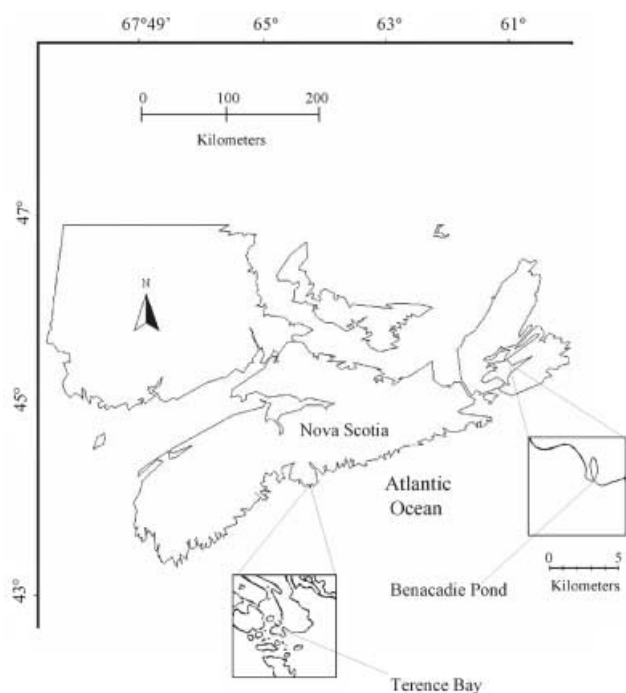


Figure 1. Location of study sites at Terence Bay and Benacadie in Nova Scotia, Canada.

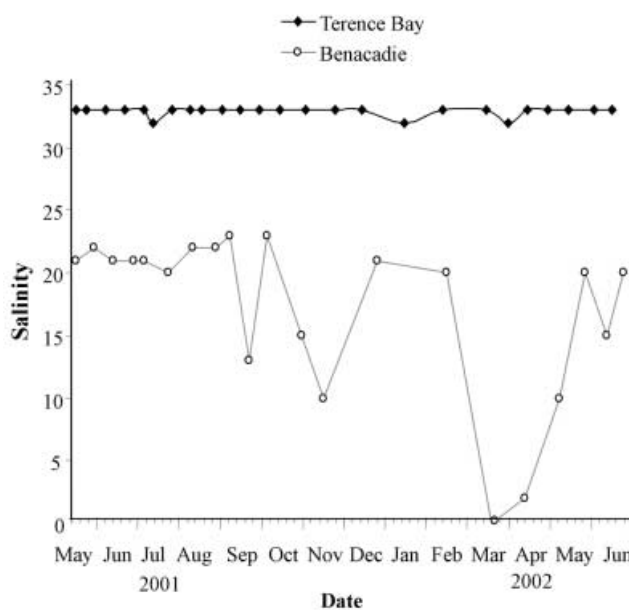


Figure 2. Surface salinity at Terence Bay and Benacadie, Nova Scotia, sampled biweekly from June 2001–July 2002.

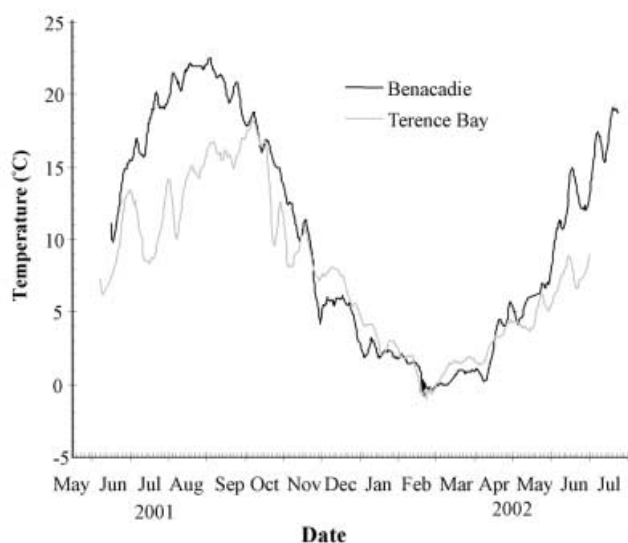


Figure 3. Mean surface-water temperatures (averaged over 12 h period) at Terence Bay (grey line) and Benacadie (black line), Nova Scotia, measured by a HOBO temperature logger attached to the substrate at <1 m depth between May 2001 and June 2002.

