## SHORT COMMUNICATION

# Geographical expansion of the invader *Caprella scaura* (Crustacea: Amphipoda: Caprellidae) to the East Atlantic coast

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Abstract Caprella scaura (Templeton in Trans Entomol Soc Lond 1:185–198, 1836) is a native species to the western Indian Ocean. It was first described from Mauritius and later reported from several regions of the world. During the last decade, the species spread out of the Adriatic Sea, and in 2005, C. scaura was reported in Gerona, on the northeastern coast of Spain. The present study shows the recent rapid expansion of the species to the East Atlantic. During a sampling survey of harbours along the Strait of Gibraltar (Dec 2009–June 2010), we found high densities of C. scaura associated with the bryozoans Zoobotryon verticillatum Della Chiaje, 1822, in Chipiona and Bugula neritina (L.) in Cádiz, Atlantic coast of southern Spain; on the other hand, during May 2009, an important population of C. scaura was also found in the Canary Islands (Tenerife) associated with aquaculture resources. A total of 1,034 individuals of C. scaura were studied, and we confirm that the populations are effectively established, with high densities and reproducing females during the whole year. The population from Cádiz was characterised by smaller specimens but a higher number of eggs per female. These differences could be related to environmental conditions, mainly sea water

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Laboratorio de Bentos, Departamento de Biología Animal, Facultad de Biología, Universidad de la Laguna, 38206 La Laguna, Tenerife, Canary Islands, Spain temperature and to other factors such as competition with other species, or availability of food or substrate. Significant correlation was found between female size and number of eggs in the three populations, but egg size did not vary with female body length. The morphometric relation length/width of the second gnathopod was also calculated and compared between sexes: larger males presented longer gnathopods at the three sites. The most probable introduction vector of this species is shipping; in fact, the Strait of Gibraltar is characterised by an intense shipping traffic. Also, we have observed that the native Caprella equilibra Say, 1818, is being displaced by C. scaura in the harbour of Cádiz, where this species reach densities of 35,945 ind/ 1,000 g of B. neritina. Further experimental studies are necessary to explore the potential danger of this species, which might spread into natural habitats too.

# Short communication

Biological invasions occur worldwide and are considered today as one of the greatest threats to ocean and coastal marine ecosystems (Ruiz et al. 2000; Hayes and Sliwa 2003; Montelli 2010). Introduced species are those that were transported by human activities from their original, or historically known, areas of distribution (Somaio Neves et al. 2007). They can be considered invasive when interfering with the establishment and survival of native species with concurrent ecological or socio-economical costs (Elliott 2003). Most introduced species are not invasive, although they may become so if environmental variability favours invasion (Silva et al. 2004). Ballast water, fouling of commercial vessels and aquaculture are generally considered the main vectors responsible for species movement of introduction across the oceans, but also touristic



Fig. 1 Lateral view of Caprella scaura from the Strait of Gibraltar

harbours can represent a sink of alien species (Savini et al. 2006). They provide suitable habitat for settlement in the local fouling community, and consequently, they could play an important role in the diffusion of invasive species along the littoral by recreational boating (Bulleri and Airoldi 2005; Glasby et al. 2006; Bulleri and Chapman 2010). In fact, harbours and ports are likely sites of first introductions and structures common to ports, harbours and marinas provide new habitats and substrata for potentially invasive species (Floerl and Inglis 2003).

