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Invasion dynamics of the European shore crab, *Carcinus maenas*, in Australia

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Abstract In Australia and most other invaded locations, rates of range expansion by the European shore crab, *Carcinus maenas*, are typically only a few kilometres per year, despite a planktonic duration upwards of 50 days and off-shore larval development. This relatively static distribution is punctuated by rare episodes of long-distance and large-scale spread, some of which appear to be related to unusual oceanographic conditions and some of which are likely to be human assisted. These observations suggest, first, that long planktonic duration and off-shore development in a marine invertebrate does not preclude very localised recruitment, and, second, that this recruitment norm may be punctuated by brief episodes of wide scale mixing of propagules. Punctuated dispersal has previously been suggested to account for large-scale biogeographic patterns of distribution and speciation, but may also have implications for the processes that stabilise structured spatial metapopulations.

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Introduction

How far and in what directions planktonic larvae disperse are fundamental data for understanding the dynamics of marine populations (Sinclair 1987; Cushing 1995). Yet this information is known only for a few species with particularly short planktonic duration, measured in hours rather than the more typical weeks or months (e.g. Gotelli 1987; Reed et al. 1988). Tagging larvae is impractical given their small size and fragility, and alternative approaches, such as genetic studies or use of natural phenotypic tags (e.g. body composition), from which dispersal could be inferred, are of limited value in the face of even low levels of mixing or suffer from limited resolution and reliability (Hartl and Clark 1989; Thresher 1999).

Introduced species provide another opportunity to assess the role of planktonic processes in marine population dynamics, through an analysis of the processes that facilitate or hinder their dispersal and range expansion (e.g. Grosholz 1996). Comparisons of the behaviour of the same introduced species in different invaded locations may allow generic principles to be distinguished from processes specific to particular sites. The European shore crab, *Carcinus maenas* (Decapoda: Portunidae), provides opportunities for such comparisons. From its original distribution along the Atlantic coast of Europe, the species has established populations in South Africa (Le Roux et al. 1990), Australia (Zeidler 1978), and on the east and west coasts of North America (Williams 1984; Cohen et al. 1995; Grosholtz and Ruiz 1995). It has also been reported from Brazil, Panama, Hawaii and Ceylon, but it is not clear if it has established in these tropical regions. A closely related species, *Carcinus mediterraneus*, has invaded Japan (Geller et al. 1997).

C. maenas appears to have an unexceptional larval development, with a planktonic duration of up to about 50 days and late-stage larvae distributed well across the continental shelf (Roff et al. 1986; Lindley 1987;

Queiroga 1996). Consequently, inferences drawn about its patterns of dispersal and connectivity are likely to have broad application among coastal marine organisms. We assessed this invader's patterns of dispersal and connectivity by examining its abundance and demography at nested spatial scales at sites across Australia.

C. maenas was first recorded in Port Phillip Bay, Victoria, in the late 1800s, apparently introduced in the dry ballast of wooden vessels from Europe (Fulton and Grant 1902). In the hundred years since, it has become widely distributed throughout Port Phillip Bay (Sinclair 1997) and along the south-east coast of Victoria (MRGVM 1984). It was reported in southern New South Wales in 1971 (Hutchings et al. 1989), in South Australia in 1976 (Zeidler 1978; Rosenzweig 1984) and in Tasmania, an island state about 200 km south of Port Phillip Bay, in 1993 (Gardner et al. 1994). The species has also been reported in Western Australia, based on a single specimen found in the Swan River in 1965; *C. maenas* has not been reported in the area again.

In the present study, we examined in detail the current distribution and abundance of *C. maenas* in Australia, over a 5-year period, using standardised sampling techniques that allowed us to make direct comparisons between sites and over time. We combined these data with information about the historical distribution of *C. maenas* in Australia, to elucidate the mechanisms of its range expansion. We focused much of our sampling effort and analysis on Tasmania, which appeared to be a region of recent invasion and possible range expansion by *C. maenas*.

Materials and methods

Data on the distribution and abundance of *Carcinus maenas* were obtained principally by trapping. The traps, purchased commercially, were collapsible boxes, 62 cm long, 42 cm wide and 20 cm high. The traps were made of 0.4 mm diameter plastic-coated wire, covered with 1.3 cm square plastic netting, and weighted down with steel chain or lead. Crabs entered the trap through slits at the apex of inwardly directed panels at each end of the trap. Each trap was baited with about 300 g of oily fish (jack mackerel or Australian salmon), housed in a perforated "bait-saver" to prevent bait being consumed by the crabs or fish. Traps were generally set in the afternoon or evening and left to fish for 15–24 h. Catches were processed at the trap site. For each *C. maenas* caught (except during port surveys), we measured carapace width (CW) to the nearest millimetre and determined its sex. The following five trapping programs were undertaken.

Habitat survey of Tasmania

In order to determine the habitat range of the species prior to undertaking large-scale geographic comparisons, we set traps at a wide range of shore-accessible, shallow-water sites around Tasmania during January–April 1996 (Fig. 1). We were able to sample relatively few sites along the south and west coasts, because of limited road access in those areas. However, subsequent work reported below suggests there was little likelihood of finding *C. maenas* along these coasts, which are rocky and very exposed. At each locale, we distributed from 4 to 15 traps, fishing the range of habitat types. Sampling was supplemented at all sites by qualitative surveys (visual scans of apparently suitable habitats, >15 min) for evidence of the crab and exuvia.

