

## Seasonal population dynamics of the non-native *Caprella mutica* (Crustacea, Amphipoda) on the west coast of Scotland

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**Abstract.** Information on the life history and population dynamics of non-native species is essential to understand the process of invasion and impacts on invaded ecosystems. The non-native marine caprellid amphipod *Caprella mutica* has successfully established populations on coastlines throughout the temperate northern hemisphere and in New Zealand in the southern hemisphere. The introduction mechanism has been surpassed and it is now important to understand its ecology and biology in non-native habitats. The seasonal population dynamics of *C. mutica* were investigated over 18 months at four sites with different levels of anthropogenic disturbance on the west coast of Scotland. Abundance of *C. mutica* fluctuated seasonally at all sites, peaking during June to October. The highest abundance recorded on a single mesh collector was 319 000 individuals m<sup>-2</sup> in August 2004 at one of the fish farms. Both seasonal and site-specific factors influenced the population dynamics of *C. mutica*. Both males and females were significantly larger and more abundant at the fish farm sites. Individuals displayed reproductive characteristics at a smaller size at the fish farm sites, indicating earlier maturity. The results suggest that anthropogenic disturbance and artificial resource enhancement contribute to the global establishment success of non-native *C. mutica*.

**Additional keywords:** aquaculture, invasion biology.

### Introduction

Information on the life history and population dynamics of non-native species is essential to understand the process of invasion, and impacts on invaded ecosystems (García-Meunier *et al.* 2001). Population biology can help to predict ecological impacts of non-native species (Ricciardi and Rasmussen 1998; Krylov *et al.* 1999), develop management practices and policies (Goodwin *et al.* 1999; Townsend 2003), and identify whether efforts to contain, eradicate, or even take no action, would be more practical (Allendorf and Lundquist 2003). The ecological impact of non-native species cannot always be predicted from knowledge of their biology in their native habitat (Krylov *et al.* 1999; Rosecchi *et al.* 2001). It is critical that the basic characteristics of an invader's distribution in space and time in the new habitat are understood before many questions concerning a non-native species can be answered (Flores and Paula 2002; Parker *et al.* 2003; Phillips and Shine 2006).

Only a small proportion of introduced species become established following introduction (Lodge 1993; Williamson 1996). Although propagule pressure and environmental mismatch are the primary determinants of the successful establishment of a species (e.g. Colautti and MacIsaac 2004; Colautti *et al.* 2006), life history characteristics might also aid

establishment success and facilitate subsequent spread in a new habitat (Newsome and Noble 1986; Nichols *et al.* 1990). Non-native species that spread rapidly once established are often 'r' strategists, i.e. those that respond opportunistically when conditions are favourable, including the ability to take advantage of disturbed habitats (Lodge 1993; Van Der Velde *et al.* 1998). Characteristics of 'r' strategists, shared by aquatic crustacean invaders, include high fecundity and growth rates, short life span and generation time, production of several generations per year and early sexual maturity (Van Der Velde *et al.* 1998; Devin *et al.* 2004). Having these life history traits does not guarantee success as an invader, but it does indicate that a species is equipped to invade a suitable habitat if given the opportunity.

Caprellid amphipods are marine crustaceans living from the littoral zone to depths of over 1500 m. Many species in the F. Caprellidae exhibit the characteristics described above, and thus may be considered as prime candidates to establish and spread in areas where they are not native (provided appropriate transportation vectors are available). To date, *Caprella acanthogaster*, *C. californica*, *C. mutica*, *C. natalensis*, *C. scaura* and *C. simia* have been identified outside of their native range (Ashton 2006, and references therein; Watling and Carlton 2007). Of these, *C. mutica* in particular has successfully

invaded a wide range of new ecosystems in association with anthropogenic activities and vectors. The native habitat of *C. mutica* is the sub-boreal coastal waters of north-east Asia, but it has now been described from all oceanic coastlines in the northern hemisphere (Ashton *et al.* 2007a), and from New Zealand in the southern hemisphere (Inglis *et al.* 2006). The population and production biology of *C. mutica* in its native range in Possjet Bay, Sea of Japan has been investigated by Fedotov (1991) and Vassilenko (1991). However, given the widespread distribution of non-native *C. mutica*, it is necessary to understand its ecology and biology in non-native habitats. *Caprella mutica* was first identified on the west coast of Scotland in 2000 (Willis *et al.* 2004), and is now widely distributed on artificial substrates on both the east and west coasts of Scotland (Cook *et al.* 2007). Artificial substrates (e.g. marinas, aquaculture facilities, oil platforms) often experience regular anthropogenic disturbance. Disturbance has been suggested an important characteristic in the invasibility of communities (Hobbs and Huenneke 1992; Burke and Grime 1996). For example, Colautti *et al.* (2006) found that communities experiencing more disturbance and greater resource availability sustained greater establishment rates and proliferation of invaders. Therefore, the association of *C. mutica* with disturbed and resource-supplemented habitats in its non-native range might also contribute to its establishment success.

The aim of this study was to investigate the seasonal population dynamics of non-native *C. mutica* in areas of anthropogenic disturbance on the west coast of Scotland. Sites with different anthropogenic disturbances were used for the study to determine whether population characteristics (abundance, size–frequency distribution and sex ratio) or reproductive biology (size at maturity, and fecundity as both proportion of ovigerous females in the population and number of eggs per ovigerous female) typify those of an ‘*r*’ strategist and therefore contribute to the success of newly established non-native populations.

## Materials and methods

### Site description

The Lynne of Lorne, on the west coast of Scotland, has a large sea loch in the north (Loch Linnhe) and opens to the Atlantic continental shelf in the south (Pearson 1970; Fig. 1). The area experiences freshwater runoff from Loch Linnhe and Loch Etive, and there is also exchange of oceanic water through the Sound of Mull to the west. Tides are semidiurnal, with an average tidal range of 3.5 m. All the study sites were located on the eastern side of the Lynne of Lorne, close to the entrance to Loch Etive (Fig. 1).