In spite of having direct development, peracarids and, in particular, caprellids are able to disperse large distances associated with detached aquaculture buoys and other artificial substrata ("rafting"), or as a part of the fouling communities of ships and boats (Thiel et al. 2003; Astudillo et al. 2009). Caprella scaura Templeton 1836 (Fig. 1) is a native species to the western Indian Ocean. It was first described from Mauritius and later reported from several regions of the world (Krapp et al. 2006) (Fig. 2). During the last decade, C. scaura spread out of the Adriatic Sea, and, in 2005, it was reported in Gerona, on the north-eastern coast of Spain (Martínez and Adarraga 2008), indicating that it is probably invading the whole Mediterranean. Caprella scaura is mainly a detritivore (Guerra-García and Tierno de Figueroa 2009) and has aggressive behaviour among individuals, especially males in the presence of receptive females (Lim and Alexander 1986; Schulz and Alexander 2001). Courtship and mating involve exploration of the female by the male using antennae and maxillipeds followed by moulting of the female and copulation (Lim and Alexander 1986). Caprella scaura has parental care (Lim and Alexander 1986; Aoki 1999). Although the species seems to prefer Bugula neritina as a substrate (pers. observ.), Guerra-García (2003) reported no specific habitat selection: specimens were collected on bryozoans, red and brown algae, seagrasses (Lim and Alexander 1986; Takeuchi and Hino 1997; Guerra-García and Thiel 2001) or sponges (Serejo 1998). Furthermore, the complete mitochondrial genome of *C. scaura* has been recently published (Ito et al. 2010), with an emphasis on the unique gene order pattern and duplicated control region. The diploid number is 2n = 24, with 12 pairs of metacentric chromosomes (Krapp et al. 2006).

During a sampling survey of the harbours along the Strait of Gibraltar, we found C. scaura associated with the bryozoans Zoobotryon verticillatum Della Chiaje, 1822, in Chipiona harbour (36°44'46''N, 6°25'46''W) (Dec 2009) and Bugula neritina (L.) in the harbour of Cádiz (36°32'29''N, 6°17'61''W) (June 2010), on the Atlantic coast of southern Spain. An important population of C. scaura was also found in the Canary Islands (IEO Installations, Santa Cruz de Tenerife), associated with aquaculture tanks (28°29'58''N, 16°11'48''W) (May 2009). Specimens from the three locations (Fig. 3) were collected and studied in detail. Photographs of each specimen were taken with a Motic K-400L stereomicroscope. The number of eggs per female was counted and photographed with a Leica CME microscope. Measures such as total body length, length and width of gnathopod 2 and diameter of eggs-long axiswere taken using software Scion Image Alpha 4.0.3.2© (2000-2001 Scion Corporation).

A total of 1,034 individuals of C. scaura were studied. The sampling effort was similar in the three locations, and three replicate samples of substrate were collected in all sites. The largest population was found in Cádiz (Fig. 3), where C. scaura was the dominant species on the bryozoan Bugula neritina (reaching densities of 35,945 ind/1,000 g of B. neritina), but was also abundant on the bryozoans Zoobotryum verticillatum and Tricellaria inopinata and the hydroid Eudendrium sp. In aquaculture tanks of Canary Island, we measured densities of 3,080 ind m<sup>-2</sup>. Taking into account the large differences in the total number of specimens of each population, we selected randomly the same number of specimens from each location (n = 35) to conduct a balanced ANOVA design for length comparison. The length of male specimens from Chipiona (11.8  $\pm$ 3.7 mm, Mean  $\pm$  SD) and Canary Islands (9.6  $\pm$  3.9 mm) was significantly higher than the length of males from Cádiz (5.2 ± 2.6 mm) (one-way ANOVA,  $F_{2.102} = 39.1$ , p < 0.001, Tamhane post hoc test: Cadiz-Chipiona p = 0.0001, Cádiz-Canary Islands p = 0.0001, Chipiona-Canary Islands p = 0.051). A similar pattern was obtained for mature females, with smaller specimens in Cádiz  $(5.4 \pm 0.8 \text{ mm})$  than in Chipiona  $(7.4 \pm 0.6 \text{ mm})$  or Canary Islands (7.5  $\pm$  0.8 mm) (one-way ANOVA,  $F_{2.102} = 77.2$ , p < 0.001, Tamhane post hoc test: Cadiz-Chipiona



**Fig. 2** Distribution of *Caprella scaura*. *White circles* indicate the most recent sites (after 2000) where the species has been found. *Star symbols* indicate the localities registered during the present study, representing the first record to East Atlantic. Data of distribution have been taken from Templeton (1836), McCain (1968), McCain and Steinberg (1970),