This coarse analysis of habitat preferences was complemented in March 1996 by an intensive sampling program throughout Georges Bay (Fig. 2), an area in which our earlier samples indicated *C. maenas* was abundant (Fig. 1). Sixty-four traps were set over a 2-day period at 38 sites, which covered the range of habitats in the bay and just outside its mouth. Traps were set in lines of two or three, perpendicular to shore, to determine possible changes in abundance with depth, at 20 of the sites inside the bay; the other six inner sites and all 12 sites outside the bay each had a single trap. At each site, we recorded depth, substratum type and percent vegetative cover, visually where water clarity allowed and with a scissor sediment grab where it did not. We repeated the trapping a year later (February 1997), for 18 sites within the bay (outer sites not sampled because of zero catch rates there in 1996), with five traps at each, arranged parallel to the shoreline and set 30 m apart.

Assessment of temporal variability in catch rates

Day-to-day, seasonal and annual variability in catch rates was quantified by repeated sampling of sites on the east coast of Tasmania from 1996/1997 to 2000/2001. In the first year, we sampled three sites [Little Swanport, Hendersons Lagoon and Lords Point (in Georges Bay)]. In 1997/1998 and 1998/1999, we expanded our sampling to include three more sites: Moulting Bay (in Georges Bay) and two sites in Blackman Bay (for site locations, see Figs. 1, 2). Five traps were set at each site, parallel to the shoreline, approximately 30 m apart and at a depth of about 0.5 m mean low water. Sampling intervals were approximately monthly during summer and autumn (December through April), but were less regular and more infrequent during winter and spring.

National Port surveys

The distribution of *C. maenas* around Australia was determined as part of a national program to assess the distribution and abundance of introduced species in Australian ports. Port survey sampling protocols have been reported by Hewitt and Martin (1996). Sampling took place over a 4-year period in representative ports all around Australia (Fig. 3), usually for only one to two nights per port and at different times of the year (though predominantly spring–summer), depending upon the requirements for each port survey. The number of traps set varied from one to nine per port, depending upon the extent of habitat that appeared to be suitable for *C. maenas*. The number of crabs caught in each trap per overnight set was recorded. At all sites, we supplemented the trapping with visual surveys of suitable habitats for the crabs or their ecdyses, and by questioning local fishers, beachwalkers and other water users.

Mainland Australia surveys

We obtained more detailed information on the distribution and abundance of *C. maenas* in southern Australia by undertaking a detailed trapping survey of Victoria (20 sites), southern New South Wales (7 sites) and South Australia (8 sites) in September–October 1998 (Fig. 1). Sampling locations included areas where the crab had been reported, as well as areas that appeared to be suitable crab habitat. At each site, we set five traps in the shallow subtidal, in a line parallel to the shoreline and approximately 30 m apart, which were then fished overnight (15–24 h). Between December 1998 and March 1999, we re-sampled some sites in Victoria, to assess possible seasonal differences in crab abundance and to look for evidence of recruitment.

