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

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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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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 LT₅₀, 28.3 ± 0.4 °C), and salinities
29 lower than 16 (48 h LC₅₀, 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 LC₅₀ 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 ± 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 ($100 \mu\text{m}$; salinity ~ 35)
98 and five pieces of 5 mm mesh (150 cm^2) 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 ± 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 (χ^2) to test whether the data fits the Probit model. When χ^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 ± 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 LC₅₀ (\pm 95% C.L.) was 18.7 ± 0.2 . The
167 lower LC₅₀ for females (18.0 ± 0.3) was significantly higher ($P < 0.05$) than that for
168 males (19.3 ± 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 LT₅₀, 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 LC₅₀ (18.7 ± 0.2) is higher than that of *C. scaura*
201 and *C. equilibria*, with 24 h LC₅₀ 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 LC₅₀ 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 LC₅₀ 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

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260

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345 crustacean invader in the Laurentian Great Lakes basin. *Canadian Journal of*
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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).

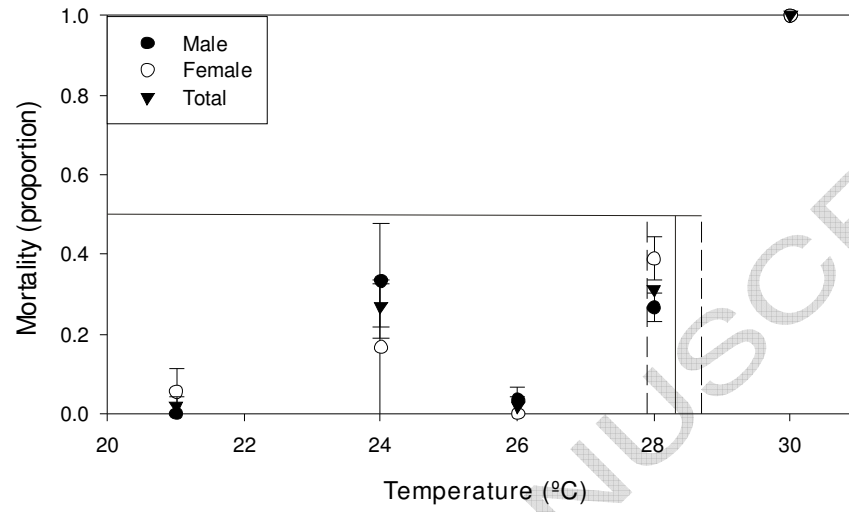
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361 Figure 1.

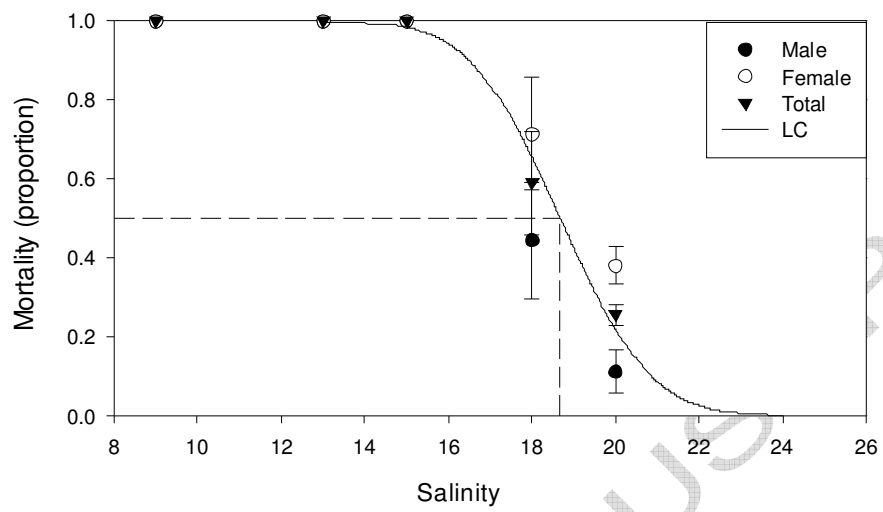


362

363

363

364 Figure 2.



365

366

367