MATERIALS AND METHODS

Study sites

The coastal site was a wave-sheltered location at Terence Bay, Halifax County, Nova Scotia, Canada (44°27'N 63°43'W) (Figure 1). This site has fully saline waters (practical salinity of 33) and a mean tidal range of approximately 1.6 ± 0.5 m. The site in the Bras d'Or Lakes was at Benacadie, Cape Breton County (45°54'N 60°43'W) (Figure 1). This site was located in the narrow (~25 m wide at narrowest point) channel connecting Benacadie Pond (1.5 km long by 0.5 km wide) to the main Bras d'Or Lake (Figure 1). The Lakes are characterized by low salinity (typical practical salinity of 20–26), a wide temperature range, (they often freeze over in winter and may reach $>25^{\circ}\text{C}$ in summer), and a mean tidal range of approximately 0.3 ± 0.1 m. The small tidal fluctuations in the Lakes are frequently obscured by atmospheric events (Petrie, 1999) and are, thus, difficult to predict. Temperature was continuously monitored at each site with a HOBO Stowaway Tidbit temperature logger (accuracy $\pm 0.2^{\circ}\text{C}$ at 21.1°C) anchored subtidally to the substrate. Salinity was measured every two weeks with a hand-held, temperature-compensated refractometer (WestoverTM model RHS-10ATC).

Sampling of larvae and juveniles

The abundance of zoeae in the water column (~10 cm below the sea surface) was sampled approximately biweekly from 25 May 2001 to 25 June 2002 at Terence Bay, and from 30 May 2001 to 3 July 2002 at Benacadie, with a battery-powered bilge pump at a rate $\sim 141 \text{ min}^{-1}$. Because zoeae may avoid the narrow opening, a funnel (0.15 m in diameter) was affixed to the input hose. All

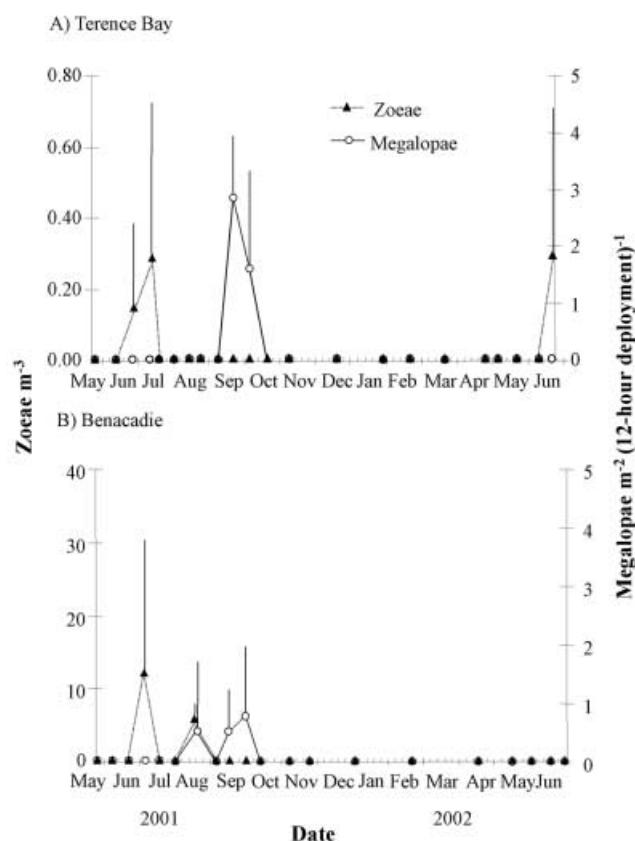


Figure 4. *Carcinus maenas*. Abundance of zoeae (mean \pm SD, $N=2$) and megalopae (mean \pm SD, $N=5$) at Terence Bay (A), and Benacadie (B), sampled biweekly from June to December 2001 and from May to June 2002, and monthly from December 2001 to April 2002.

samples were collected during daylight hours at both sites, and during high tide at Terence Bay. Sampled volumes ranged from 1.54 to 5.41 m^3 . Two replicate samples were pumped at each site. At Benacadie, both samples were pumped in the channel, but from 4 July until 2 September 2001, the second sample was pumped from the pond. After 2 September 2001, two replicate samples were collected from each of the pond and channel, until the pond froze in January 2002. Sampling resumed in April 2002. The sampled water was pumped through a $63\text{-}\mu\text{m}$ net and the contents of the cod end were collected, preserved in 80% ethanol, and later sorted under a microscope. Zoeae were identified according to Rice & Ingle (1975).