Fig. 3 Number of specimens of *Caprella scaura* studied during the present work

p = 0.0001, Cádiz-Canary Islands p = 0.0001, Chipiona-Canary Islands p = 0.951). The number of eggs was significantly higher in females of Cádiz (41.4 ± 12.8, n = 22) than in the other two localities (Canary Islands: 29.7 ± 15.5, n = 19; Chipiona: 29.6 ± 9.4, n = 23) ( $F_{2.66} = 7.0, p < 0.01$ , Tamhane post hoc test: Cadiz-Chipiona p = 0.003, Cádiz-Canary Islands p = 0.015, Chipiona-Canary Islands p = 1.00). In this case, to have the same number of replicates in all sites (n = 23), we used mean values to replace the missing replicates, adjusting the degrees of freedom of the residual. However, the mean size of eggs (measured as the long axis length) was similar at the three localities: 0.22 mm ± 0.02 (Cádiz), 0.21 ± 0.01 (Canary Islands) and 0.24 ± 0.04 (Chipiona). A significant correlation was found between female size and number of eggs for

Arimoto (1976), Lim and Alexander (1986), Laubitz (1991,1995), Ren and Zhang (1996), Coles et al. (1999), Guerra-García and Thiel (2001), Guerra-García (2003, 2004), Guerra-García and Takeuchi (2003, 2004), Foster et al. (2004), Krapp et al. (2006), Martínez and Adarraga (2008). Possible pathways of introduction are indicated with *question marks* 

the three localities (Chipiona: r = 0.49, p < 0.05; Cádiz: r = 0.67, p < 0.01; Canary Island: r = 0.61, p < 0.01) (Fig. 4). Although the parallelism test did not show differences between the slopes of regression lines, the equality of lines test showed significant differences between Cádiz and the other two sites (Cádiz-Canary Islands,  $F_{2,37} = 17.5$ , p = 0.0001; Cádiz-Chipiona,  $F_{2,41} = 19.5$ , p = 0.0001; Chipiona-Canary Islands,  $F_{2,38} = 1.3$ , p = 0.3); for a given size of the female, a higher number of eggs was measured in Cádiz. On the other hand, egg size did not significantly correlate with female body size nor the number of eggs in any of the three localities (Fig. 4). A clear correlation between the ratio length/width of the gnathopod 2 and the body size was obtained for males in the three localities (Chipiona: r = 0.78, p < 0.01; Cádiz: r = 0.55, p < 0.01; Canary Island: r = 0.72, p < 0.01), while no correlation was measured for females (Fig. 5). In general, larger males showed more elongate gnathopods 2, provided with stronger "poison tooth". Although there is no conclusive evidence that caprellids produce a toxin with this tooth, the extensive array of tegumental glands suggest that the secretions may have an offensive or defensive function in aggressive encounters (Schulz and Alexander 2001).

The coloration and external anatomy of *C. scaura* appeared quite similar to the bryozoan *Bugula neritina*, so the affinity of *C. scaura* for *B. neritina* can be attributed to its cryptic adaptation to this substrate. A similar association has been reported for *Caprella californica*, a species close to *C. scaura* (Keith 1971), which has recently expanded around the coastline of Australia (Montelli 2010). Keith (1971) proposed at least two means of colour regulation for *C. californica*: (1) by cuticular tanning and (2) by



**Fig. 4** Correlations between female size, number of eggs and eggs size for *Caprella scaura* collected during the present study in the three populations. Only the females with a close brood pouch were considered for this study

physiological colour changes brought about by expansion and contraction of chromatophores.

