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# The spreading of the non-native caprellid (Crustacea: Amphipoda) *Caprella scaura* Templeton, 1836 into southern Europe and northern Africa: a complicated taxonomic history

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## Abstract

*Caprella scaura*, originally described by Templeton (1836) from Mauritius and later reported as several "forms" or "varieties" from numerous areas of the world, was found for the first time in the Mediterranean in 1994. Since this report, the species has been found in several Mediterranean locations. To explore the current distribution of *C. scaura* in the Iberian Peninsula and adjacent areas, we surveyed marine fouling communities from 88 marinas along the whole Iberian Peninsula and North Africa, 3 from Italy, 1 from France, 1 from Malta and 1 from Greece between June 2011 and June 2012. The results of this survey report the first confirmed record of *C. scaura* in Corsica (France), Crete (Greece) and Morocco, and confirm an extensive distribution of *C. scaura* along the Spanish Mediterranean coast and the Strait of Gibraltar. The species was absent along the north Atlantic coast of Spain and the upper distribution limit for the eastern Atlantic coast is the locality of Cascais, on the south coast of Portugal. All populations studied belong to the same morphological form, which match the "varieties" *C. scaura typica* from Brazil and *C. scaura scaura* from Mauritius, suggesting that (1) these two forms correspond to the same "variety"; (2) this "variety" is the only one that is expanding its distribution range and (3) the remaining "varieties" of *C. scaura* complex could represent distinct species with a restricted distribution.

**Keywords:** Non-indigenous species, invasive species, first record, introduction pattern, fouling community, Mediterranean Sea.

## Introduction

Biological invasions are part of the anthropogenic global change and are considered one of the greatest threats to marine ecosystems (Ruiz *et al*., 2000, Occhipinti-Ambrogi, 2000). The Mediterranean Sea is one of the areas in the world that is most affected by these invasions. Over 1000 introduced species have been recorded in this area, 159 of these correspond to alien crustaceans (Zenetos *et al*., 2012). The subphylum Crustacea includes the most successful species among aquatic alien invaders (Engelkes & Mills, 2011). However, although the number of alien crustaceans has increased noticeably in the last two decades (Galil, 2009), the number of alien species belonging to the amphipods is still underestimated (Zenetos *et al.*, 2010). Caprellid amphipods, commonly known as skeleton shrimps, are small marine crustaceans that are common in many littoral habitats, where they form an important trophic link between primary producers and higher trophic levels (Woods, 2009). The morphology of caprellids, with reduced appendages on the abdomen that are used for swimming in other amphipod crustaceans (Takeuchi & Sawamoto, 1998), as well as the lack of a planktonic larval stage, suggest that the cosmopolitan distribution of certain littoral caprellids could be facilitated by the fact that they are often associated with fouling communities on floating objects and vessels (Thiel *et al*., 2003; Astudillo *et al.*, 2009). In other occasions, hidden diversity refutes cosmopolitan distribution in some caprellid species complexes traditionally considered as a single cosmopolitan species (Cabezas *et al.*, 2013). This is particularly pronounced in smaller-bodied and taxonomically more challenging taxa (Carlton, 2009).

In 1994, an unusual-looking caprellid characterized by an acute cephalic projection (Krapp *et al*., 2006), was found associated with the fouling community from the Lagoon of Venice, in Italy (Sconfietti & Danesi, 1996). This caprellid, identified as *Caprella scaura* Templeton, 1836 [sensu lato], was the first alien caprellid in the Mediterranean Sea. Since this record, the species has been reported from several Mediterranean countries including Greece (Krapp *et al*., 2006), Spain (Martínez & Adarraga, 2008), Turkey (Bakir & Katagan, 2011) and Tunisia (Ben Souissi *et al*., 2010). The species was frequently found associated with the fouling communities of arti-

ficial structures such as boats, buoys, floating pontoons, aquaculture tanks or cages, but also seagrasses and seaweeds in enclosed bays.