Megalopae were also sampled biweekly, from May 2001 to June 2002, usually on the same day as zoeae, using artificial floating collectors, used previously for *Carcinus maenas* (Moksnes & Wennhage, 2001). These consisted of a 40 cm long PVC pipe (16 cm i.d.) frame surrounded by a sleeve of hog's hair air-conditioning filter material, and moored ~ 10 cm below the surface. The surface area of the filter material was 0.4 m^2 . Five collectors were deployed below the low tide line at each site, for 12-h periods during daylight, to minimize possible emigration of megalopae from the collectors at night (Moksnes & Wennhage, 2001). From September 2001 until the end of the sampling period, the collectors were deployed near sunset for 24 h because of reduced daylength. Upon retrieval, the

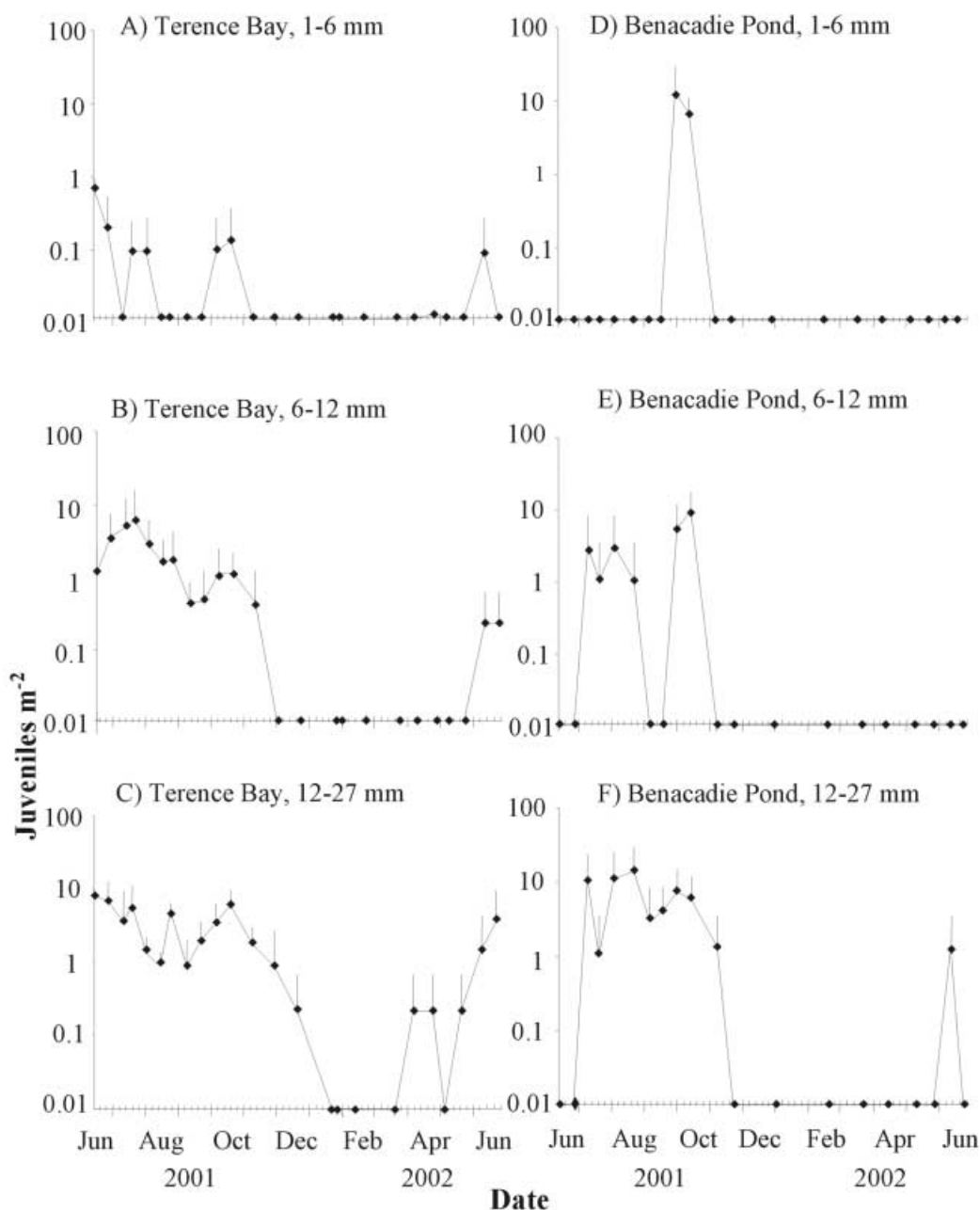


Figure 5. *Carcinus maenas*. Mean abundance of juveniles (\pm SD) in three size-classes averaged over three intertidal zones at Terence Bay (A, B & C) ($N=3$), and in <15 cm depth at Benacadie (D, E & F), as determined by biweekly 0.25 m² quadrat sampling ($N=6$) from June 2001 to July 2002.

