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### ► To cite this version:

Gail V. Ashton, Kate J. Willis, Michael T. Burrows, Elizabeth J. Cook. Environmental tolerance of: implications for its distribution as a marine non-native species. *Marine Environmental Research*, 2007, 64 (3), pp.305. 10.1016/j.marenvres.2007.02.003 . hal-00501909

**HAL Id: hal-00501909**

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Submitted on 13 Jul 2010

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## Accepted Manuscript

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PII: S0141-1136(07)00036-0  
DOI: [10.1016/j.marenvres.2007.02.003](https://doi.org/10.1016/j.marenvres.2007.02.003)  
Reference: MERE 3103

To appear in: *Marine Environmental Research*

Received Date: 21 December 2006  
Revised Date: 8 February 2007

Please cite this article as: Ashton, G.V., Willis, K.J., Burrows, M.T., Cook, E.J., Environmental tolerance of *Caprella mutica*: implications for its distribution as a marine non-native species, *Marine Environmental Research* (2007), doi: [10.1016/j.marenvres.2007.02.003](https://doi.org/10.1016/j.marenvres.2007.02.003)

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1 **Environmental tolerance of *Caprella mutica*: implications for its distribution as a**  
2 **marine non-native species**

3

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19

20

20 **Abstract**

21 Physiological tolerances limit the distribution of marine species, with geographical  
22 ranges being set by environmental factors, such as temperature and salinity, which  
23 affect the rates of vital processes and survival of marine ectotherms. The  
24 physiological tolerances of the non-native marine amphipod *Caprella mutica* were  
25 investigated in laboratory experiments. Adult *C. mutica* were collected from a fish  
26 farm on the west coast of Scotland and exposed to a range of temperatures and  
27 salinities for 48 h. *C. mutica* were tolerant of a broad range of temperature and salinity  
28 conditions, with 100% mortality at 30 °C (48 h LT<sub>50</sub>, 28.3 ± 0.4 °C), and salinities  
29 lower than 16 (48 h LC<sub>50</sub>, 18.7 ± 0.2). Although lethargic at low temperatures (2 °C),  
30 no mortality was observed, and the species is known to survive at temperatures as low  
31 as -1.8 °C. The upper LC<sub>50</sub> was greater than the highest salinity tested (40), thus it is  
32 unlikely that salinity will limit the distribution of *C. mutica* in open coastal waters.  
33 However, the species will be excluded from brackish water environments such as the  
34 heads of sea lochs or estuaries. The physiological tolerances of *C. mutica* are beyond  
35 the physical conditions experienced in its native or introduced range and are thus  
36 unlikely to be the primary factors limiting its present distribution and future spread.

37

38 **Keywords**

39 Biological invasion, caprellid amphipod, non-native distribution, physiological  
40 tolerance, salinity tolerance, temperature tolerance

41

41 **Introduction**

42 The marine amphipod *Caprella mutica*, a native of north-east Asia, is now widely  
43 distributed in the northern hemisphere between latitudes 35°N and 70°N, representing  
44 a considerable extension to its native latitudinal range (Ashton *et al.*, in press). The  
45 non-native populations discovered to date are restricted to temperate oceanic coasts  
46 that experience temperatures ranging from 0 to 22 °C, similar to that of the native  
47 habitat, which has an annual seawater temperature range of -1.8 to 25 °C  
48 (Schevchenko *et al.*, 2004).