*Caprella mutica* was first recorded at Dunstaffnage fish farm (56°27.090'N, 05°27.733'W) in 2000 (Willis *et al.* 2004). In addition to Dunstaffnage fish farm (hereafter referred to as Dunstaffnage), three artificial sites near Dunstaffnage likely to support populations of *C. mutica* and having different levels of anthropogenic disturbance were included in this study: Saulmore fish farm (56°27.115'N, 05°24.669'W), Dunstaffnage Marina (56°27.041'N, 05°25.961'W), the Scottish Association for Marine Science (SAMS) pontoon (56°27.026'N, 05°26.358'W), hereafter referred to as Saulmore, Marina and Pontoon respectively.

Dunstaffnage fish farm is located in the Lynne of Lorne (Fig. 1) and produces Atlantic salmon (*Salmo salar*). The depth at the site ranged from 30 to 40 m (below Chart Datum, C. D.). The residual current direction is north-east, although there are strong currents to the south-west when the tide ebbs out of Lochs Linnhe and Etive (C. J. Cromey, unpubl. data). Saulmore fish farm is located in a bay close to the mouth of Loch Etive (Fig. 1), raising sea trout (*Salmo trutta*). The depth at the site is 7 m. This site is subject to considerable freshwater runoff from Loch Etive, which plays an important role in the physical characteristics of the area. The outflow from Loch Etive into the Lynne of Lorne causes a clockwise eddy in the bay on the ebbing tide, and in the opposite direction on the flood tide (G. V. Ashton, M. T. Burrows, K. J. Willis and E. J. Cook, pers. obs.). Dunstaffnage Marina is a recreational boating marina located in Dunstaffnage Bay, a sheltered bay between the mouth of Loch Etive and the Lynne of Lorne (Fig. 1). The marina is operational throughout the year. The marina pontoons are moored in a water depth of 4 m. The characteristics of the bay are similar to those experienced at Saulmore fish farm, although the influence of Loch Etive is less pronounced. SAMS has a moored pontoon on the opposite side of Dunstaffnage Bay to the marina (Fig. 1). This site is shallower than the marina (3 m) but is influenced by the same water currents. The pontoon experienced minimal anthropogenic disturbance for the duration of the study.

### Experimental protocol

Fortnightly sampling started in January 2004 and continued for 18 months. Sampling at Dunstaffnage Fish Farm began in July 2004 and continued for 14 months. Every fortnight, three weighted plastic meshes (25 × 10 cm, mesh size 5 mm; Clean-ups, EGL Homecare, Essex, UK; Ashton 2006) were deployed at each site at a depth of 4 m; each deployment was separated by a distance of 2 m, enabling detection of abundance down to a minimum of 40 individuals m<sup>-2</sup> (i.e. 1 individual in 250 cm<sup>2</sup>). The meshes were recovered eight weeks after deployment. On several occasions, weather conditions made it unsafe to collect the meshes, and resulted in the loss of several meshes over the study period. Individuals of *C. mutica* were removed from the meshes and preserved in 90% ethanol.

Temperature was recorded at a depth of 4 m every 30 min during the study using Tiny-Tag dataloggers (±0.1°C; Gemini Data Loggers, West Sussex, UK). Seawater temperatures recorded at the four sites followed the same annual trend for the first 12 months; subsequently only one datalogger was deployed (at Dunstaffnage). Water-column profiles of temperature and salinity were recorded at each site on each sampling occasion using a Sea-Bird SBE 19 SeaCat Profiler (Sea-Bird Electronics, Washington, USA).

### Laboratory procedures

Individuals of *C. mutica* collected in the field were observed under an Olympus SZX9 stereomicroscope. If the sample was considered too large (>300 individuals), a sub-sample was taken using a plankton splitter (Hiwatari and Kajihara 1984). Body length to the nearest 0.1 mm was measured from the front of the head to the end of pereonite VII, using PC-based digitising software. Females were identified by the presence of oostegites,