collectors were soaked in fresh water for a minimum of 30 min, and the fresh water sieved for megalopae, which were preserved in 80% ethanol for later examination under the microscope. Megalopal abundances were standardized to the number of megalopae per m² of collector area per 12-h deployment.

At each site, abundance of juveniles was determined approximately biweekly from May 2001 to July 2002 (except monthly from December 2001 to March 2002) as weather and ice conditions permitted, using six replicate quadrats (0.5×0.5 m). At Terence Bay, the sampling site is a continuous, gradually sloping ($<20^\circ$) granitic bedrock outcrop. Because of the magnitude of tidal activity, the horizontal extent of the intertidal habitat is ~ 12 m. In

native macrotidal habitats, juvenile green crabs are most abundant in the high intertidal zone (Hunter & Naylor, 1993). Because such data are not available for non-native habitats and to maximize collection of juveniles, at Terence Bay, six quadrats were placed in each of three intertidal zones (their mid height defined as the height above mean low low water (MLLW) and by the dominant macroalgal species: low zone: 0.45 m, *Fucus vesiculosus* (Linnaeus); mid zone: 1.1 m, *Ascophyllum nodosum* (Linnaeus); and high zone: 1.5 m, *A. nodosum* and *F. spiralis* (Linnaeus)). Abundance of juveniles was then averaged across the three zones. At the microtidal Benacadie Pond, six quadrats were placed in <15 cm water depth. The substrate in the pond along the edge of the channel is sand, whereas the deeper parts of