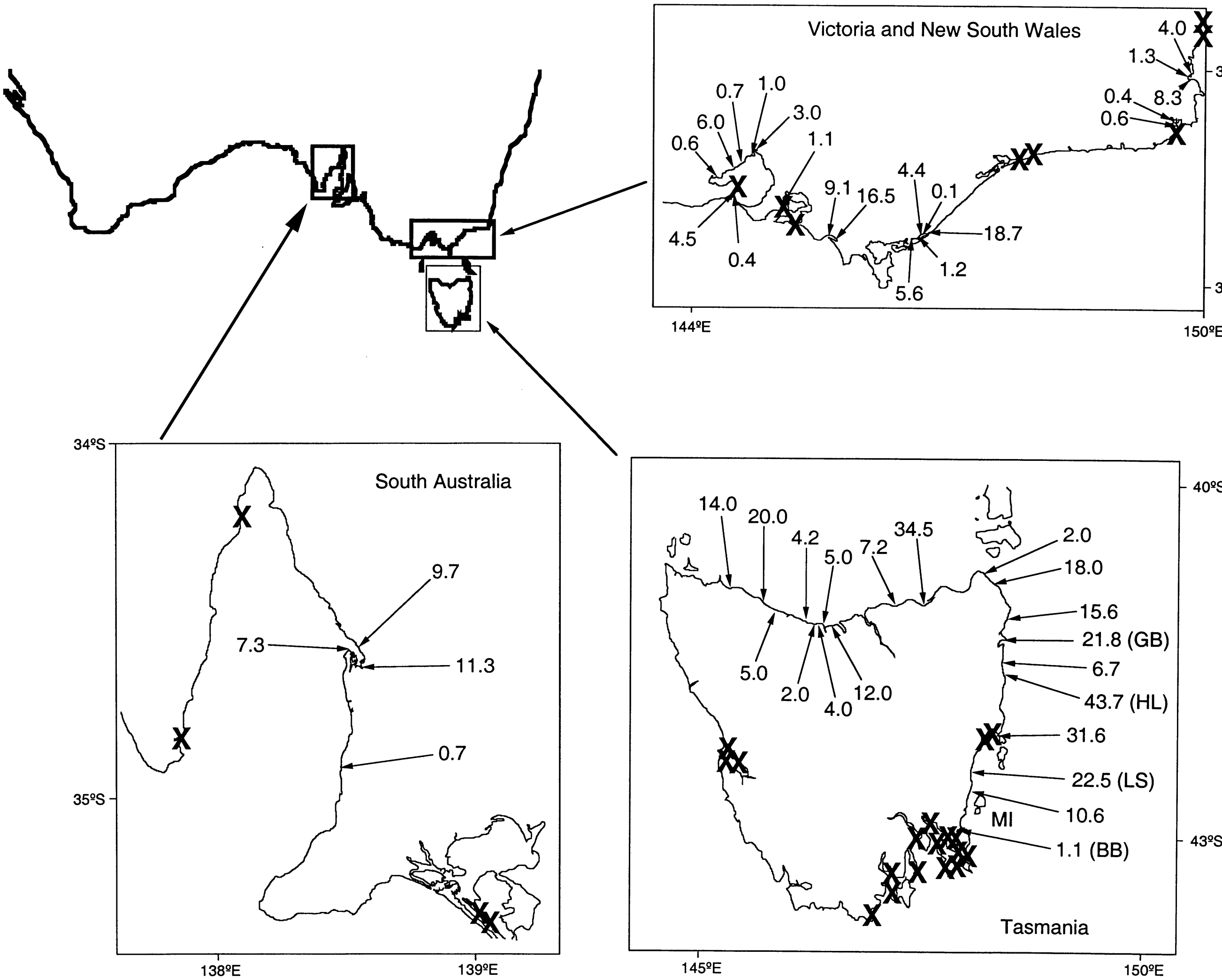

Fig. 1 Mean number per trap of *Carcinus maenas* caught at sites in South Australia, Victoria and New South Wales, and Tasmania, between July 1996 and March 2000. *Cross* indicates a zero catch. In most cases, at least five traps were set at each site, though the sampling intensity and temporal coverage differed widely among sites (see "Materials and methods") (*GB* Georges Bay; *HL* Hendersons Lagoon; *LS* Little Swanport; *MI* Maria Island; *BB* Blackman Bay)

Tasmanian surveys and monitoring

Methods and locations for long-term sampling at sites along the east coast of Tasmania are reported above. In addition, since 1997 we have set traps opportunistically at a variety of sites within and outside the apparent current range of *C. maenas* in Tasmania (Fig. 4), in order to ascertain the limits of its distribution. In all cases, five traps were set in shallow subtidal areas, in a line parallel to the shoreline. A few of the sites have been repeatedly sampled over the years (in March/April, 1997 and 1998), whereas others were "exploratory" or followed reports of *C. maenas* in areas outside of its known area of abundance.

Data processing

Processing of trap catches in both the Tasmanian and mainland Australian surveys included the noting of any gravid females and the developmental stage of their eggs, as determined by egg colour (stage 1 = bright orange or yellow to stage 5 = dark grey/black). We also opportunistically examined the ovaries of subsamples of females taken from trap catches, scoring ovaries from stage 1 to 5 (stage 1 = ovary not visible or transparent to stage 5 = ovary bright orange, fully ripe).

Information on the presence/absence of juvenile (≤ 15 mm CW) crabs was obtained as a by-product of shore surveys done in Tasmania and mainland Australia to examine the impacts of *C. maenas* on native benthic fauna. These surveys involved removing and sieving (through 2.8 mm mesh) the top 5 cm of sediment within quadrats (generally 1×1 m), sampled across different levels on the intertidal shore. Other censuses of juveniles were done more opportunistically, during the trap surveys for adult crabs, which usually involved digging and sieving as described above, but also searching under rocks exposed during ebb tides. Modal analysis of size-frequency distributions and tagging studies of juveniles indicate they can reach a carapace width of 50–60 mm in their first year (Lewis 1997).

Data on oceanographic conditions in the south-eastern Australian region were obtained from the coastal monitoring station maintained at Maria Island (east coast of Tasmania, see Fig. 1) by CSIRO since 1940. The Maria Island station and the relationship between its data and regional changes in coastal circulation have been discussed by Harris et al. (1987).

Statistical analyses used the Statview package.

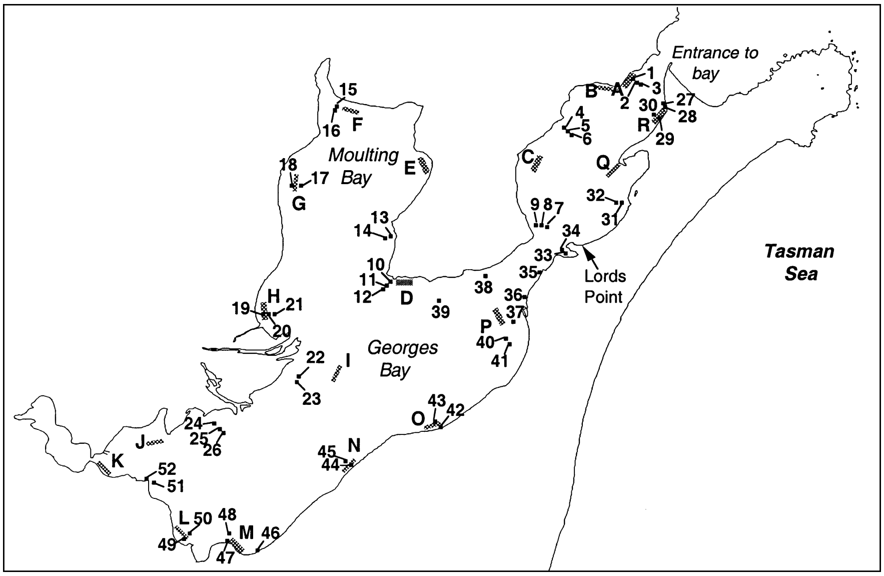

Fig. 2 Location of sampling sites for *Carcinus maenas* in Georges Bay in March 1996 (*numerals*) and February 1997 (*letters*)