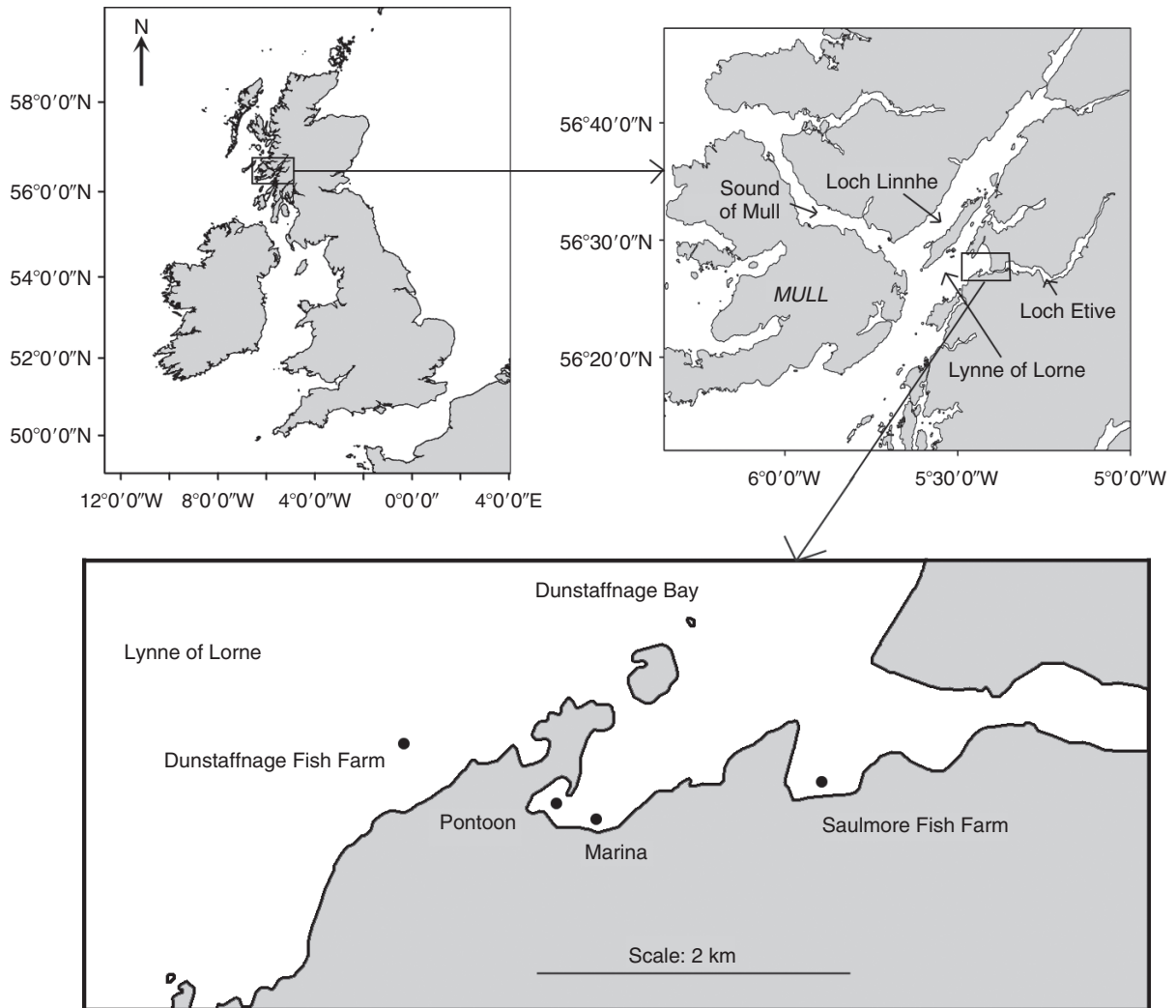


Fig. 1. Map of east Lynne of Lorne showing location on the west coast of Scotland and the position of sampling sites.

the anterior position of gnathopod II and a lack of setation on pereonites I and II, and males by the distal position of gnathopod II and extension and setation of pereonites I and II (Laubitz 1970; Arimoto 1976). Identification of ovigerous females was through the presence of eggs in the brood pouch. Individuals that were smaller than 4 mm, or lacking characteristics of either sex, were defined as juveniles. Eggs were counted from up to 10 haphazardly-selected ovigerous females in each sample by dislodging them from the brood pouch using a dissecting needle and fine paint brush.

Statistical analysis

Differences in salinity at 4 m and throughout the whole water column at the four sites were analysed using one-way ANOVA after confirming data met the assumption of this parametric test. A significant result was followed by a *post-hoc* pairwise Mann–Whitney test (Zar 1996). MINITAB (version 13) was used for all statistical analyses.

As a solution to the difficulties posed by the preponderance of zero counts, generalised linear models of categorised

(ordinal) abundance were used to test the significance of factors influencing the abundance of *C. mutica*. The continuous scale of the original abundance data was sliced to create ordinal data (Guisan and Harrell 2000). Slices were logarithmically spaced to give seven categories of abundance, each increasing by one order of magnitude (e.g. Category 1 included abundances >0–1 with a logarithmic midpoint of 0.31622, Category 2 included abundances of >1–10 with a logarithmic midpoint of 3.1622, etc.). Male, female and juvenile abundance data were treated separately. Site was used as a factor in the model. ‘No individuals at Dunstaffnage’ was used as a reference value. The cosine and sine of the angular equivalent of the day of the year ( $\theta$ ;  $2\pi * \text{Julian day} / 365$ ) were used as covariates in the model to incorporate seasonality ( $\text{Cos } \theta$  and  $\text{Sin } \theta$  respectively). The following model was then estimated:

$$LP(\leq \text{category at site}) = a\text{Category} + b\text{Site} + c \text{Cos } \theta + d \text{Sin } \theta + e\text{Site} \times \text{Cos } \theta + f\text{Site} \times \text{Sin } \theta$$

where  $LP$  equals logit probability, and  $a$  through  $f$  were coefficients. The 'goodness of fit' of the models was assessed by the Somers'  $d_{yx}$  (Somers 1962).

Logit probabilities were then back-transformed to give cumulative odds ratios i.e. the probability of being in the test category or less. The probability of being in a category ( $x$ ) was therefore:

$$P(x) = P(\leq x) - P(\leq x - 1)$$

Predicted probabilities were used to calculate expected abundance at 7-day intervals by summing the product of the logistic midpoint of each category multiplied by the expected probability:

$$E(Y) = \Sigma P(\text{Cat}2) \times 3.1622 + \dots + P(\text{Cat}6) \times 3.1622$$

where 3.6122 is the logarithmic midpoint of Category 2, and so on.

The probability of being in Category 7 (100 000–1 000 000 individuals  $\text{m}^{-2}$ ) was less than 0.05 in all instances; however, because of the large value of the midpoint, the inclusion of the term in the model led to large deviations from the sampled data. For this reason, the term was excluded from the models used to predict abundance. The significance of site, season and site-dependent season effects in all models was calculated using Student's  $t$ -tests (with a null hypothesis of the coefficients being equal to zero). A chi-square test was used to calculate the significance of differences between the sites.

Seasonal length–frequency distributions were obtained by splitting size records into 2-mm classes (Flores and Paula 2002). Lengths of males and females were compared using Student's  $t$ -test (Zar 1996). Differences in the length–frequency distribution between sites were analysed using a Kruskal–Wallis test.