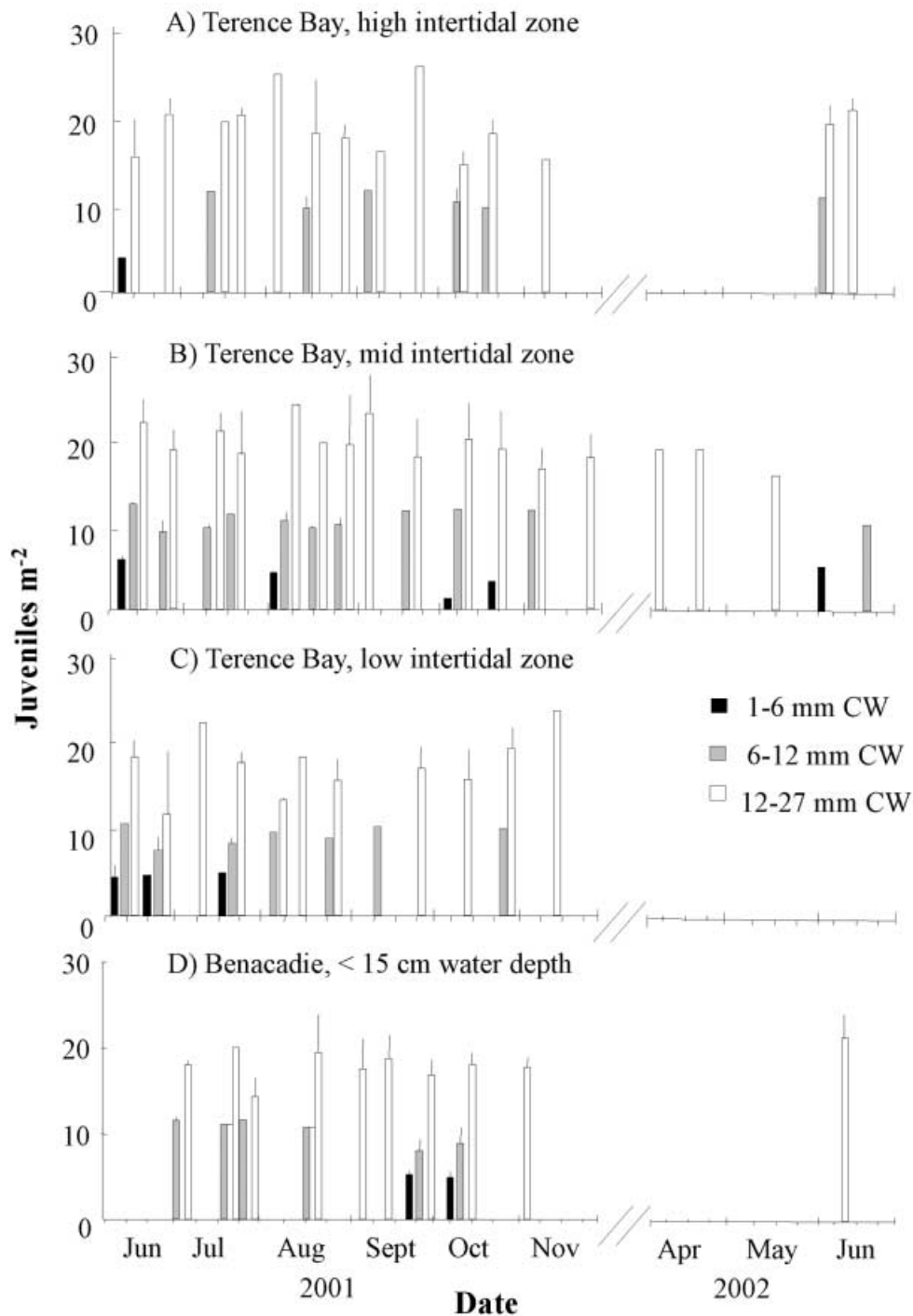


Figure 6. *Carcinus maenas*. Mean carapace width of juveniles (\pm SD, $N=2$ to 11) in each of three size-classes in the three intertidal zones at Terence Bay (A, B & C), and in < 15 cm depth at Benacadie (D), as determined by biweekly 0.25 m² quadrat sampling from June 2001 to July 2002.

the channel are granitic bedrock (grade 10°), covered with a layer (>15 cm) of coarse sand or cobbles. In each quadrat, the substrate and any macroalgae present were carefully examined for the presence of juveniles, and the substrate removed to a depth of 5 cm, if possible. Carapace widths (CWs) of captured crabs were measured to the nearest 0.1 mm using digital Vernier calipers and the crabs were subsequently released.

In Maine, USA, Berrill (1982) estimated that females of *Carcinus maenas* can reproduce at 34 mm CW. However, we

selected 27 mm as the maximum CW of a juvenile, based on the minimum size of captured ovigerous females at Benacadie. Juveniles were assigned to one of three size-classes, 1–6, 6–12, and 12–27 mm CW, respectively. The 1–6 mm CW size-class included newly settled juveniles, while the 6–12 mm CW size-class represented juveniles which had already survived one winter. These size-classes were based on the findings of Berrill (1982) that newly settled *C. maenas* on the central coast of Maine grow to a mean of \sim 6 mm CW before winter, and reach 13–25 mm

Table 1. Number of trapped adult female *Carcinus maenas* in each of four reproductive stages (1, non-reproductive; 2, bearing orange eggs in early stage of development; 3, bearing dark, mature eggs with no empty egg capsules; 4, spawning or recently spawned, bearing dark mature eggs and empty eggs capsules, or remains of eggs capsules). The percentage of the total trapped in each stage is given in parentheses.