*Caprella scaura* [sensu lato] was described for the first time by Templeton in 1836 from individuals collected in Mauritius, in the south Indian Ocean. About 50 years later, Mayer (1890, 1903) recognized 6 "formae" (= varieties): *C. scaura* f. *typica* (1890), including the specimens described by Templeton and others found in Brazil and Australia, *C. s.* f. *diceros* (1890) from Japan, *C. s.* f. *cornuta* (1890) from Chile and Brazil, *C. s.* f. *spinirostris* (1890) from Chile, *C. s.* f. *californica* (1903) from California and *C. s.* f. *scauroides* (1903) from Hong Kong and Japan. According to recent rules of nomenclature, these varieties are now treated as subspecies (Krapp *et al.*, 2006; Takeuchi & Oyamada, 2012). Mayer (1903) grouped these subspecies in two separate groups, one for specimens without a ventral spine between the insertions of gnathopods 2, including *C. s. typica*, *C. s. diceros* and *C. s. cornuta*, and the other group for specimens with a ventral spine between the gnathopods 2, including the remaining specimens. In 1947, Utinomi (1947) added a seventh subspecies without a ventral spine, *C. s. hamata*. Dougherty & Steinberg (1953) separated *C. s. californica* as a distinct species and re-established Stimpson's (1857) name *C. californica* and McCain & Steinberg (1970) synonymized the other two subspecies with ventral spine, *C. s. scauroides* and *C. s. spinirostris*, with *C. californica* [sensu lato]. Recently, Takeuchi & Oyamada (2012) proposed *C. s. scauroides* to a species level based on differences with *C. californica* [sensu stricto] from California. In summary, at the present time, three valid species have been recognized: *C. scaura*, *C. californica* and *C. scauroides*.

Krapp *et al.* (2006) conducted a detailed revision of *C. scaura* species and found that Arimoto (1976) referred to *C. scaura typica* as *Caprella scaura* (in part), probably considering that *C. scaura typica* described by Mayer was different from individuals of *C. scaura* described by Templeton, as pointed out by Krapp *et al.* (2006). These authors classified the individuals from Mauritius as *C. scaura scaura* to separate them from the subspecies *C. scaura typica,* according to currently valid taxonomical rules. Differences in both forms were mainly attributed to the dorsal tuberculation pattern in males. Krapp *et al*. (2006) concluded that the morphology of the Mediterranean populations of Italy and Greece matches that of *C. scaura scaura*. However, differences between the subspecies *C. s. typica* and *C. s. scaura* are not clear and these authors also suggested that a more detailed observation of the growth stages in juveniles, adults and hyperadults is necessary to study the morphological variation within populations.

In the Iberian Peninsula *Caprella scaura* was recorded for the first time in 2005 by Martínez & Adarraga (2008) in Girona, located on the north eastern coast of Spain. These authors identified the Spanish population as *C. scaura scaura* and predicted, based on the high density of specimens found, a future invasion along the Iberian Mediterranean coast and adjacent areas. Only five years later, *C. scaura* was reported from two recreational marinas of southern Spain and one aquaculture tank in Tenerife (Canary islands, eastern Atlantic) (Guerra-García *et al.*, 2011). However, there are many areas that remain unexplored and several questions that remain unresolved, for example: (1) Has *C. scaura* expanded throughout the Spanish Mediterranean coast and adjacent areas? (2) What is the northernmost distribution limit of *C. scaura* along the Atlantic coast of southern Europe? (3) Which "subspecies" is invading the Mediterranean Sea? In this paper we study the current distribution of *C. scaura* in southern Europe and northern Africa and analyze its global distribution to address these questions and understand the invasion pattern of this species in its introduced range.

## Materials and Methods

A total of 88 marinas were surveyed along the whole Iberian Peninsula and North Africa during the summer of 2011. Additionally, 3 marinas in Italy, 1 in Corsica (France), 1 in Malta and 1 in Crete (Greece) were also surveyed in the summer of 2012 (Fig. 1, Table 1). At each site, fouling communities proliferating on artificial hard substrata including floating pontoons, ropes, buoys and ship hulls were inspected for the presence of caprellids. When caprellids were detected on a particular type of fouling substratum (hydroids, bryozoans or macroalgae), several colonies (at least three) of the host substratum were taken by hand and fixed in situ in 90% ethanol to examine the samples later in the laboratory for the presence of *Caprella scaura*.