Binary logistic modelling was used to investigate differences between the proportion of males, females and ovigerous females found at each site during the study (using a model similar to that described above). Coefficients of the parameters in the model were used to predict sex ratios over an annual cycle. Seasonal differences in the number of eggs per female and the ratio of number of eggs to the length of female were analysed using general linear models. Where the seasonal component was not significant, General Linear Modelling (GLM), with length as a covariate, was used to investigate between-site differences in the number of eggs per female. Significant between-site differences in the length–frequency distribution and number of eggs per female were followed by *post-hoc* pairwise comparisons using the Mann–Whitney test (Zar 1996).

## Results

### *Environmental data*

Seawater temperatures ranged from 7.4°C (April 2004) to 14.3°C (September 2004), varying from the late winter minima in February–March and late summer maxima in August–September. Salinity at 4 m varied between 16.5 (Saulmore, December 2004) and 34.5 (all sites, March 2005). Salinity at Dunstaffnage varied least throughout the study period. Salinity at the other sites varied inconsistently but tended to be lower and more variable when sampling was carried out close to low tide.

There were significant differences in salinity between the four sites at 4 m (ANOVA:  $F_{3,98} = 9.82$ ,  $P < 0.001$ ) and throughout the water column (ANOVA:  $F_{3,98} = 8.84$ ,  $P < 0.001$ ). Salinity at both 4 m and throughout the entire water column was consistently higher at Dunstaffnage than at the Marina and Pontoon (Mann–Whitney test:  $P < 0.001$ ). Saulmore was the least saline site (Mann–Whitney test:  $P = 0.02$ ).

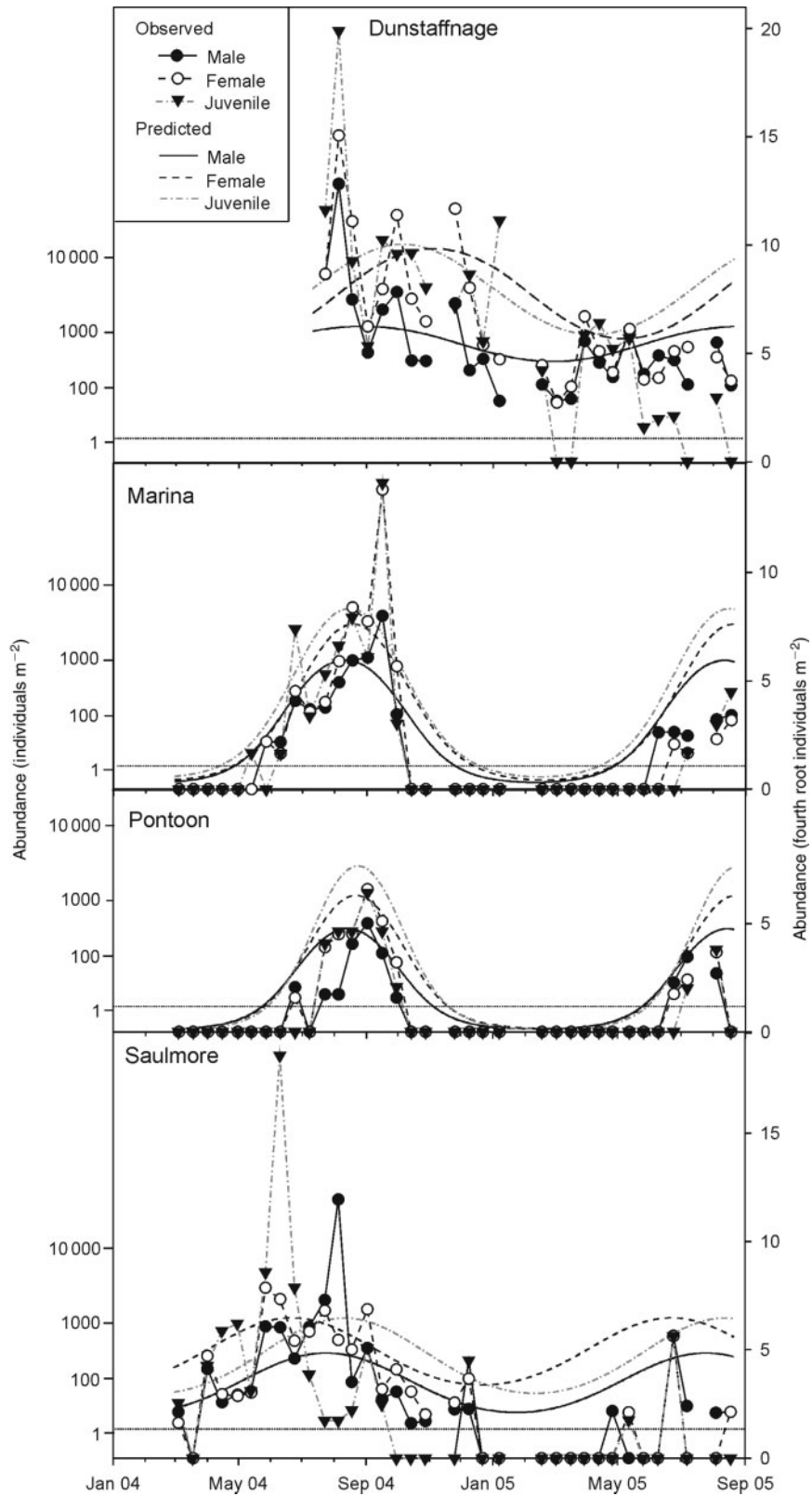
### *Population characteristics*

Abundances of *C. mutica* fluctuated seasonally at all sites (Fig. 2). Dunstaffnage was the only site where individuals were found on every sampling occasion. Populations at the Marina and Pontoon displayed clear seasonal differences, with a complete absence of individuals from October to May and highest abundances in August and September (Fig. 2). The highest abundance recorded on a single mesh was 319 000 individuals  $\text{m}^{-2}$  in August 2004 at Dunstaffnage. The high abundances of *C. mutica* at all sites were largely explained by high numbers of juveniles. At the Pontoon, the maximum abundance of 2900 individuals  $\text{m}^{-2}$  was recorded on 5th August 2004. When all dates were considered together, juveniles were more abundant than males or females, except at the Pontoon where abundances of females and juveniles were similar (Table 1), and females were generally more abundant than males at all sites.