49 Environmental factors are likely to play an important role in influencing the present  
50 and future global distribution of *C. mutica*, as physiological tolerances result in ranges  
51 being set by physical characteristics that affect the rates of vital processes and survival  
52 (Vermeij, 1996). Temperature and salinity are often considered to be the principle  
53 variables affecting growth, reproduction and survival of marine ectotherms (Kinne,  
54 1970a; Kinne, 1970b), and can act singly or in combination to influence distribution  
55 patterns (Wiederholm, 1987; Stauffer & Boltz, 1994). Previous work has shown that  
56 while temperature does not limit the latitudinal distribution of *C. mutica* on the west  
57 coast of Scotland (Ashton *et al.*, in press), it does influence global distribution  
58 patterns of caprellid amphipods (Laubitz, 1970; Thiel *et al.*, 2003). For example,  
59 temperature is the primary factor limiting the distribution of caprellids in Australasia  
60 and Southern Chile (Thiel *et al.*, 2003), and in the North Pacific (Laubitz, 1970), with  
61 most species occurring in the 10 to 15 °C temperature range, and only a few in the  
62 sub-antarctic 5 to 10 °C range. The relatively disjunctive non-native distribution of  
63 *C. mutica* within the region experiencing temperatures between 0 to 22 °C, suggests  
64 that either range expansion is still underway, or factors other than temperature are  
65 affecting its establishment at a global scale.

66 A wide salinity tolerance is typical of many amphipod species (Kinne, 1970a), with  
67 several caprellid species displaying tolerance to salinities lower than 15 (Takeuchi *et*  
68 *al.*, 2003). Upper salinity tolerance limits are unlikely to be a limiting factor, as  
69 illustrated by Takeuchi *et al.* (2003), who found the salinity tolerance of four *Caprella*  
70 spp. to be greater than 34. In the native habitat of *C. mutica*, salinities range from 11  
71 to 35 (Schevchenko *et al.*, 2004). The presence of *C. mutica* in Scottish sea lochs that,  
72 at times, receive considerable freshwater inputs (Ashton *et al.*, in press), suggests that  
73 this caprellid is relatively tolerant of low salinities.

74 Tolerance of a wide range of environmental conditions is suggested as a characteristic  
75 of successful non-native species (Van der Velde *et al.*, 1998; Strasser, 1999).  
76 However, it is currently unknown whether the environmental conditions experienced  
77 by *C. mutica* throughout its distribution range correspond with its environmental  
78 tolerances. The caprellid may be limited to its current range by its physiological  
79 tolerance limits to temperature and salinity, or other factors may be limiting its  
80 biogeographic distribution. Here, we present the results of a study to investigate the  
81 lethal salinity and temperature tolerance limits of the non-native amphipod *C. mutica*  
82 on the west coast of Scotland. This study aimed to establish the physiological  
83 tolerances of the species to these two key environmental variables that are likely to be  
84 important in limiting the caprellids global distribution.

85

## 86 **Methods**

### 87 *Caprellid collection and maintenance*

88 *Caprella mutica* were collected from filamentous red algae attached to pontoon  
89 structures at Dunstaffnage fish farm (56° 27.090' N 05° 27.733' W) in June 2005 and

90 2006. The animals were transported in sea water, still attached to the algae, in 10 L  
91 buckets. Animals were acclimatised to laboratory conditions for 48 h at a constant  
92 temperature ( $14 \pm 1$  °C, ambient temperature) at a photoperiod of 8 D:16 L, the  
93 photoperiod regime was maintained throughout the tolerance experiments. The  
94 buckets received constant aeration and no additional food was given.

95

#### 96 *Temperature tolerance experiments*

97 Fifteen containers (1.5 L) were filled with filtered sea water (100 µm; salinity ~35)  
98 and five pieces of 5 mm mesh (150 cm<sup>2</sup>) were added to each container. Larger,  
99 healthy-looking animals were carefully isolated from the algae using forceps and  
100 transferred to the mesh in the experimental containers. A maximum of 34 individuals,  
101 including at least five male and five female *C. mutica* were added to each container.  
102 Starting numbers in each container were recorded. Experimental containers were then  
103 transferred into water baths (60 x 30 cm) maintained at five temperatures, with three  
104 replicate containers at each temperature. The containers reached test temperatures  
105 within 10 minutes of the start of the experiment. Temperatures were maintained using  
106 either TropicMarin heaters, or a Grant chiller, and were monitored throughout the  
107 experiment with temperature data loggers (Tinytag Aquatic, TG-3100). After 48 h, the  
108 containers were removed from the water baths and animals were immediately  
109 inspected for mortality, defined as a lack of response to mechanical stimulus (gentle  
110 prodding with a blunt probe).