*Caprella scaura* is remarkable because of its size and McCain (1968) reported males and females as long as 21



**Fig. 5** Correlation between the ratio length/width for Gnathopod 2 in males and females of the three populations of *C. scaura* 

and 12 mm, respectively. Foster et al. (2004), however, reported lengths of 18 mm for males and 6-8 for females and even smaller (10 and 5 mm, respectively) for specimens collected in summer. The specimens of the present study were also smaller to those reported by McCain (1968). Foster et al. (2004) suggested that these size differences may be due to seasonal effects; for example, these authors reported that individuals, especially males, in winter populations reach much larger sizes than those observed during the summer months in coastal waters of Georgia. They attributed these apparent ecophenotypic differences in size to the decrease in predation during the colder months, in conjunction with the dampening effects of low temperature on reproductive activity. Our study seems to support this trend. Specimens from Chipiona were collected in winter (Dec 2009), while the specimens of Canary Islands and

Cádiz were collected by the end of spring and beginning of summer (May 2009 and June 2010, respectively). Sea water temperature ranges from 18.4°C (February) to 24.3°C (October) in Canary Islands and 13.6°C (January) to 23.3°C (October) in Cádiz and Chipiona. The highest temperatures in June could explain the smaller size of specimens from Cádiz and the higher number of eggs relative to those from Chipiona, just a few kilometres from Cádiz. Differences between Cádiz and Canary Islands are not so clear, since specimens were collected during the same period, with similar seawater temperature and salinity (36-36.5 psu). Probably other factors such as competition with other species, availability of substrates or food, could be determining these differences. In fact, the specimens of the three populations were collected from different substrates: Zoobotryon verticillatum in Chipiona, Bugula neritina in Cádiz and surface of aquaculture tanks in Canary Islands. Further studies should be conducted to compare the ecology and the reproductive patterns of these different populations throughout the whole year.

In recent decades, *Caprella scaura sensu lato* has widely extended its geographic distribution (Fig. 2): Coles et al. (1999) found the species in Hawaii; Foster et al. (2004) reported a range extension from the Caribbean Sea to the Florida Gulf Coast and South Carolina; Guerra-García (2003, 2004) reported the species from western Australia and Tasmania; since 1994, the species has been extending along the Mediterranean Sea. The present study represents an extension towards the East Atlantic of around 3,000 km. Krapp et al. (2006) suggested that the species could have spread across the Mediterranean probably travelling among fouling on the hulls of ships. Martínez and Adarraga (2008) also suggested that the introduction of the species in Mediterranean waters seemed to be due to the continuous circulation of yachts, although aquaculture (movement of fish cages) in certain specific zones represents another possible introduction vectors. Recreational boating has already been claimed to be responsible for the dissemination of C. scaura (Sconfietti et al. 2005; Savini et al. 2006).

According to several authors (see Martínez and Adarraga 2008), *C. scaura* appears to be a strong invader, able to colonise a wide geographical range. These authors, based on the high densities measured in Gerona (12,925 ind  $m^{-2}$ ), suggested a probable future invasion along the Iberian Mediterranean coasts and adjacent areas. In fact, the present study reveals that *C. scaura* has been already introduced along the Strait of Gibraltar and the East Atlantic coast, where it had not been reported before. Several pathways could be suggested: (1) Mediterranean specimens could have come from the native Indian Pacific, through the Suez Canal and could have extended from the Mediterranean to nearby Atlantic or (2) East Atlantic and Mediterranean specimens could have arrived from Caribbean populations. Future molecular studies would be very helpful to elucidate the invasion patterns; for example, Ashton et al. (2008) revealed multiple northern Hemisphere introductions of the invader *Caprella mutica* based on mitochondrial DNA. A low genetic divergence between native and non-native populations may enable identification of the source population, while a high genetic divergence may indicate limited gene flow, long-term isolation or different selection pressures in the non-native habitat (see Ashton et al. 2008).

During the present study, we observed that in the harbours where *C. scaura* was abundant, the native species, such as *Caprella equilibra* or *Caprella dilatata* were absent, or present in very low abundances. Furthermore, other macrofauna associated with the main substrates at these harbours (*Bugula neritina*, *Tricellaria inopinata*, *Zoobotryon verticillatum* and *Eudendrium* sp.) was also less abundant when the invasive *C. scaura* was present. Other amphipods sharing habitats with *C. scaura* in the studied populations were *Elasmopus rapax*, *Corophium acutum*, *Jassa cf falcata* and *Ericthonius brasiliensis*. Further studies based on seasonal fluctuations and ecological experiments should be conducted to evaluate the potential impact of *C. scaura* on the native species and properly address the management of this invasive species.