Likelihoods of abundance predicted using GLMs were representative of the data (Somers'  $d_{xy} = 0.72$ – $0.79$ ). The likelihood of finding *C. mutica* individuals at the Marina and Pontoon was very low for around six months over winter and spring, followed by a sharp increase and a narrow peak in abundance in September (Fig. 2). At Saulmore and Dunstaffnage, the changes in likelihood were more gradual, with presence predicted throughout the year, and a maximum predicted likelihood in October at Dunstaffnage and July to August at Saulmore (Fig. 2). Abundance varied significantly over the annual cycle ( $t$ -test of  $\text{Cos } \theta$  coefficient  $c$  v. zero,  $n = 276$ ,  $P < 0.001$ ) and the pattern of change varied at each site ( $t$ -test of  $\text{Site} \times \text{Cos } \theta$  interaction coefficient  $e$  v. zero,  $n = 276$ ,  $P < 0.001$ ). Male, female and juvenile caprellids were significantly more likely to be present and more abundant at Dunstaffnage ( $\chi^2_3$ :  $P < 0.001$ ,  $P < 0.001$  and  $P = 0.03$  respectively), and abundance values at Saulmore were also significantly greater than those at the Marina and Pontoon ( $\chi^2_3$ :  $P < 0.001$ ,  $P = 0.002$  and  $P = 0.005$  respectively).

The maximum total length recorded for males during the study was 47 mm at Dunstaffnage, whereas for females it was 29 mm at Saulmore (Table 1). Juvenile *C. mutica* ranged in body length from 0.81 to 7.95 mm. Males dominated the larger size classes and were significantly longer than females ( $t$ -test,  $n = 2387$ ,  $P < 0.001$ ; Fig. 3). Females had a unimodal size distribution, whereas males showed a more variable distribution. The length–frequency distribution varied significantly between sites (Kruskal–Wallis test,  $Z = 919.75$ ,  $\text{df} = 3$ ,  $P < 0.001$ ), with the longest individuals at Saulmore and the shortest at the Marina (both males and females; Table 1; Fig. 3).

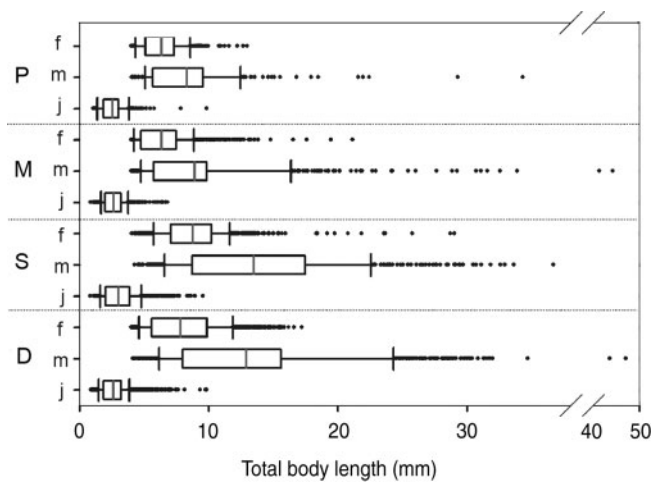
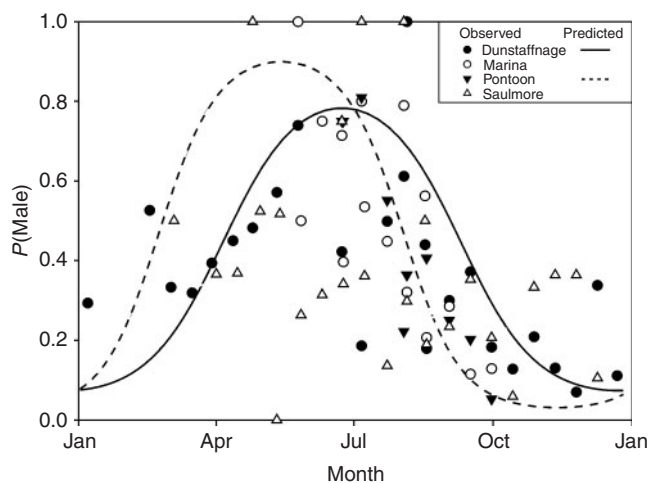
Females dominated at all sites for most of the year, but their dominance was most marked in autumn and winter (Fig. 4). The overall sex ratio was biased towards females (males/males + females:  $n = 159$ ,  $\text{mean} \pm \text{s.e.} = 0.399 \pm 0.023$ ). Sex ratio varied between sites ( $t$ -test,  $n = 74$ ,  $P < 0.001$ ), seasons ( $t$ -test,



**Fig. 2.** Seasonal abundance of male, female and juvenile *Caprella mutica* from January 2004 to September 2005 at Dunstaffnage (top), Marina, Pontoon and Saulmore (bottom). Symbols are the average fourth root (abundance  $m^{-2}$ ) ( $n = 3$ ). Curves are the predictions from Ordinal Logistic Regression, see methods for further details. The horizontal dashed line indicates the minimum detectable value (40 individuals  $m^{-2}$ ).