111 A preliminary range-finding test using temperatures of 2, 10, 22, 31 and 40°C was  
112 undertaken to define approximately the lethal tolerance limits of *C. mutica*. These  
113 temperatures were selected pragmatically in an effort to include mortality rates  
114 ranging from 0% to 100%. In the range finding test, caprellids exposed to 40 °C died

115 within 5 minutes, while at 2 °C they were immobile after 48 h, and lethargic when  
116 stimulated. The second definitive experiment used a narrower range of temperatures  
117 (21, 24, 26, 28 and 30 °C) encompassing the upper lethal limit, which was estimated  
118 to lie between 22 and 31 °C in the range finding test.

119

#### 120 *Salinity tolerance experiments*

121 Experimental procedures and conditions were as described for the temperature  
122 tolerance tests, with the exception that the salinity tolerance experiments were  
123 maintained at a temperature of  $14 \pm 1$  °C in a constant temperature room.

124 Large healthy-looking caprellids were transferred to exposure tanks (1.5 L) containing  
125 filtered sea water (100 µm) at five different salinities. Salinities were achieved by  
126 addition of artificial sea salt (Tropical Marin) to water treated by reverse osmosis.  
127 Salinity was confirmed using a portable refractometer (Atago, S/MILL) at the  
128 beginning and end of the 48 h exposure periods. After 48 h, individuals were  
129 inspected for mortality by gentle prodding with a blunt probe.

130 As above, a preliminary range-finding test was done using salinities of 0, 10, 20, 30  
131 and 40 in an attempt to incorporate concentrations causing 0% and 100% mortality. In  
132 the range finding test, caprellids exposed to a salinity of 0 were immobile within 5  
133 minutes, with 100% mortality at salinities of 0 and 10 after 48 h. The upper lethal  
134 limit was higher than 40 (<10% mortality at salinities of 30 and 40). The second  
135 definitive experiment employed a narrower range of salinities (9, 13, 15, 18 and 20)  
136 encompassing the lower lethal limit, which was estimated to lie between 10 and 20 in  
137 the range finding test.

138



139 *Statistical Analysis*

140 Median lethal  $LT_{50}$  and  $LC_{50}$  values and associated 95% confidence limits were  
141 calculated using probit (Finney, 1971) or trimmed Spearman-Kärber analysis (TSK;  
142 Hamilton *et al.*, 1977; U.S.E.P.A., 1990) using MINITAB. MINITAB uses a Chi-  
143 squared analysis ( $\chi^2$ ) to test whether the data fits the Probit model. When  $\chi^2$  rejected  
144 the Probit model ( $P > 0.05$ ), a trimmed Spearman-Kärber analysis was used to  
145 calculate a non-parametric estimate of the lethal value. A disadvantage of the TSK  
146 analysis is that it only yields the median lethal response ( $LC_{50}$ ) and 95% confidence  
147 limits. When the test results are not unimodal or symmetrical about the median lethal  
148 response, the confidence intervals (CI) can be unreliable. A pairwise students' *t*-test  
149 was used to compare differences in mortality of male and female *C. mutica* at each  
150 temperature.

151

152 **Results**153 *Temperature tolerance*

154 Following 48 h exposure to temperatures between 21 °C and 30 °C, there was a  
155 marked increase in mortality of *C. mutica* at temperatures greater than 26 °C, with  
156 100% mortality at 30 °C (Figure 1). At 24 °C, mortality was increased (~25%) relative  
157 to that at 26 °C, and similar to mortality at 28 °C. The reason for this is unknown, but  
158 may be a response to other uncontrolled experimental conditions (e.g. pH or oxygen).  
159 Mortality was <10% at temperatures of 21 °C and 26 °C. The 48 h  $LT_{50}$  ( $\pm$  95% C.L.)  
160 was  $28.3 \pm 0.4$  °C. There was no significant difference in mortality between male and  
161 female *C. mutica*.