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### References

- Aoki M (1999) Morphological characteristics of young, maternal care behaviour and microhabitat used by caprellid amphipods. J Mar Biol Assoc UK 79:629–638
- Arimoto I (1976) Taxonomic studies of caprellids (Crustacea, Amphipoda, Caprellidea) found in the Japanese and adjacent waters. Special Publications from the Seto Marine Biological Laboratory, Series 3:1–299
- Ashton GV, Stevens MI, Hart MC, Green DHm, Burrows MT, Cook EJ, Willis KJ (2008) Mitochondrial DNA reveals multiple Northern Hemisphere introductions of *Caprella mutica* (Crustacea, Amphipoda). Mol Ecol 17:1293–1303
- Astudillo JC, Bravo M, Dumont CP, Thiel M (2009) Detached aquaculture buoys in the SE Pacific: potential dispersal vehicles for associated organisms. Aquat Biol 5:219–231
- Bulleri F, Airoldi L (2005) Artificial marine structures facilitate the spread of a non-indigenous green alga, Codium fragile ssp tomentosoides, in the North Adriatic Sea. J Appl Ecol 42:1063–1072
- Bulleri F, Chapman MG (2010) The introduction of coastal infrastructure as a driver of change in marine environments. J Appl Ecol 47:26–35

- Coles SL, De Felice RC, Eldredge LG (1999) Non indigenous marine species introductions in the harbours of the south and west shores of Oahu, Hawaii. Bishop Museum Technical Report no. 15, p 212
- Elliott M (2003) Biological pollutants and biological pollution-an increasing cause for concer. Mar Pollut Bull 46:275-280
- Floerl O, Inglis GJ (2003) Boat harbour design can exacerbate hull fouling. Aust Ecol 28:116–127
- Foster JM, Heard RW, Knott DM (2004) Northern range extensions from *Caprella scaura* Templeton, 1836 (Crustacea: Amphipoda: Caprellidae) on the Florida Gulf Coast and in South Carolina. Gulf Carib Res 16:65–69
- Glasby M, Connel SD, Holloway MG, Hewitt CL (2006) Non indigenous biota on artificial structures: could habitat creation facilitate biological invasions? Mar Biol 151:887–895
- Guerra-García JM (2003) The Caprellidea (Crustacea: Amphipoda) from Mauritius Island, Western Indian Ocean. Zootaxa 232:1–24
- Guerra-García JM (2004) The caprellidea (Crustacea: Amphipoda) from Western Australia and Northern Territory, Australia. Hydrobiologia 522:1–74
- Guerra-García JM, Takeuchi I (2003) The caprellidea (Malacostraca: Amphipoda) from Mirs Bay, Hong Kong, with the description of a new genus and two new species. J Crust Biol 23:154–168
- Guerra-García JM, Takeuchi I (2004) The Caprellidea (Crustacea: Amphipoda) from Tasmania. J Nat Hist 38:967–1044
- Guerra-García JM, Thiel M (2001) The caprellid fauna (Crustacea: Amphipoda: Caprellidea) from Coquimbo, northern-central Chile with a taxonomic key for species identification. Rev Chil Hist Nat 74:873–883
- Guerra-García JM, Tierno de Figueroa JM (2009) What do caprellids feed on? Mar Biol 156:1881–1890
- Hayes KR, Sliwa C (2003) Identifying potential marine pests: a deductive approach applied to Australia. Mar Pollut Bull 46:91–98
- Ito A, Aoki M, Yokobori S-I, Wada H (2010) The complete mitochondrial genome of *Caprella scaura* (Crustacea, Amphipoda, Caprellidea), with emphasis on the unique gene order pattern and duplicated control region. Mitochondrial DNA 21:183–190
- Keith DE (1971) Substrate selection in caprellid amphipods of Southern California with emphasis on *Caprella californica* Stimpson and *Caprella equilibra* Say (Amphipoda). Pacific Sci 25:387–394
- Krapp T, Lang C, Libertini A, Melzer RR (2006) Caprella scaura Templeton 1836 sensu lato (Amphipoda: Caprellidae) in the Mediterranean. Org Div Evol 6:77–81
- Laubitz DR (1991) Crustacea Amphipoda Caprellidea: caprellids from the western Pacific (New Caledonia, Indonesia and the Philippines). In: Crosnier A (Ed) Résultats des Campagnes MUSOR-STOM. Mémoires du Museum National d'Histoire Naturelle, Paris (Serie A) Zoologice 9:101–123
- Laubitz DR (1995) Caprellidea (Crustacea: Amphipoda) from the southern and western Indian Ocean. Mésogée 54:81–100
- Lim STA, Alexander CG (1986) Reproductive behaviour of the caprellid amphipod *Caprella scaura typica* Mayer, 1890. Mar Behav Phys 12:217–230