Results

Habitat preferences

Carcinus maenas was caught at about half the sites we sampled in January 1996. Almost all sites where it was caught were soft-sediment benthos of low or moderate wave energy; most were estuary mouths or sheltered bays. Substratum type, depth and water quality were poor predictors of *C. maenas* presence or abundance: the species was caught in areas ranging from barren sand

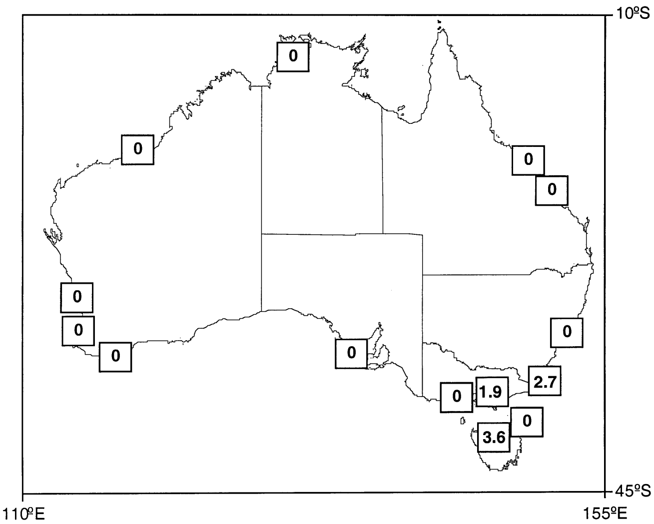

Fig. 3 Location of port surveys around Australia. The *number in each box* is the mean number of *Carcinus maenas* caught in traps deployed overnight at each site. The mainland ports surveyed are (clockwise from top centre) Darwin, Hay Point, Mackay, Newcastle, Eden/Twofold Bay, Westernport/Hastings, Portland, Port Lincoln, Albany, Bunbury, Geraldton and Port Hedland. The two Tasmanian sites surveyed are Devonport and, off the north-east, Lady Barron Island

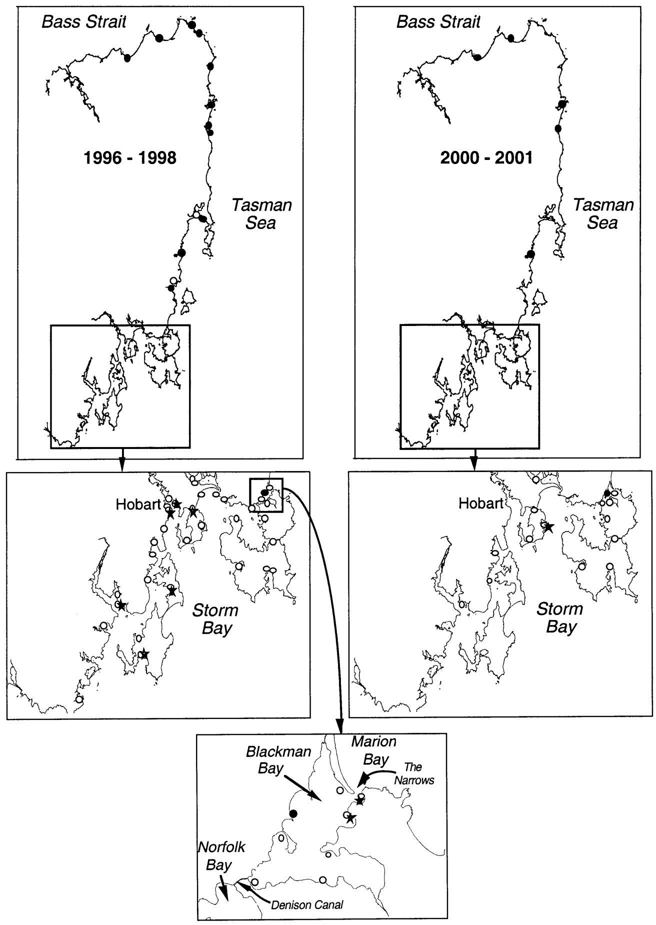

Fig. 4 Geographic distribution of *Carcinus maenas* along the east coast of Tasmania, as inferred from trapping surveys and community reports, in 1996–1998 (*left panels*) and 2000–2001 (*right panels*) (*filled circles* confirmed presence of populations; *stars* locations of "one-off" reports; *open circles* no evident *C. maenas* despite efforts to trap or otherwise locate them). *Lower middle panel*: location of *C. maenas* in Blackman Bay as indicated by a bay-wide trapping survey in January/February 1999

and fine silt to those heavily vegetated, at all depths sampled (immediately subtidal to a low-tide depth of several metres), and in turbid areas close to sources of urban run-off as well as in areas of clear oceanic water that appeared pristine. We also caught it at locations well upstream from river mouths (e.g. in the Scamander River), indicating tolerance of low-salinity environments. Nonetheless, we never caught *C. maenas* with anguilid eels or hymenosomatid crabs, both of which locally characterise brackish water habitats. Similarly, we also never caught it in exposed areas, such as open sandy beaches or rocky headlands.