The morphological characteristics used to identify *C. scaura* [sensu lato] males are (1) cephalon with an acute, bent forward, dorsal projection, (2) pereonites 1 and 2 elongate in males, (3) basis of gnathopod 2 long but no longer than pereonite 2 and (4) absence of ventral projection between the insertion of gnathopods 2 (adapted from Templeton, 1836; Mayer, 1890; Krapp *et al.*, 2006). Additional morphological features were also explored to determine the possible intraspecific variation within non-native *C. scaura* populations. These features were also explored in specimens previously collected by the authors from Mauritius, the type locality of *C. scaura scaura* and Brazil, the type locality of *C. scaura typica*, to identify the subspecies which are being dispersed between marinas in the Mediterranean and the eastern Atlantic coast of Spain.

Extensive study of published material on *C. scaura* records was also conducted to determine the current global distribution of this species. Descriptions, illustrations and photographs included in these publications were carefully analyzed to determine the particular subspecies of each record.

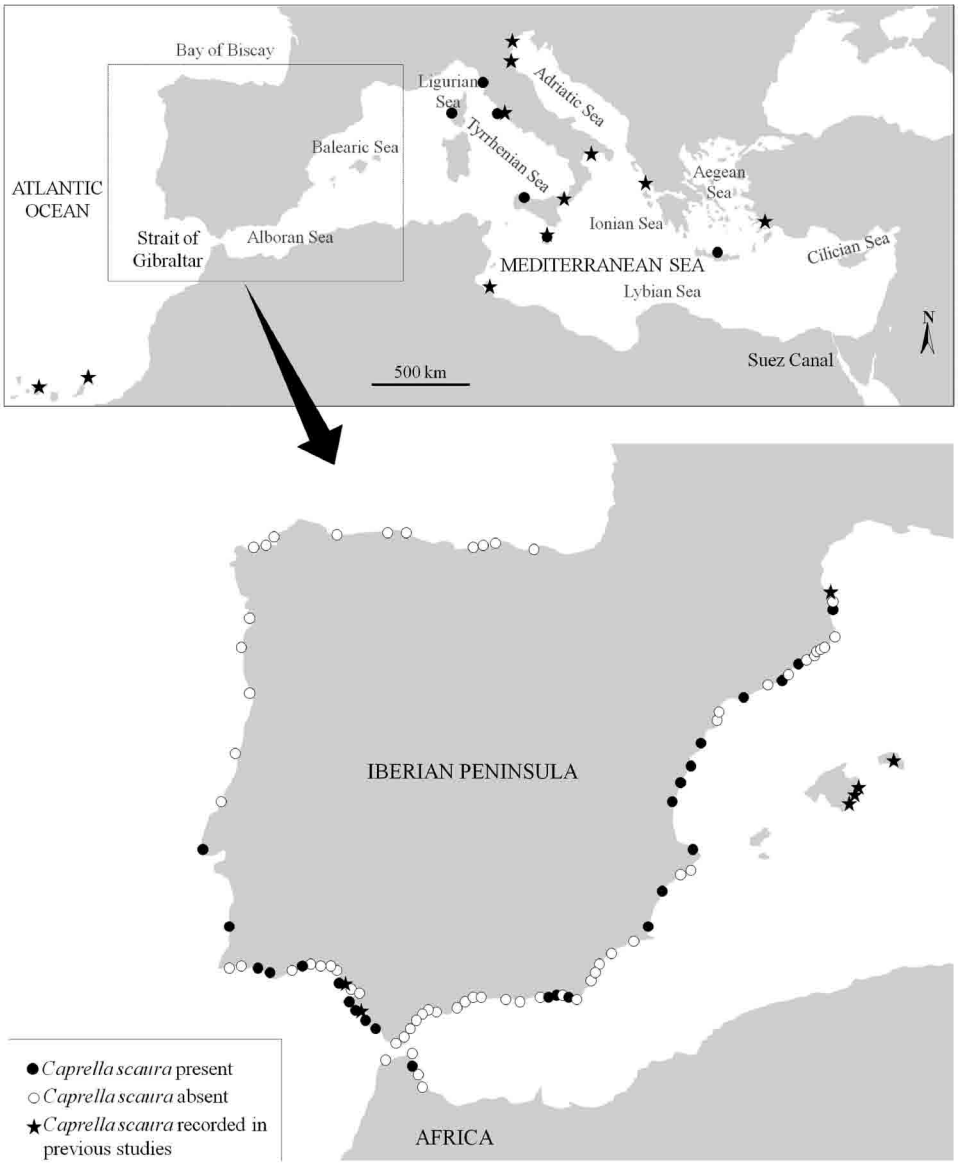


***Fig. 1:*** Location of marinas sampled for *C. scaura* in the Mediterranean Sea and the East Atlantic coast together with the records of *C. scaura* in the study area from previous studies (Canary Island and Southern Spain: Guerra-García *et al.,* 2011, Lanzarote Island: Minchin *et al.,* 2012; northeast coast of Spain: Martínez & Adarraga, 2008; Balearic Islands: Ros *et al.,* 2013a; Italy: Sconfietti & Danesi, 1996; Sacchi *et al.