**Table 1.** Summary statistics for *Caprella mutica* populations at the four sites on the west coast of Scotland from January 2004 to September 2005. The numbers of individuals used to calculate length and fecundity statistics are indicated in parentheses

Site	Sample size	Sex	Abundance (mean individuals $m^{-2} \pm s.e.$ )	Length (mean mm $\pm s.e.$ )	Fecundity (mean no. eggs per female $\pm s.e.$ )
Dunstaffnage	25	Male	1269 $\pm$ 277	12.90 $\pm$ 0.15 (828)	81.92 $\pm$ 0.13 (406)
		Female	3416 $\pm$ 850	7.80 $\pm$ 0.10 (2138)	
		Juvenile	4588 $\pm$ 1238		
Marina	35	Male	465 $\pm$ 152	8.94 $\pm$ 0.23 (547)	50.52 $\pm$ 0.37 (90)
		Female	2469 $\pm$ 1224	6.32 $\pm$ 0.36 (1204)	
		Juvenile	2624 $\pm$ 1330		
Pontoon	35	Male	102 $\pm$ 32	8.29 $\pm$ 0.29 (197)	59.39 $\pm$ 0.86 (36)
		Female	225 $\pm$ 98	6.34 $\pm$ 0.08 (415)	
		Juvenile	228 $\pm$ 81		
Saulmore	35	Male	532 $\pm$ 37	11.58 $\pm$ 0.14 (522)	71.71 $\pm$ 0.12 (207)
		Female	1710 $\pm$ 128	7.57 $\pm$ 0.04 (5043)	
		Juvenile	2140 $\pm$ 213		

**Fig. 3.** Length–frequency distribution of *Caprella mutica* collected from January 2004 to September 2005 at: P, Pontoon; M, Marina; S, Saulmore; D, Dunstaffnage (f, female; m, male; j, juvenile).**Fig. 4.** Observed and predicted values of sex ratio ( $P(\text{Male}) = \text{male}/(\text{male} + \text{female})$ ). Predicted values were calculated using Binary Logistic Models as described in the text (Somers'  $d_{yx} = 0.56$ ).

$n = 74$ ,  $P < 0.001$ ), and displayed different seasonal patterns at each site ( $t$ -test,  $n = 74$ ,  $P = 0.025$ ).

#### Reproductive biology

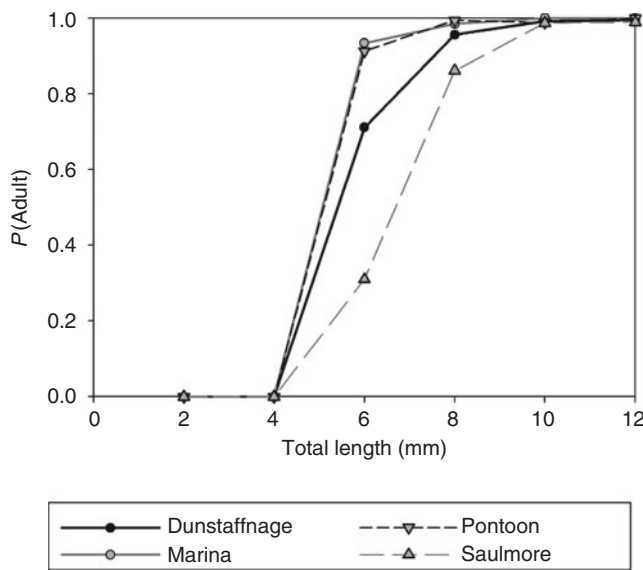
Juveniles developed adult morphological characteristics at a smaller size at the Marina and Pontoon compared with Dunstaffnage, with juveniles attaining greater length before maturing at Saulmore (Fig. 5). Ovigerous females were found throughout the study period (Fig. 6). Proportions of ovigerous females varied between sites, seasons and exhibited different seasonal patterns at each site ( $t$ -test,  $n = 71$ ,  $P < 0.05$  for all variables). The predicted proportion of ovigerous to non-ovigerous females was greatest in spring and summer (April–October). The number of eggs per female was highly variable (range = 3–363, mean = 74, s.d. = 47.7; Fig. 7), but was significantly related to female length (Spearman's Rank Correlation coefficient,  $r_s = 0.469$ ,  $n = 739$ ,  $P < 0.01$ ). There was no significant difference in fecundity estimates as a function of female length between sites ( $t$ -test,  $n = 739$ ,  $P = 0.46$ ).

#### Discussion

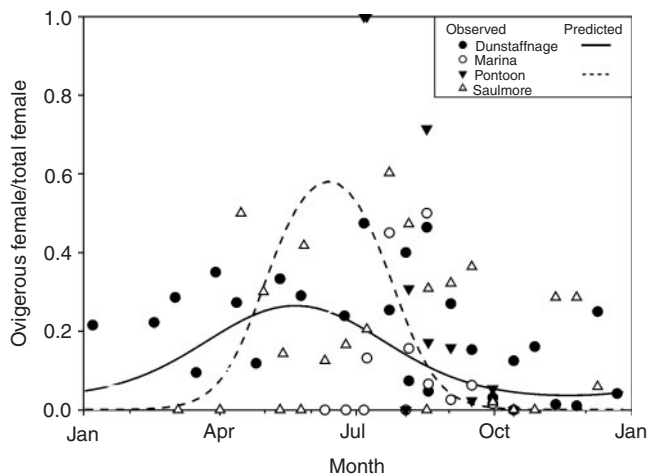
This is the first study on the seasonal population biology of the non-native *Caprella mutica*. Large fluctuations in abundance were observed at all four study sites on the west coast of Scotland, with population characteristics and reproductive output varying in response to seasonal and site-specific factors.