The detailed assessment of habitat preferences carried out at Georges Bay (see Fig. 2) in 1996 and 1997 produced much the same picture. Catches were extremely patchy, and there were few obvious correlations between the abundance or presence of *C. maenas* and any environmental variable measured. Only two generalities could be inferred from the Georges Bay data. First, we caught no *C. maenas* outside of the bay itself, i.e. in exposed coastal areas. Second, catches were highest in shallow areas. At the sites where *C. maenas* were caught and where traps had been set at different depths (range: 1–6 m), the crabs were only caught in the shallowest traps. However, we rarely found adult *C. maenas* in the intertidal zone, except during a flood tide.

Temporal variability in catch rates

Long-term Tasmanian data indicate that catch rates of *C. maenas* vary widely day-to-day, seasonally and inter-annually. In the most extreme example, we caught 159 crabs in five traps set at Lords Point (Georges Bay) on 3 January 1997; 1052 *C. maenas*, in the same five traps set 13 days later; and 1372 crabs, in the five traps set 28 days after that. Differences between samples could not easily be attributed to any obvious difference in weather or water condition, and only in part to recruitment. Excluding young-of-the year <45 mm CW from the analysis still results in catches differing amongst weeks by a factor of four (144, 576 and 486 large adults for the three sampling dates, respectively).

Temporal variation in catches only in part reflects a weak annual cycle of abundance/catchability. Catches tended to be highest in summer (December–February) and lowest during winter (June–August), but, overall, seasonal differences were not significant for the sites at which we had the most comprehensive data sets (Moulting Bay: differences among seasons for catches of adults >55 mm CW, ANOVA $F_{1,22}=0.11$, NS; for young-of-the-year ≤40 mm CW, $F_{1,22}=0.78$, NS; Lords Point: for adults, $F_{1,20}=0.79$, NS; for young-of-the-year, $F_{1,20}=0.80$, NS).

Over the 5-year sampling period, catches declined at most sites in Tasmania (Fig. 5). For the three sites where *C. maenas* was common and that we sampled repeatedly from 1997/1998 to 2000/2001 (Moulting Bay, Lords Point and Little Swanport), differences between sites and

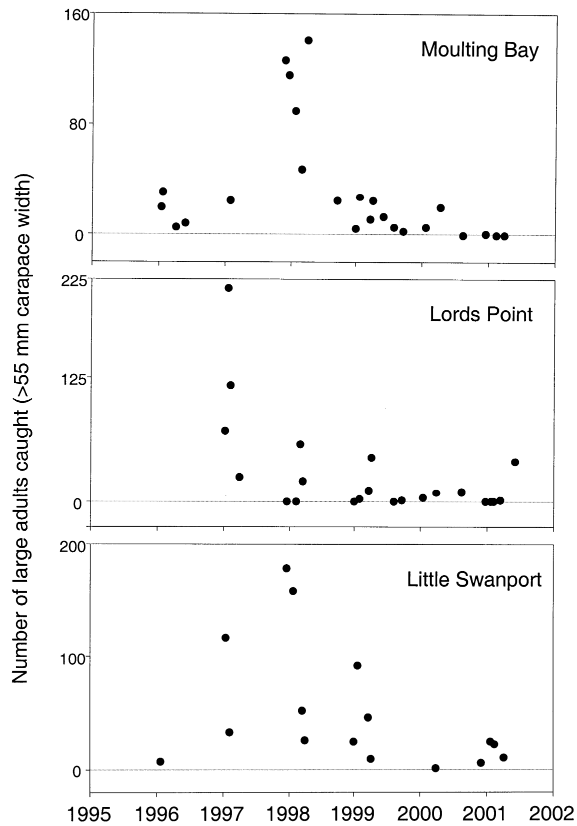

Fig. 5 *Carcinus maenas*. Catch rates (mean number per trap) of large adults (>55 mm CW) at three long-term monitoring sites, from January 1996 to May 2001. For locations, see Figs. 1, 2

the site×year interaction factor are not significant ($F_{2,186}=0.32$, NS and $F_{6,186}=0.33$, NS, respectively). However, differences among years are highly significant ($F_{3,186}=3.68$, $P=0.013$). Sparse data for other Tasmanian sites also indicate declines between 1996 and 2001. All four sites along the north coast of Tasmania sampled in January/February 1996 and again in January/February 2001 showed drops in catch rates (number of crabs per trap per day) ranging from 39% to 90%.

Current distribution of *C. maenas* in Australia

C. maenas were caught only in the port surveys in south-eastern Australia (Tasmania, Victoria and southern New South Wales) (Fig. 3). We caught no *C. maenas* at two of the ports surveyed in that region (Portland, Victoria; Lady Barron Island, Tasmania), but both are relatively exposed, high wave-energy habitats where, based on the analysis above, we would not have expected to find it. We have been unable to find any evidence, other than the "one-off" specimen collected in Western Australia, referred to above, that the species is present in Australia anywhere other than the south and south-eastern coasts.

In our more intensive spring/summer sampling of mainland and Tasmanian sites, we caught *C. maenas* at 25 of 45 locations (Fig. 1), indicating a localised population in St. Vincent Gulf, South Australia, and a consistent presence at sites all along the coasts of central and south-eastern Victoria and of north, north-eastern and eastern Tasmania. The species was also present at sites in southern New South Wales, but it was absent from the sites we sampled in eastern Victoria (east of and including Lakes Entrance to Mallacoota Inlet), suggesting a disjunct distribution. The species has not been reported further north in New South Wales, nor have we found it in our qualitative sampling in the Sydney region.