Site	Date	Number of females	Developmental stage of eggs				
			1	2	3	4	
Terence Bay	14/06/01	5	5 (100)	0	0	0	
	27/06/01	14	14 (100)	0	0	0	
	11/07/01	2	2 (100)	0	0	0	
	19/07/01	8	6 (75)	2 (25)	0	0	
	01/08/01	6	5 (83)	1 (17)	0	0	
	14/08/01	19	19 (100)	0	0	0	
	23/08/01	36	27 (75)	8 (22)	0	1 (3)	
	07/09/01	20	17 (85)	2 (10)	0	1 (5)	
	20/09/01	15	15 (100)	0	0	0	
	04/10/01	22	19 (86)	0	3 (14)	0	
	06/11/01	25	25 (100)	0	0	0	
	27/11/01	24	24 (100)	0	0	0	
	17/12/01	4	4 (100)	0	0	0	
	24/01/02	3	3 (100)	0	0	0	
	15/02/02	0	0	0	0	0	
	02/04/02	0	0	0	0	0	
	01/05/02	0	0	0	0	0	
	16/05/02	6	6 (100)	0	0	0	
	04/06/02	29	29 (100)	0	0	0	
	17/06/02	10	10 (100)	0	0	0	
	Benacadie	24/05/01	16	16 (100)	0	0	0
		06/06/01	4	4 (100)	0	0	0
		21/06/01	29	29 (100)	0	0	0
04/07/01		129	91 (71)	10 (8)	15 (12)	13 (10)	
15/07/01		93	84 (90)	6 (6)	0	3 (3)	
29/07/01		68	68 (100)	0	0	0	
17/08/01		114	114 (100)	0	0	0	
01/09/01		59	59 (100)	0	0	0	
13/09/01		9	9 (100)	0	0	0	
27/09/01		71	71 (100)	0	0	0	
10/10/01		104	104 (100)	0	0	0	
04/11/01		22	22 (100)	0	0	0	
19/11/01		67	67 (100)	0	0	0	
28/12/01		2	2 (100)	0	0	0	
16/02/02		0	0	0	0	0	
21/03/02		0	0	0	0	0	
13/04/02		0	0	0	0	0	
10/05/02	7	7 (100)	0	0	0		
13/06/02	9	9 (100)	0	0	0		
25/06/02	31	18 (58)	11 (35)	1 (3)	1 (3)		

CW in their second summer. Our 12–27 mm CW size-class included older juveniles, which were still reproductively immature.

Trapping of adults

To examine patterns in reproduction, adult *Carcinus maenas* were trapped approximately biweekly from May 2001 to July 2002, except from December 2001 to May 2002 at Benacadie and to April 2002 at Terence Bay, when they were trapped monthly. At each site, three replicate cylindrical eel traps were used (60 cm long and 35 cm in diameter), with a mesh size of 1.25 cm, and baited with whole mackerel or herring. Traps were deployed subtidally

for ~4 hours [shown previously to provide an adequate sample size (B. Cameron, unpublished data)], and, at the macrotidal Terence Bay site, on a mid-ebb to mid-flood daytime tide to eliminate biases in trapping efficiency arising from tidal migration. Female crabs were examined for the presence of eggs on the pleopods, and the condition of the pleopods was recorded. Trapped female crabs were placed in one of four categories based on visual examination of external features: (1) non-reproductive, showing no evidence of egg production or larval release, and with pleopods clear of debris; (2) bearing orange eggs in an early stage of development; (3) bearing dark-coloured mature eggs but with no signs of empty egg capsules; and (4) recently-spawned, carrying dark-coloured mature eggs

and empty egg capsules, or carrying no eggs but with obvious egg capsule remnants on their black pleopods.

RESULTS

Environmental factors

At Terence Bay, salinity was typical of a coastal location, remaining relatively constant at ~ 33 throughout the sampling period (Figure 2). In contrast, surface salinity was consistently lower at Benacadie and ranged between 0 and 23 (Figure 2). On several occasions in early spring and autumn (3 and 19 November 2001, 21 March and 10 May 2002), surface salinities were low (0–12) because of snow and ice melt and run-off. Mean water temperature fluctuated throughout the year at both sites, and generally was lower at Terence Bay (-1.7°C to 18.9°C) than the Bras d'Or sites (-1.3°C to 25.5°C) (Figure 3).

Larval abundance

In Terence Bay, *Carcinus maenas* zoeae were present from June to July 2001 and in June 2002 (Figure 4A). On 20 September 2001, a moulted exoskeleton of a zoea was also identified. At Benacadie, zoeae were present from July to August 2001 (Figure 4B). The greatest abundance of zoeae-I in a pump sample (25 individuals m^{-3}) was recorded inside the pond at Benacadie on 4 July 2001. At Terence Bay, megalopae were present in late September and early October 2001 (Figure 4A), whereas at Benacadie they were present from mid-August to late September 2001 (Figure 4B). Interestingly, although there was a difference of ~ 1 order of magnitude in zoeal abundance between sites, megalopal abundance was similar.