*,1998; Sconfietti *et al.,* 2005; Krapp *et al.,* 2006; Galil, 2008; Eleftheriou *et al*., 2011; Malta: Fernandez-Gonzalez *et al.,* 2011; Greece: Krapp *et al*., 2006; Turkey: Bakir & Katagan, 2011; Tunisia: Ben-Soussi *et al.,* 2010).

## Results

### *Distribution of* C. scaura *in southern Europe and northern Africa*

*Caprella scaura* was present in thirty one marinas, being recorded for the first time on the islands of Corsica (France) and Crete (Greece), and in Morocco (Fig. 1, Table 1). The species was present in fourteen marinas distributed along the Mediterranean coast of the Iberian Peninsula and ten marinas of the Atlantic coast of the Iberian Peninsula. It was absent along the north Atlantic coast of Spain and the upper distribution limit on the eastern Atlantic coast is the locality of Cascais, on the south coast of Portugal.

As regards microhabitat use, it was found to be associated with the erect bryozoan *Bugula neritina* primarily, but also with other bryozoans such as *Zoobotryon verticillatum* and, along the southern Atlantic coast of Spain, with the invasive *Tricellaria inopinata* (Table 1). It was also occasionally found associated with the hydroids *Eudendrium* sp. and *Pennaria disticha*, and the seaweeds *Gelidium* sp., *Halopteris scoparia*, *Cladostephus spongiosus*, *Dictyota dichotoma* and *Corallina elongata* (Table 1).

### *Intraspecific morphological variation within introduced populations*

The specimens collected in the study area share the same morphology. This morphology was similar to other

**Table 1.** Presence/absence records of *Caprella scaura* from different fouling substrates collected in marinas from 2011 and 2012.