In Tasmania, catches of *C. maenas* were consistently highest at north-eastern sites and, in particular, at upper Georges Bay and Henderson Lagoon (highest catches of 428 and 288 crabs from a single overnight trap set, respectively, and mean catch rates of 34.5 and 43.7 crabs $trap^{-1}$ $night^{-1}$, respectively). Catches in excess of 100 crabs from a single trap set were also taken at three other north-eastern sites (Ansons Bay, Great Swanport and Little Swanport). The species was also taken at sites all along the north coast of Tasmania and along the east coast as far south as Blackman Bay (Fig. 1). Qualitative sampling at Flinders Island, to the north-east of Tasmania proper, indicated *C. maenas* was present, but apparently in low numbers. Trapping at numerous sites south and south-west of Blackman Bay yielded no *C. maenas*. However, there have been several "one-off" finds of live *C. maenas* or carapaces south of the bay (Fig. 4). Most were associated with oyster or mussel farms. We followed up each of these reports with trapping and SCUBA searches, but in all cases failed to find any additional specimens.

The southernmost extent of *C. maenas* distribution in Tasmania appears to have changed little, if at all, over the 5 years of this study (Fig. 4, upper panels). In Blackman Bay, the distribution of the crab has been essentially static since sampling began (Fig. 4, lower panel). Although we occasionally collected ovigerous females at the one site in the bay where the crabs are common, reports of juveniles are sparse and in all cases limited to areas in or around racks of seed oysters that, in turn, are brought into the bay from sites farther north along the Tasmanian coasts. Despite considerable effort, particularly in 1999, we have been unable to find juveniles elsewhere in the bay, even though habitats appear very suitable for them. Size-frequency distributions for the one site at which we did catch adults indicated young-of-the-year (50–60 mm CW) in 1997 and 1998, suggesting recruitment in both years.

Invasion history of Tasmania

Gardner et al. (1994) reported the first collection of what were in retrospect young-of-the-year *C. maenas* in Georges Bay in mid-1993. The species' arrival in the region at about that time has been substantiated by marine farmers in the area, who had never seen it before then. Farther south along the east coast, we received a first report, from a marine farmer, of the species in Blackman Bay in 1995 (L. Cleaver, personal communication), but our size-frequency data for that site in 1996 indicate 2- to 3-year-old individuals (Proctor et al., unpublished data), suggesting it arrived there more or less simultaneously with its arrival in north-eastern Tasmania. We have few data and no reliable qualitative accounts of the crab's arrival in north-western Tasmania, but our size-frequency data for the region for 1996 indicate three year classes being present.

Whether the broad-scale invasion of Tasmania was caused directly by recruits sourced from the mainland or a rapid spread from a small population seeded into Tasmania from either Victoria or South Australia is not known. A detailed survey for exotic marine species at Devonport, north central Tasmania, provides strong evidence of exotic species being introduced into the area by coastal shipping from Port Phillip Bay (CRIMP 1996), so that a human-assisted invasion of Tasmania is plausible. However, oceanographic data for the Tasmanian east coast, from the Maria Island long-term monitoring station (see Fig. 1), show unusually warm winters from 1988–1991, i.e. immediately preceding the discovery of *C. maenas* in Tasmania (Fig. 6). Warm sea-surface temperatures at Maria Island are markers of the East Australian Current, a poleward flowing sub-tropical water mass (Harris et al. 1987). The series of warm years prior to the invasion by *C. maenas* suggest a period of prolonged greater than usual influence of these currents along the Tasmanian east coast, which would be consistent with a southward transport of larvae from Victoria to Tasmania. If so, it implies that *C. maenas* was present in Tasmania for 2–4 years prior to being reported, although perhaps in small numbers.

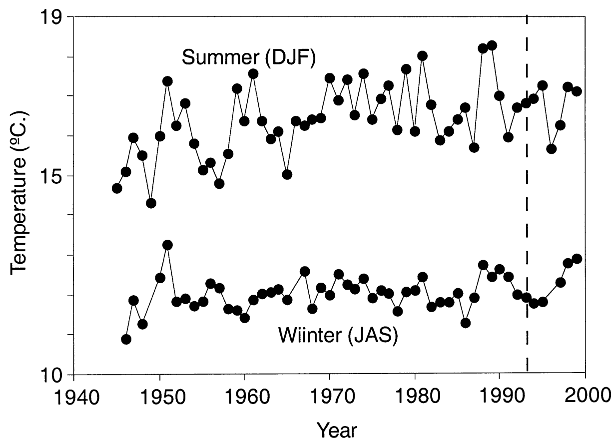

Fig. 6 Winter (Jul/Aug/Sep) and summer (Dec/Jan/Feb) mean surface-water temperatures at the Maria Island monitoring station off the east coast of Tasmania (see Fig. 1, for location). *Dashed vertical line* indicates year *Carcinus maenas* was first detected in Tasmania

Discussion

Carcinus maenas' planktonic development involves four zoeal stages and a megalopal stage (Rice and Ingle 1975). Early-stage larvae exit coastal areas rapidly, are transported to the mid-continental shelf, as much as 37 km off-shore, and then return to coastal habitats to settle (Roff et al. 1986; Lindley 1987; Queiroga 1996). Total duration of the planktonic stage varies with temperature, but is upwards of 36–50 days (Williams 1968; Dawirs 1985). At this planktonic duration, *C. maenas* would be considered a "true long-distance disperser", based on the criteria of Thorson (1961). Its off-shore planktonic development presumably also facilitates long-distance transport (Queiroga 1996). Therefore, we would have predicted that once substantial populations had been established at points of first invasion, these sites would act as "beachheads" from which the species would spread rapidly. At the minimum, we would have expected to find or have reports of juvenile *C. maenas* at sites all along the coast down-current from its established populations, even if these juveniles subsequently disappeared.