- Martínez J, Adarraga I (2008) First record of invasive caprellid *Caprella scaura* Templeton, 1836 sensu lato (Crustacea: Amphipoda: Caprellidae) from the Iberian Peninsula. Aquat Invasions 3:165–171
- McCain (1968) The Caprellidae (Crustacea: Amphipoda) of the Western North Atlantic. US Nat Mus Bull 278:1–147
- McCain JC, Steinberg JE (1970) Amphipoda-I, Caprellidea-I, Family Caprellidae. In: Gruner HE, Holthuis LB (eds) Crustaceorum Catalogus, Part 2. Dr. W. Junk N.V, Den Haag, pp 1–78
- Montelli L (2010) The recent geographical expansion of Caprella californica (Caprellidea: Caprellidae) around the coastline of Australia. Biol Invasions 12:725–728
- Ren X, Zhang CH (1996) Fouling Amphipoda (Crustacea) from Dayawan, Guangdong province, China (South China sea). Institute of Oceanology, China Academy of Sciences 1: 58–78
- Ruiz GM, Fofonoff PW, Carlton JT, Wonham MJ, Hines AH (2000) Invasion of costal marine communities in North America: apparent patterns, processes and biases. Annu Rev Ecol Syst 31:481– 531
- Savini D, Marchini A, Forni G, Castellazzi M (2006) Touristic harbours and secondary spread of alien species. Biol Mar Mediterr 13:760–763
- Schulz MK, Alexander CG (2001) Aggressive behaviour of *Caprella scaura* typical Mayer, 1890 (Crustacea: Amphipoda). Mar Fresh Behav Physiol 34:181–187
- Sconfietti R, Mangili F, Savini D, Occhipinti-Ambrogi A (2005) Diffusion of the alien species *Caprella scaura* Templeton, 1836 (Amphipoda: Caprellidae) in the Northern Adriatic Sea. Biol Mar Mediterr 12:335–337
- Serejo CS (1998) Gammaridean and caprellidean fauna (Crustacea) associated with the sponge *Dysidea fragilis* Johnston at Arraial de Cabo, Rio de Janeiro, Brazil. Bull Mar Sci 63:363–385
- Silva JSV, Frenandes FC, Souza RCCL, Larsen KTS, Danelon OM (2004) Água de Lastro e Bioinvasão. Editora Interciência, Rio de Janeiro, p 270
- Somaio Neves C, Moreira Rocha R, Bettini Pitombo F, Roper JJ (2007) Use of artificial substrata by introduced and cryptogenic marine species in Paranaguá Bay, southern Brazil. Biofouling 23:319–330
- Takeuchi I, Hino A (1997) Community structure of caprellid amphipods (Crustacea) on seagrasses in Otsuchi Bay, northeastern Japan, with reference to the association of *Caprella japonica* (Schurin) and *Phyllospadix iwatensis* Makino. Fisheries Sci 63:327–331
- Templeton R (1836) Descriptions of some undescribed exotic Crustacea. Trans Entomol Soc London 1:185–198
- Thiel M, Guerra-García JM, Lancellotti DA, Vásquez N (2003) The distribution of littoral caprellids (Crustacea: Amphipoda: Caprellidea) along the Pacific coast of continental Chile. Rev Chil Hist Nat 76:203–218