#### Population characteristics

The population abundances of *C. mutica* at all sites increased in spring to a peak in late summer (August–September), followed by a decline during winter. This cycle was in phase with annual sea water temperatures in the area and was similar to the seasonal population dynamics of *C. mutica* in its native habitat in Possjet Bay, Sea of Japan (Fedotov 1991), where abundance ranged from  $25.3 \pm 5.2$  (average  $\pm$  s.e.) individuals  $m^{-2}$  in April (spring) to  $1223.3 \pm 89.7$  individuals  $m^{-2}$  in June (summer). Populations of *C. mutica* on the west coast of Scotland were more abundant compared with those in the native habitat; abundance in excess of 10 000 individuals  $m^{-2}$  was recorded at three sites in this study (with a maximum of  $\sim 319\,000$



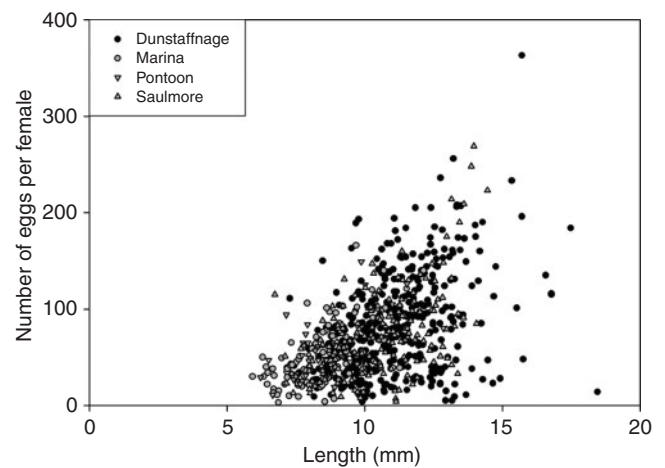
**Fig. 5.** Body length of *Caprella mutica* at sexual maturity (mm). Sample sizes:  $n = 7974, 4877, 1245, 4450$  for Dunstaffnage, Marina, Pontoon and Saulmore respectively.  $P(\text{Adult})$  is the proportion of individuals of that size class determined to be sexually mature.



**Fig. 6.** Observed and predicted ratio of ovigerous females to all females at all sites. Predicted values were calculated using Binary Logistic Models as described in the text (Somers'  $d_{yx} = 0.58$ ).

individuals  $m^{-2}$ ), compared with a maximum of 2600 individuals  $m^{-2}$  in the native habitat (Vassilenko 2006). Several factors could be contributing to the high abundance of *C. mutica* in non-native habitats, such as enhanced food supply at the fish farm sites (Cook *et al.* 2006), the availability of space created by the artificial structures (Stachowicz *et al.* 1999, 2002; Locke *et al.* 2007), a favourable physical environment (Crawley 1986; Occhipinti–Ambrogi 2007), or a lack of native competitors, predators, diseases and/or parasites (Van Der Velde *et al.* 1998; the ‘enemy release hypothesis’: Colautti *et al.* 2004).

The recognised non-native distribution of *C. mutica* continues to expand (Ashton *et al.* 2008; Woods *et al.* 2008), and



**Fig. 7.** Relationship between number of eggs per female and female length of *Caprella mutica* at the four sampling sites.

although high abundance and rapid population increases might contribute to the invasive success of *C. mutica* (Ehrlich 1989; Van Der Velde *et al.* 1998), population fluctuations will also affect localised spread and establishment. *Caprella mutica* individuals were present at Dunstaffnage for the duration of the study, suggesting long-term establishment at this location. However, as in the native habitat (Fedotov 1991), abundance was low at all sites during winter, indicating high mortality or migration events. Individuals were only present at Saulmore for eight months of the year and were apparently absent from the Marina and Pontoon sites for six or seven months, between October and May or June, respectively. Environmental factors do not explain the observed differences in population characteristics at the four sites. It is unknown whether these populations migrate elsewhere during this time (possibly to deeper waters: Fedotov 1991) or become locally extinct and are reintroduced from a perennial source (e.g. Dunstaffnage). Fluctuating populations could make *C. mutica* susceptible to extinction (Pimm 1988). However, the rapid rate of population increase of *C. mutica* at these sites (from 0 to  $>1000$  individuals  $m^{-2}$  in 2 months at both the Marina and Pontoon) is likely to contribute to its invasion success at new locations. Individuals were significantly larger at Saulmore and Dunstaffnage than at the pontoon; this size difference is found throughout development, with juveniles at Saulmore reaching a larger size before sexual diagnostic characters become apparent. The larger size of the females also contributes to the higher fecundity of *C. mutica* at the fish farms. The artificial fish feed, high in protein and lipids, has been shown to increase growth of crustacean species (Deering *et al.* 1997; Sheen and Wu 1999), and most likely produces a similar response in *C. mutica* at the fish farms. Enhanced quantities of phyto- and zooplankton associated with fish farms (Doi *et al.* 2008; Navarro *et al.* 2008), as well as other organisms attached to the cage structures (Cook *et al.* 2006; Doi *et al.* 2008) could also contribute to this increased growth.

Increased body size in the introduced range is common in invasive marine invertebrates (Grosholz and Ruiz 2003), and the successful establishment of the comparatively large *C. mutica* may be another example in agreement with this trend in

crustaceans. However, it has recently been disputed whether larger body size implies better invasion success in marine bivalves (Miller *et al.* 2002; Roy *et al.* 2002). Males are typically larger than females, with the maximum length of male *C. mutica* recorded in this study (47 mm) similar to that in the native range of Japan (50 mm; Nishimura 1995), but greater than that recorded in Possjet Bay, Russia (Fedotov 1991; Vassilenko 1991).

As in the native range (Fedotov 1991), and in common with many amphipods (Costello and Myers 1989, and references therein; Powell 1990), female *C. mutica* dominated the populations for most of the year, with males only dominating populations in the summer. Sex-ratio fluctuations in amphipods have been attributed to several factors, including differential rates of production, growth, longevity or mortality (Naylor *et al.* 1988; Beare and Moore 1996) or selective predation on females (Caine 1979). The influence of sex-biased characteristics has not previously been suggested as determining the invasion success in other taxa and is considered unimportant to the establishment success of non-native *C. mutica*.