Juvenile abundance

Juveniles of all size-classes were slightly more abundant at Benacadie Pond than Terence Bay (Figure 5). At Terence Bay, few individuals 1–6 mm CW were present from June to October 2001 and in June 2002 (Figure 5A). In contrast, juveniles 1–6 mm CW were present at Benacadie only in autumn 2001, when they showed a distinct peak in abundance (Figure 5D). Juveniles 6–12 mm CW were present from June to November 2001 and in June 2002 at Terence Bay (Figure 5B) and from July to October 2001 at Benacadie Pond (Figure 5E). Juveniles 12–27 mm CW were present from June to December 2001 and from April to June 2002 at Terence Bay (Figure 5C), and they were present from July to November 2001 and in June 2002 at Benacadie Pond (Figure 5F). At Terence Bay, densities of 1–6 and 12–27 mm CW juveniles did not vary among intertidal zones (Figure 6). In contrast, the 6–12 mm CW size-class appeared to move higher in the intertidal through the season (Figure 6).

Reproductive females

Reproductive females were found throughout the summer at Terence Bay, but they were only found in late June and in July at Benacadie (Table 1). Although the peak in number of reproductive females corresponds closely to the peak in zoeal abundance at this site, the presence of

ovigerous females is not determined accurately by trapping. When females are carrying eggs they remain buried in the substrate for extended periods of time and feed sporadically, and therefore their abundance may be severely underestimated in the traps.

DISCUSSION

Temporal patterns in the reproduction of *Carcinus maenas* were similar between the coastal site at Terence Bay and the site in the Bras d'Or Lakes. Zoeae-I and megalopae were collected in summer and autumn 2001 at the two sites (Terence Bay: zoeae-I from June to July and megalopae from September to October; Benacadie Pond: zoeae-I from July to August and megalopae from August to September), but zoeae were not found at Benacadie in spring and early summer 2002. Although the presence of zoea was sporadic in samples from Terence Bay in summer 2001, reproductive females were present throughout summer and autumn at this site, indicating a reproductive season of ~ 5 months (June to October). Reproductive females were only collected in late June and July at Benacadie, but it is doubtful this reflects the reproductive period at this site. It is possible that after July most berried females were carrying eggs at a more advanced developmental stage, and thus were less active and not collected in the traps. In combination, the timing of the presence of reproductive females and zoea at Benacadie indicate a similar reproductive period as at Terence Bay. Although zoeal abundance was greater by 1–2 orders of magnitude at Benacadie Pond than Terence Bay, approximately the same total numbers of megalopae were collected at each site throughout the settlement period. These results suggest increased dilution of zoea upon their release at Terence Bay, associated with the pronounced tidal mixing at this site. Alternatively, zoeal mortality may be much greater at Benacadie Pond than Terence Bay.

No zoeae-II, -III or -IV were collected at either site, which is particularly surprising for Benacadie, given the large number of zoeae-I found there. It is possible that zoeae-I are flushed out of the pond, develop in the main lake, and subsequently return as megalopae. Larval stages of the related blue crab, *Callinectes sapidus*, are known to utilize tidal stream transport to regulate their horizontal position (Epifanio, 1995). Zoeae and megalopae of *Carcinus maenas* have shown endogenous tidal swimming rhythms in the United Kingdom (Zeng & Naylor, 1996a,b), although Swedish populations in microtidal environments (similar to Benacadie Pond) have been shown to lack this behaviour (Queiroga et al., 2002). Alternatively, the later zoeal stages at Benacadie may avoid surface waters or exhibit high rates of mortality. Additional sampling of larger volumes at high spatial resolution in the Pond and in the Lake would enhance our understanding of these patterns.

At Terence Bay, the abundance of 1–6 mm CW juveniles was greatest in summer 2001, and mean CW of the 1–6 mm CW size-class was greater in June 2001 and 2002 than on the other sampling dates. These results suggest that the small juveniles found in spring are probably those that settled in fall of the previous year. At Benacadie, there was a pronounced pulse in 1–6 mm CW recruits in September and October 2001, most likely resulting from

the recorded influx of competent megalopae. A similar pulse was documented in autumn 2004 (Breen & Metaxas, unpublished data). Since the 1–6 mm CW size-class was recorded at this site only in autumn and not in spring of either 2001 or 2002, it is likely that new recruits may grow quickly before they overwinter. The lower numbers of small juveniles observed in spring at Benacadie suggest that winter mortality may be high at this site. The substrate at Benacadie is coarse sand and is frequently rearranged by strong wave action throughout the year, and by ice scour in winter. Alternatively, juveniles may migrate into deeper water during winter, as they are known to do in the native range (Pihl & Rosenberg, 1982), and may not have been present during early spring sampling.