162

163 *Salinity tolerance*

164 100% mortality was observed following 48 h exposure of *C. mutica* to salinities lower  
165 than 15 (Figure 2). At a salinity of 18, individuals were lethargic and less responsive  
166 to stimulation than those at 20. The lower 48 h LC<sub>50</sub> ( $\pm$  95% C.L.) was  $18.7 \pm 0.2$ . The  
167 lower LC<sub>50</sub> for females ( $18.0 \pm 0.3$ ) was significantly higher ( $P < 0.05$ ) than that for  
168 males ( $19.3 \pm 0.4$ ).

169

170 **Discussion**

171 Adult *C. mutica* collected on the west coast of Scotland were tolerant of a wide range  
172 of temperature and salinity conditions in 48 h laboratory exposures. The upper  
173 thermal tolerance limit of *C. mutica* (48 h LT<sub>50</sub>, 28.3 °C) was higher than maximum  
174 temperatures experienced in its non-native Scottish habitat (16 °C; Ashton *et al.*, in  
175 press), or in its native habitat (25 °C, Schevchenko *et al.*, 2004). The lower lethal  
176 temperature was not determined as there was no mortality at the lowest temperature  
177 tested (2 °C), although the caprellids were immobile after 48 h at 2 °C and were  
178 lethargic when stimulated. After 48 h at a salinity of 18, *C. mutica* were lethargic, and  
179 at salinities lower than 16, 100% mortality was observed. These salinity values are  
180 also higher than those recorded in the native and non-native habitat of the caprellid  
181 (11 and 10.5 respectively; Schevchenko *et al.*, 2004; Ashton *et al.*, in press).

182 The current experiments were run for a period of 48 hours, and therefore only give an  
183 indication of the short-term tolerance of *C. mutica*. However, the thermal tolerance  
184 limits recorded in this study suggest that *C. mutica* could survive introduction to the  
185 tropics or the poles, extending its current distribution. In the northern hemisphere, *C.*  
186 *mutica* has been introduced to both coasts of North America, from 37.5 to 48.5 °N and

187 to the Atlantic coasts of Europe from 49.5 to 69.1 °N. In the southern hemisphere, *C.*  
188 *mutica* has only been described from New Zealand (Ashton *et al.*, in press). Sea  
189 surface temperatures at the equator are relatively stable at 26 to 27 °C throughout the  
190 year (Tait, 2001), slightly lower than the 48 h upper lethal limit of 28 °C. However,  
191 the ability of *C. mutica* to survive prolonged exposure to high temperatures is  
192 unknown, and it is also possible that earlier life stages may not be as tolerant to high  
193 temperatures as the adults.

194 In its native habitat, populations of *C. mutica* survive at temperatures as low as -  
195 1.8 °C, and non-native populations have established in areas that freeze at the surface  
196 during winter, such as Passamaquoddy Bay, Canada (Ashton *et al.*, in press). Given  
197 the lethargic state of the caprellids after 48 h at 2 °C in the present study, it is likely  
198 that growth and reproduction are reduced, or cease, at such low winter temperatures.

199 The salinity tolerance of adult *C. mutica* is similar to or slightly less than that of other  
200 *Caprella* species. The lower 48 h LC<sub>50</sub> (18.7 ± 0.2) is higher than that of *C. scaura*  
201 and *C. equilibria*, with 24 h LC<sub>50</sub> values of 7.5 and 11.5 respectively (Cockman &  
202 Albone, 1987), noting that these values are for 24 h exposures, not 48 h. For other  
203 *Caprella* species, *C. danilevski*, *C. subinermis*, *C. penantis* and *C. verrucosa*, 48 h  
204 LC<sub>50</sub> values ranged from 12 to 17 (Takeuchi *et al.*, 2003). The increased salinity  
205 tolerance of male *C. mutica* in the present study may reflect the sexual dimorphism of  
206 the species (the males are considerably larger) or differences between the sexes in  
207 resource allocation to reproduction (Hoback & Barnhart, 1996). It is surprising,  
208 however, that this trend was not observed with temperature, which might be expected  
209 to produce a greater physiological response (Davenport & Davenport, 2005).