#### *Reproductive biology*

At Dunstaffnage, juveniles (0–10 mm) were present throughout the study, indicating continuous reproduction or delayed growth of over-wintering juveniles. Seasonality of reproduction, similar to that observed in the native region (Fedotov 1991), was observed at the three other sites, where juveniles (and adults) were absent in the winter (November–January), and most abundant in spring and summer at Saulmore, and in summer and autumn at the Marina and Pontoon. Within its native range, average water temperatures can fall to 0°C (Fedotov 1991). The minimum water temperature recorded in this study was 7.4°C (April 2004). Adult *C. mutica* have been shown to tolerate temperatures <2–28°C, and salinities down to 19 over a short (48 h) exposure period (Ashton *et al.* 2007b). Warmer winter temperatures on the west coast of Scotland could enable year-round reproduction and survival of juveniles, as recorded at Dunstaffnage. However, the absence of juveniles at three of the sites in winter indicates that temperature is not the only limiting factor. Early developmental stages of crustaceans have reduced tolerance to changes in salinity and temperature (Maranhão *et al.* 2001; Tsoi *et al.* 2005), so greater fluctuations in environmental conditions might have limited the presence of juveniles at the Marina, Pontoon and Saulmore (temperature, salinity and suspended sediment regimes will be more marked at these shallower sites). The year-round input of feed at the fish farms could also contribute to the maintenance of juvenile *C. mutica* individuals at Dunstaffnage and Saulmore. In addition, at Saulmore, the increased freshwater influence during winter reduces the survival of juvenile *C. mutica* here.

There was a positive correlation between *C. mutica* female length and the number of eggs produced, as found for *C. mutica* and other caprellids in their native ranges (Caine 1979; Vassilenko 1991), and a common trend in amphipods (Powell 1990; Sainte-Marie 1991). The artificial nutrient enrichment at Dunstaffnage and Saulmore might be responsible for the larger, more productive female *C. mutica* at these sites (either directly or through enhancing the associated flora and fauna), but did not affect fecundity in terms of number of eggs per female body

length. The high fecundity of *C. mutica* would allow rapid population growth and expansion in newly-established populations, thus contributing to its success as a non-native species. However, in its native range *C. mutica* is not the most fecund caprellid species (Vassilenko 1991), so other characteristics must also contribute to its success outside its native range.

#### *Anthropogenic influence*

Anthropogenic activities influenced the population dynamics and characteristics of *C. mutica* at both fish farm and non-fish farm sites (i.e. Marina and Pontoon). The enhanced food supply can be beneficial to epibiotic communities at caged fish farm sites (Cook *et al.* 2006). Artificial feed has the potential to influence all aspects of the population biology of *C. mutica*, in particular the rate of population increase and size of individuals (Stirling and Okumus 1995; Cook *et al.* 2006). As opportunistic feeders (Keith 1969), *C. mutica* could be feeding directly on the fish feed, on the algal growth, which is enhanced by dissolved organic nutrients (e.g. Rhodophyta) (Troell *et al.* 1997), and/or on enhanced plankton abundance in the close vicinity of the cages (Cook *et al.* 2006; Navarro *et al.* 2008; Cook *et al.* 2009). Without the continuous input of feed, food supply at the Marina and Pontoon might be much reduced relative to the fish farms, especially in winter when productivity in the area is minimal (Grantham 1981).

Space is a limiting resource in subtidal epifaunal habitats (Dayton 1971; Sutherland and Karlson 1977) and influences invasion success in other communities (e.g. Burke and Grime 1996; Stachowicz *et al.* 2002). The success of *C. mutica* at the fish farms might reflect enhanced availability of space at these sites. Cage nets, which are suspended in the water column, provide favourable habitat for *C. mutica* that is similar to the algal beds where they are found in their native range (Vassilenko 2006). Although available space is enhanced with the addition of floating structures at the Marina and Pontoon, the quantity and quality of space suspended in the water column is reduced in comparison to the fish farms, and the rigid properties of the structures are likely to be less favourable. Caprellids favour highly branched substrata, especially those that allow encirclement by the pereopods (e.g. hydroids and filamentous algae: Caine 1978), and the fibres in the nets offer such substrata. At the Pontoon and Marina, *C. mutica* depend on epibenthic fouling organisms to provide suitable attachment sites.

Disturbance also promotes species invasions (Crawley 1986; Cohen 2002; Stachowicz *et al.* 2002), and non-native species are generally first identified in human-impacted, highly disturbed sites. However, it should be noted that non-natives generally originate from and are released into human-impacted sites, and that these sites are the most intensively studied (Cohen 2002). Fish farms are highly disturbed environments where nets are regularly lifted for pharmaceutical treatments, harvesting, grading, and air-drying to reduce epibiotic growth, continually providing new space for opportunistic species to establish. The specific effects of disturbance on invasibility and invasion success are confounded by differences in species properties, ecosystem properties and propagule pressure (Lonsdale 1999). The intensity, timing and sequence of disturbance events will also be important in determining its effect on ecological communities (Fukami 2001). Thus, the difference in disturbance



regimes may help to explain the different population dynamics at the four sites.

## Conclusions

Several factors influence the establishment success of a species, including vector associations, propagule pressure, environmental mismatch and chance (Colautti and MacIsaac 2004; Colautti *et al.* 2006). *C. mutica* has repeatedly overcome these and is now widespread on artificial structures in disturbed environments in the northern hemisphere (Ashton *et al.* 2007a), and range expansion is also underway in the southern hemisphere (Willis *et al.* 2009). Aquaculture sites appear to provide optimal conditions and refuges for *C. mutica* and other non-native species, greatly enhancing their probability of establishment. The commensal nature of *C. mutica* in its native habitat suggests that management is unlikely to be necessary. However, the high abundances of *C. mutica* in non-native environments, combined with their competitive nature (Shucksmith 2007), are of some concern. Any eradication attempts of this or other motile invertebrates should note that sites would be at risk of re-introduction of *C. mutica* from any neighbouring sources in late spring. Furthermore, the apparent absence of *C. mutica* in surface waters in winter does not necessarily denote complete absence at a site.

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