| | | | | SUBSTRATES | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Bryozoans | | | Hydroids | | Macroalgae | | | | |
| **Country** | **Locality** | **Date** | **Coordinates** | *Bugula neritina* | *Tricellaria inopinata* | *Zoobotryon verticillatum* | *Eudendrium* sp. | *Pennaria disticha* | *Gelidium* sp. | *Halopteris scoparia* | *Cladostephus spongiosus* | *Dictiota dichotoma* | *Corallina elongata* |
| PORTUGAL | Cascais | 09-May-11 | 38º 41' N; 9º 26' W | ✓ | | | | | | | | | |
| | Sines | 09-May-11 | 37º 57' N; 8º 51' W | ✓ | | | | | | | | | |
| | Albufeira | 10-May-11 | 37º 05' N; 8º 15' W | ✓ | | | | | | | | | |
| | Faro | 11-May-11 | 37º 00' N; 7º 56' W | ✓ | | ✓ | | | | | | | |
| SPAIN | Isla Canela | 16-May-11 | 37º 11' N; 7º 20' W | ✓ | | | | | ✓ | | | | |
| | Chipiona | 17-May-11 | 36º 44' N; 6º 25' W | ✓ | ✓ | ✓ | | | | | | | |
| | Rota | 17-May-11 | 36º 36' N; 6º 21' W | ✓ | ✓ | ✓ | | | | | | | |
| | Cádiz | 17-May-11 | 36º 32' N; 6º 17' W | ✓ | ✓ | ✓ | | | | | | | |
| | Conil | 17-May-11 | 36º 17' N; 6º 08' W | ✓ | ✓ | | | | | | | | |
| | Barbate | 17-May-11 | 36º 11' N; 5º 56' W | ✓ | ✓ | | | | | | | | |
| | Almerimar | 01-Jul-11 | 36º 41' N; 2º 47' W | ✓ | | | | | | | | | |
| | Roquetas | 01-Jul-11 | 36º 45' N; 2º 36' W | ✓ | | | | | | | | | |
| | Almería | 01-Jul-11 | 36º 49' N; 2º 27' W | ✓ | | ✓ | | | | | | | |
| | Torrevieja | 29-Jun-11 | 37º 58' N; 0º 41' W | ✓ | | | | | | | | | |
| | Alicante | 29-Jun-11 | 38º 20' N; 0º 29' W | ✓ | | | | ✓ | | | | | ✓ |
| | Denia | 28-Jun-11 | 38º 50' N; 0º 6' W | ✓ | | ✓ | | | | | | | ✓ |
| | Valencia | 28-Jun-11 | 39º 25' N; 0º 19' W | ✓ | | ✓ | | | | | | | |
| | Borriana | 28-Jun-11 | 39º 51' N; 0º 4' W | ✓ | | | | | | | | | |
| | Oropesa | 28-Jun-11 | 40º 04' N; 0º 8' E | ✓ | | | | | | | | | |
| | Benicarló | 27-Jun-11 | 40º 24' N; 0º 26' E | ✓ | | ✓ | | | | | | | |
| | Tarragona | 27-Jun-11 | 41º 06' N; 1º 15' E | ✓ | | | | | | ✓ | ✓ | ✓ | |
| | Vilanova | 27-Jun-11 | 41º 12' N; 1º 43' E | ✓ | | ✓ | | | | | | | |
| | Barcelona | 26-Jun-11 | 41º 22' N; 2º 10' E | ✓ | | ✓ | | | | | | | |
| | L'Estartit | 25-Jun-11 | 42º 03' N; 3º 12' E | ✓ | | ✓ | | | | | | | |
| MOROCCO[a] | Marina Smir | 30-May-11 | 35º 45' N; 5º 20' W | ✓ | | ✓ | | | | | | | |
| ITALY | Livorno | 30-May-12 | 43º 32' N; 10º 18' E | ✓ | | | | | | | | | |
| | Civitavecchia | 29-May-12 | 42º 05' N; 11º 47' E | ✓ | | | | | | | | | |
| | Palermo | 08-Oct-11 | 38º 08' N; 13º 22' E | ✓ | | ✓ | | | | | | | |
| FRANCE[a] | Ajaccio | 31-May-12 | 41º 55' N; 8º 44' E | ✓ | | | ✓ | | | | | | |
| MALTA | Gzira | 09-Jul-12 | 35º 54' N; 14º 29' E | ✓ | | ✓ | | | | | | | |
| GREECE | Heraklion | 18-May-12 | 35º 20' N; 25º 08' E | ✓ | | | | | | | | | |

[a]First record of *Caprella scaura* in this country

specimens collected by the authors in previous studies for the Canary Islands (Guerra-García *et al.*, 2011) and the Balearic Islands (Ros *et al.*, 2013a). However, intraspecific morphological variations, affecting the dorsal tuberculation pattern of males and females mainly, were usually found within *C. scaura* populations collected from the same locality. These variations may have some implications for the identification of the subspecies, variety or form that is spreading along the study area. In the case of males, the dorsal pattern of tuberculation on pereonites 1-3 and especially on pereonite 5 exhibited the highest variation. The males with the most pronounced dorsal body protuberance pattern had a small distal dorsal protuberance or tubercle at the end of pereonites 1-3, close to the junction with the adjacent pereonite, specially visible on pereonites 2 and 3 (Fig. 2B and C), and two pairs of tubercles on pereonite 5 (Fig. 2D). Pereonite 6 used to present a pair of knobs but in hyperadults another pair of knobs may be present.