This does not appear to be the case in Australia. Our data confirm that despite being present there for >100 years, locally abundant and clearly reproductive *C. maenas* still have a very restricted distribution in Australia. It is now widely present on the coasts of central and eastern Victoria, but this constitutes a range expansion from the apparent site of introduction (Port Phillip Bay) of only a few hundred kilometres. The easternmost edge of its present distribution, in southern New South Wales, was apparently reached only in the 1970s. In 1986, the species was reported slightly farther along that coast, in Twofold Bay, New South Wales (Hutchings et al. 1989); our survey of that region 12 years later (in September 1998) indicates no further spread up the coast in the intervening period. In South Australia, where the species was also first reported in the 1970s, the farthest point we found *C. maenas* from Adelaide, the point of first discovery, was only about 40 km along the coast. This equates to a mean rate of spread of about 1.7 km year^{-1}; it would be less if the species was present in Adelaide for a period prior to being discovered. In practice, the conspicuous nature of the crab in shallow water, its large size and distinctive appearance relative to native crabs, and extensive biological work in Australia's coastal habitats over the last half century, suggest it is unlikely the species existed undiscovered for very long either in New South Wales or South Australia.

The slow rate of range expansion is also evident in Tasmania. As noted, it took >100 years for the species to spread across Bass Strait from Victoria to Tasmania, a distance of only a few hundred kilometres, despite potential island stepping stones and current gyres that routinely circulate water across the strait (Middleton and Black 1994). Following the initial invasion in the early 1990s, there appears to have been little or no further range expansion. In the 5 years of this study, the southernmost limit of the species along the Tasmanian east coast (Blackman Bay) has not shifted even on a scale of kilometres. This is despite: (1) environmental conditions and habitats south of Blackman Bay that appear well suited for the species, as evidenced by (2) the occasional very healthy individual *C. maenas* collected south of the bay, often associated with an aquaculture facility, (3) ovigerous females in at least 1997 and 1998 in Blackman Bay, suggesting potential colonists are available, and (4) a shipping canal, only a few kilometres from where we routinely collect *C. maenas*, between Blackman Bay and similar embayments to the south, through which large volumes of water exchange daily. Even within Blackman Bay, we have been unable to find juvenile *C. maenas* anywhere other than one aquaculture facility, despite reproductive populations and habitats throughout the bay that appear to be well suited to the species.

This slow rate of spread in Australia is unlikely to be due to adverse environmental conditions. Coastal temperature and salinity regimes throughout the southern part of Australia are, with the exception of a few isolated sites, well within the tolerance ranges of the species. *C. maenas* adults tolerate salinities as low as 6‰, and temperature ranges from below freezing to as high as 35°C (Cuculescu et al. 1998; Rainbow and Black 2001), although larval development requires a more limited salinity range [in excess of 10‰ (Dawirs 1985; Anger et al. 1998)]. The species breeds over a temperature range of about 4°C to 18–26°C (Naylor 1965). Minimum winter water temperatures in the southernmost part of Australia (Tasmania) rarely go below 8°C. Temperature maxima in summer across most of southern Australia, with the exception of a few hypersaline embayments in South Australia, are in the low- to mid-20s. Sheltered habitats suitable for the species are widely distributed along the coast. Empirically, the finding of "one-off" specimens outside the current range of *C. maenas*, invariably healthy, indicate that adverse environmental conditions do not limit the distribution of the species locally.

Rates of range expansion by invasive *C. maenas* in other parts of the world appear to differ widely among sites (Grosholz 1996). In South Africa, *C. maenas* spread about 15 km along the coast from its initial point of invasion in Cape Town between 1983 and 1990 (Le Roux et al. 1990); this equates to a rate of range expansion of 1.9 km year^{-1}. The discovery of the species much farther up the coast, at Saldanha Bay, in 1990, appears to be the result of a saltatory dispersal event, possibly human assisted. Saldanha Bay is an area of aquaculture activities (C. Hewitt, personal communication), and the presence of the species outside its continuous range in association with aquaculture facilities there, is reminiscent of our observations in Tasmania and those by Yamada et al. (2000) off the American west coast. Off the eastern coast of North America, the species took 79 years (1872–1951) to spread from Cape Cod to southern Canada, a distance of about 690 km (Glude 1955). This equates to an average rate of spread of 8.7 km $year^{-1}$. Glude (1955) apparently expected a faster spread for the species, presumably based on its long planktonic duration, and attributed the slow spread to water temperatures that, for much of the region, were historically less than the species' minimum tolerance. In contrast, *C. maenas* appears to have spread quickly along the Californian coast. Following its initial detection in 1989 or 1990, the species spread throughout San Francisco Bay (maximum distance of about 80 km) in only 3 years (Cohen et al. 1995), apparently through natural dispersal. Although there are a number of mechanisms that could have facilitated its spread around the bay (a bait industry, heavily fouled tyres used as bumpers on vessels), none of these are strongly implicated as important in its spread (J. Carlton, personal communication). Between 1993 and 1994, the species spread from San Francisco Bay as far north as Bodega Harbor, a distance of about 120 km (Grosholz and Ruiz 1995). Subsequently, the species spread to Oregon and possibly southern Washington in 1996, and to Vancouver Island, Canada, in 1998 (Yamada et al. 2000). Yamada et al. (2000) note that the sites involved in the 1996 event were all areas of oyster aquaculture and, further, that the industry transports seed oysters to these sites from areas in California in which *C. maenas* had established by 1993. Both Grosholz and Ruiz (1995) and Yamada et al. (2000) emphasise the episodic pattern of range extension, with rapid spread along the coast occurring at about 3-year intervals (Yamada et al. 2000). The mean rate of spread north from San Francisco Bay, between 1993 and 1999, was about 200 km $year^{-1}$.