At Terence Bay, mean abundance of the 6–12 mm CW size-class was greatest in summer 2001, suggesting that juveniles overwinter in the 1–6 mm CW size-class, and enter the 6–12 mm CW size-class in their second season. Berrill (1982) found that in Maine, where water temperature exceeded 10°C for five months of the year, juveniles grew to 13 to 25 mm CW by their second winter. At Terence Bay, surface-water temperature was greater than 10°C for only four months of the year, making our results comparable with those in Berrill (1982) if we assume similar growth rates at these lower temperatures. At Benacadie, mean abundance of the 6–12 mm CW size-class was greatest in autumn 2001. The apparent faster growth of juveniles at Benacadie than at Terence Bay is not surprising, given that mean water temperatures at Benacadie were significantly warmer during and after the settlement period (~20°C and ~14°C at Benacadie and Terence Bay, respectively). Mean water temperature at Benacadie from June 2000 to June 2001 was 10.1°C, while it was only 7.7°C at Terence Bay during the same period. Additionally, mean surface-water temperatures at Benacadie were greater than 10°C for approximately 5.5 months per year.

At Terence Bay, abundance of 1–6 and 12–27 mm CW juveniles did not vary among intertidal zones, most likely because of reduced predation in the low and mid zones. In their native range, juvenile *C. maenas* are most abundant in the high zone (Hunter & Naylor, 1993). Abundance was greatest in the low zone in June, in the mid zone in July and August, and the high zone in October. This pattern may reflect the additive effect of predation on the distribution of recruits over the growing season. Adult *C. maenas* migrate into the intertidal zone to forage at high tide (Hunter & Naylor, 1993) and readily consume smaller members of their species (Ropes, 1967). Alternatively, as water temperatures increase in summer, causing adult *C. maenas* to become more active, small juveniles may migrate higher into the intertidal zone to avoid being preyed upon. The 1–6 mm CW size-class may be too small for adult crabs to prey upon, while the pattern for the 12–27 mm CW size-class may be confounded by migration to deeper water as these individuals approach maturity.

Our results indicate that *Carcinus maenas* can reproduce successfully in the low-salinity environment of the Bras d'Or Lakes. Females are known to prefer water of higher salinity than males (Dries & Adelung, 1982), and most likely remain at greater depths in Benacadie Pond.

According to Broekhuysen (1936), embryonic development requires a salinity of at least 20 at 16–17°C, which is within the range of bottom temperatures and salinities observed in the deeper part of the channel and pond (B. Cameron, unpublished data). As a salinity of 20 is generally considered to be the lower limit for successful larval development (Nagaraj, 1993; Anger et al., 1998), larvae could develop successfully in the Lakes, although they may be periodically exposed to lower salinities for short periods. Dries & Adelung (1982) suggested that larvae from Baltic populations may be capable of developing at a salinity of 15 at 18°C, but no supportive data were provided.

Our results also indicate that *C. maenas* can successfully reproduce in the cold waters of coastal Nova Scotia. Berrill (1982) predicted that this species would not be able to reproduce successfully further north than the central coast of Maine, due to the delay in spawning and development caused by cold temperatures. It has been suggested that the recent rapid expansion in *C. maenas* populations in Atlantic Canada may be due to cryptic invasions of this species from different areas of the native range (J. Roman, Harvard University, personal communication). The populations of *C. maenas* in the western Gulf of Maine have been shown to be of a different genetic lineage than those in the Gulf of St Lawrence, which is, in turn, home to a lineage that is not found elsewhere in North America and may be derived from populations in the North Sea (J. Roman, Harvard University, personal communication). Populations from the eastern Gulf of Maine along the coast of Nova Scotia to Halifax apparently display a mixture of these two lineages. Thus, the expansion of *C. maenas* into 'cold' waters may be due to separate introductions originating from cooler parts of the native range, such as Iceland, where summer water temperatures rarely reach 10°C. Similarly, invasions from resident populations in the Baltic into the Bras d'Or Lakes may be responsible for the low salinity tolerance of the zoeae in this habitat.

The higher degree of tidal mixing at Terence Bay presumably results in increased advection of locally produced zoeae away from this site. Also, because of the coastal location of Terence Bay, recruits may originate from a wide geographical area, rather than locally. In contrast, at Benacadie the lack of strong tidal currents coupled with short larval development period may result in a localized pool of recruits. The adaptability of the reproductive cycle of *C. maenas* to a wide range of temperatures and salinities, combined with the possibility of invasions of different genetic lineages can have a pronounced influence on the invasive success of this species and our ability to predict it.

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