Protuberances on pereonites 1-3 were scarcely present and were only found in some small males (Fig. 2A-C), with the majority of the males being dorsally smooth on these pereonites (Fig. 2E-G). However, protuberances on pereonite 5 were frequently found. These tubercles gradually disappear as the male increases in length, but some hyperadult males may also have one or two pairs of tubercles on this pereonite (Fig. 2H-J). The length of the cephalic projection is also variable but in general is short and acute. The females with the most pronounced dorsal body protuberance pattern had a protuberance at the end of pereonites 1-4, a pair of protuberances in the middle of pereonite 2 and 6, a central projection on pereonites 3 and 4, and two pairs of protuberances in the middle of pereonite 5 (Fig. 3A-E). These "spiny" females coexist with smooth ones (Fig. 3F), but the two pairs of tubercles on pereonite 5 are usually present in all of them. The same morphological variations in the dorsal protuberance pattern of males and females were also observed in individuals collected previously from Mauritius and Brazil. Interestingly, in all cases, pereonite 4 of males were dorsally smooth.

A comparative analysis was carried out between the different subspecies of *C. scaura* according to this evidence (Table 2). We consider that the "form" or "forms" that better match the subspecies that are present in the marinas of southern Europe and northern Africa are *C. scaura scaura* from Mauritius, but also *C. scaura typica* from Rio de Janeiro, Brazil.