We draw three general conclusions from these data.

First, when *C. maenas* is collected outside its known ranges, it is often in association with aquaculture activities in Tasmania, off the west coast of North America and, possibly, in South Africa. The reason for this association is not clear. Yamada et al. (2000) suggested that it could reflect aggregation or higher rates of survival by recruits in areas of high food availability. Alternatively, it could result from enhanced detection of the pest by aquaculturists familiar with local biota or from inadvertent dispersal of small *C. maenas* in aquaculture shipments outside of its extant range.

Second, with the exception of the American west coast, the rate of spread of *C. maenas* has the same order of magnitude as the demonstrated ability of tagged individuals to walk along the coast. Gomes (1991) reports that, after at most 6 months of freedom, most individuals she tagged in lagoons along the coast of Portugal were re-caught between 1 and 10 km from the point of tagging; a few moved >15 km during that interval. This equals or exceeds the annual rate of range expansion observed in most studies. The exception is the American west coast which, as noted above, might be confounded by long-distance movements of aquaculture stock. At most sites, it is not necessary to invoke larval transport at all to account for observed rates of range expansion.

Third, several observations nonetheless indicate larval transport is at least episodically important, though the evidence of its broader importance is mixed. *C. maenas* in many invaded regions occurs principally, or only, in sheltered embayments, requiring a mechanism such as planktonic dispersal (or human assistance) to expand its range between embayments. Nearly simultaneous first arrival of *C. maenas* all along the north and north-east coasts of Tasmania, a similar observation along the coasts of Washington and southern Canada by Yamada et al. (2000) and in southern California by Grosholz and Ruiz (1995) all suggest widespread recruitment mediated by larval dispersal. Both the invasion of Tasmania and spread along the American west coast may be associated with unusual oceanographic events (in the case of Tasmania, several years of unusually warm coastal water, and off the American coast, the strong poleward currents during an El Niño event), though in neither case is the connection as yet more than a supposition.

Grosholz and Ruiz (1995) note that the range expansion of *C. maenas* out of San Francisco Bay in 1993 would be consistent with the rate of longshore transport predicted by local current measurements, a planktonic duration in excess of 60 days and a single 15-day bout of slack winds, which would allow the development of northerly longshore transport. However, similar hydrodynamic studies and models for larval dispersal predict a much more extensive distribution of the species along the coast of South Australia (Fowler et al. 2000). Further, opportunities for larval dispersal do not appear limiting, and cannot easily explain why it took nearly a century for the species to spread from Victoria to Tasmania, a distance of only a few hundred kilometres and an area subject to frequent north–south water movements (Middleton and Black 1994).

Overall, the pattern of invasion and range extension by *C. maenas* appears to consist of periods of stasis or slow spread punctuated by rare, large-scale saltatory events, such as its introduction to Adelaide and possibly New South Wales in the 1970s, the invasion of Tasmania in the 1990s and the spread of *C. maenas* up the North American west coast, also in the early 1990s. The reason for such saltatory dispersal events across these invasions remains unclear. The static phase is reminiscent of the lags often seen in invasive species between first inoculation and subsequent range expansion, for which numerous theories have been proposed (see review by Crooks and Soule 1999). Our observations suggest that for *C. maenas* slow rates of range expansion are the norm. This may often be the result of as yet unidentified situation-specific factors, such as locally intense predation slowing spread or net off-shore current regimes preventing recruitment (e.g. south of Blackman Bay). However, our data suggest that range stasis is also likely to reflect well-developed mechanisms that normally return settling post-larvae to parental environments (Zeng and Naylor 1996; Queiroga 1998) and/or survival by new settlers that is enhanced in areas where the adults are already established.

Direct measurements of the spread of planktonic larvae for any marine species are rare, due to practical limitations of tagging and tracking the larvae. The general assumption is that long planktonic durations and off-shore larval development facilitate dispersal and hence maintain high levels of connectivity among population sub-units. Although we address this issue obliquely, slow range expansion by a well-established and highly fecund introduced species implies that for many marine invertebrates, even those with long planktonic phases, the norm may actually be highly localised recruitment. Relative stasis punctuated by rare conditions that result in wide-scale mixing of propagules has previously been suggested to account for biogeographic patterns of distribution at large-space scales and for speciation, in invertebrates (Gosline 1968; Scheltema 1986) and fishes (Rosenblatt 1967; Brothers and Thresher 1985). Our data suggest that it also may be a useful model for connectivity in coastal communities. This has implications for the stability of and gene flow in structured, spatial marine metapopulations.

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