210 In the native habitat, *C. mutica* individuals experience salinities as low as 11  
211 (Schevchenko *et al.*, 2004), considerably lower than the 48 h LC<sub>50</sub> in this study. Thus,

212 the current realized distribution of *C. mutica* with respect to salinity is beyond its  
213 fundamental niche described here. This is contrary to the expectation for marine  
214 ectotherms (Sprague, 1963; Tait, 2001). In coastal habitats, *C. mutica* are probably  
215 able to survive fluctuating salinity conditions during the tidal cycle and short periods  
216 of exposure to low salinity during periods of heavy rainfall. However, prolonged  
217 exposure to salinity lower than 18 is likely to adversely affect the caprellid, and may  
218 explain why populations are absent from the upper reaches of Scottish sea lochs that  
219 regularly experience low salinities (Ashton pers. obs.).

220 The broad physiological tolerance of adult *C. mutica* would suggest that changing  
221 temperature and salinity conditions experienced during transport through equatorial or  
222 polar regions would be unlikely to adversely affect individuals in ballast water (Witt  
223 *et al.*, 1997) or on ships' hulls (Minchin and Gollasch, 2003). Species distributions  
224 that are limited by thermal tolerances are expected to change in response to climate  
225 change (e.g. marine mammals, Tynan & DeMaster, 1997; coral reefs, Hoegh-  
226 Guldberg, 1999; pelagic ecosystems, Boyd & Doney, 2002). Predicted rates of range  
227 expansion in terrestrial environments include 6.1 km per decade (Parmesan & Yohe,  
228 2003) and 12.5 - 24.8 km per decade (Hickling *et al.*, 2006). In particular, evidence  
229 suggests that many invasive species possess traits that will enable them to capitalize  
230 on the various elements of global change, exacerbating the impacts of invasions on  
231 stressed ecosystems (Dukes & Mooney, 1999). Climate change will be important in  
232 determining the future distribution of *C. mutica*, which can be expected to extend  
233 polewards.

234 In addition to environmental conditions, the success of non-native species is also  
235 influenced by the frequency of introduction events, which are generally more  
236 common in temperate waters (Minchin & Gollasch, 2003; Drake & Lodge, 2004)

237 compared to tropical or polar regions, propagule pressure (the frequency and size of  
238 introduction events), and biotic interactions in the recipient region such as  
239 competition, facilitation and predation (Bruno *et al.*, 2005). Thus, the current  
240 distribution of *C. mutica* is likely to reflect a combination of introduction  
241 opportunities, as well as favourable abiotic and biotic conditions in these areas.

242 Broad physiological tolerance and plasticity are commonly cited as characteristics of  
243 successful invading species (Van der Velde *et al.*, 1998), with temperature and  
244 salinity tolerances often combining to limit the potential distributions of marine  
245 species (Wiederholm, 1987; Stauffer & Boltz, 1994). Given the broad temperature  
246 and salinity tolerance of adult *C. mutica* observed in this study, the caprellid is likely  
247 to be limited to marine habitats experiencing a temperate climate (not exceeding  
248 26 °C), and regions where salinity does not drop below 18 for extended periods of  
249 time. Evidence suggests that dispersal via human vectors is increasing the distribution  
250 of *C. mutica* at a faster rate than climate change (Ashton, 2006). Therefore, at present  
251 human dispersal will be the most important factor in determining the range expansion  
252 of *C. mutica*.

253

254

## 255 **Acknowledgements**

256 We thank A. Keay for help with the experimental setup and H. Brown and  
257 R. Shucksmith for assistance with field collection of *C. mutica*. This work was funded  
258 through a PhD studentship by the UK Natural Environmental Research Council  
259 (NER/S/A/2003/11899).

260

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- 347  
348

348

349 **Figure Legends**

350

351 Figure 1. Mortality of *C. mutica* following 48 h exposure to temperatures between 21  
352 and 30 °C (mean  $\pm$  S.E., n = 3). Reference lines indicate 48 h  $LT_{50} \pm 95\%$  CI  
353 (broken lines) estimated using TSK analysis.

354

355 Figure 2. Mortality of *C. mutica* following 48 h exposure to salinities between 9 and  
356 20 (mean  $\pm$  S.E., n = 3). LC indicates lethal concentration of percentile  
357 mortalities; the broken reference line indicates the lower 48 h  $LC_{50}$  (estimated  
358 using Probit analysis).

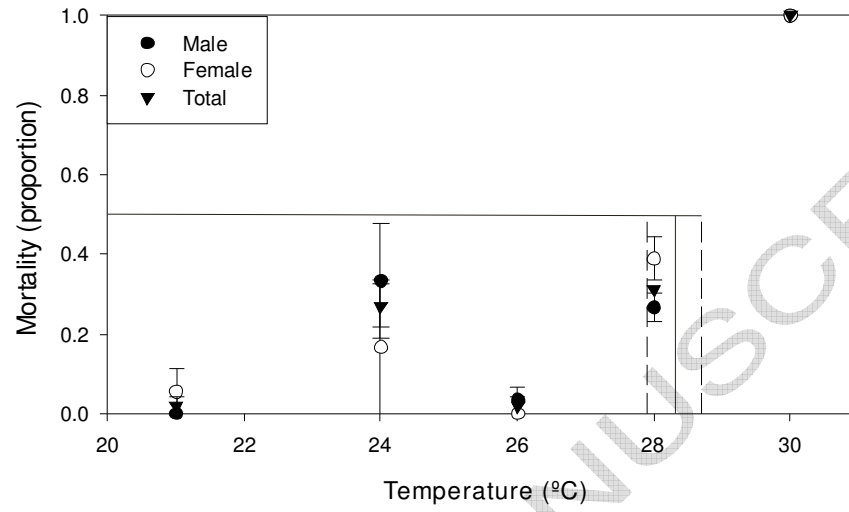
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361 Figure 1.



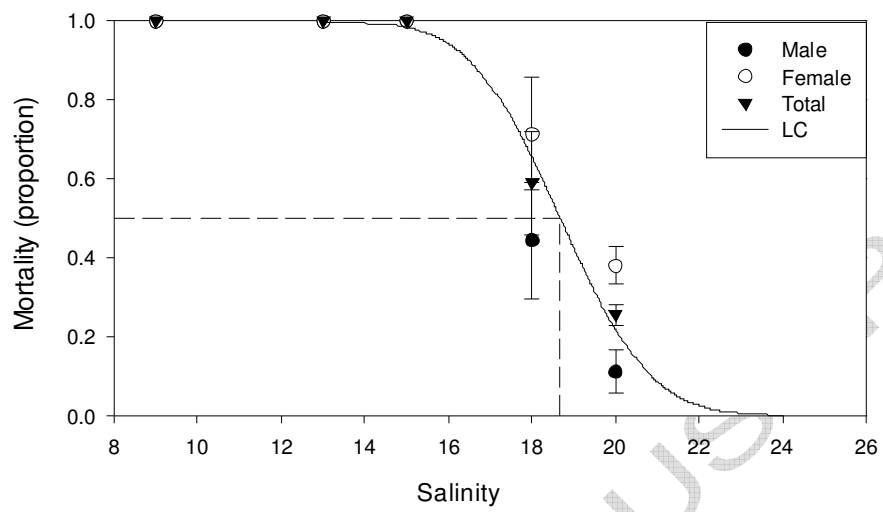
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364 Figure 2.



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