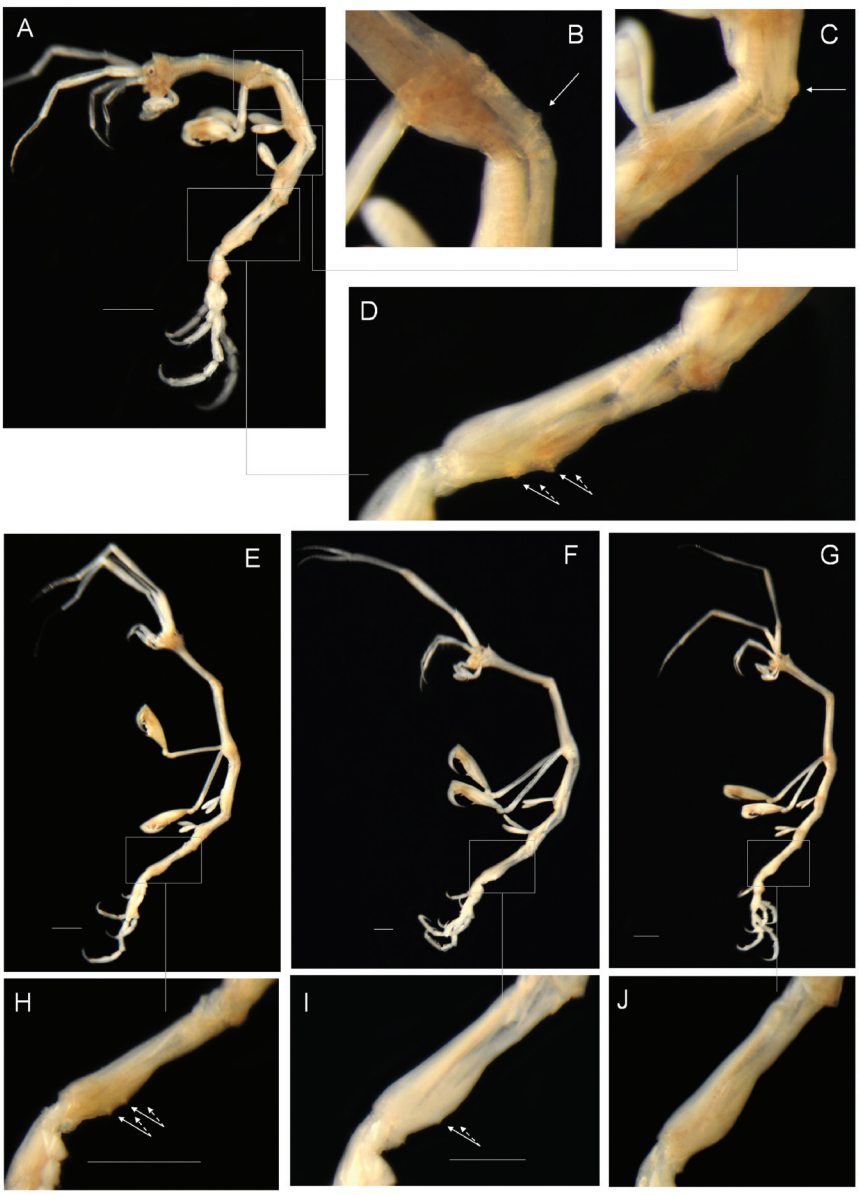


***Fig. 2:*** Intraspecific variations found in the dorsal tubercles of *C. scaura* males. A) Small male with a marked dorsal protuberance pattern. B-D) Detail of tubercles of pereonite 2, 3 and 5 respectively. E-G) Hyperadult males with different pattern of tubercles in pereonite 5. H-J) Variations in tubercles of pereonite 5. Dotted arrows show the presence of another tubercle, not visible in the photograph, which is part of the pair of tubercles. All individuals belong to the same locality: Cádiz, Spain. Scale bars: 1mm.

**Table 2.** Comparison of different morphological characters traditionally used to distinguish the different forms of *Caprella scaura*. The two subspecies that match with the specimens collected in the present study are highlighted in grey.

| | *C. scaura scaura* | *C. scaura typica* | *C. scaura cornuta* | *C. scaura diceros* | *C. scaura hamata* | *C. scaura collected* |
|---|---|---|---|---|---|---|
| Type locality | Mauritius | Brazil | Brazil | Japan | Japan | |
| Description references | Templeton (1836) | Mayer (1890; 1903) | Dana (1853) Mayer (1890; 1903) | Stebbing (1888); Mayer (1890) | Utinomi (1947) in Arimoto (1976) | |
| Maximun male body lenght (mm) | 14 | 21 | 18 | 35 | 15 | 23 |
| Cephalic projection | Short, acute | Short, acute | Short, blunt | Long, acute | Long, acute | Short, acute |
| Flagellum antenna 1 | Presence of fused articles | Presence of fused articles | Absence of fused articles | Presence of fused articles | Presence of fused articles | Presence of fused articles |
| Pereonite 4 | Smooth | Smooth | Long, oblong, distally process in some males | Lateral tubercles and distally strong process | Dorsal and lateral tubercles and distally strong process | Smooth |
| Pereonite 5 | "*Spiny*"; two pairs of dorsal processes in small males which disappear in hyper adult males (based on our examination of specimes from Mauritius) | Two pairs of dorsal processes occasionally present in males (McCain, 1968) | ? | Two pairs of dorsal processes in males | Two pairs of dorsal processes in males | Two pairs of dorsal processes in males which gradually disappear in hyper adult stages |

## Discussion

*Caprella scaura* was present in 33 percent of sampled marinas. This represents a successful spread of a species, which was found for the first time in Mediterranean coastal areas just two decades before the current study, i.e. in 1994 (Sconfietti & Danesi, 1996).

### *Which "subspecies" is spreading in the Mediterranean and the eastern Atlantic coastal area? A morphological and biogeographical approach*

Although *C. scaura* comprises a complex of several forms or subspecies, all populations spreading in the Mediterranean and the eastern Atlantic coastal area share the same morphology. This morphology includes a number of intraspecific variations in characters that are traditionally used to distinguish two forms, *C. scaura typica* and *C. scaura scaura*. In particular, the presence of two pairs of tubercles on pereonite 5 was attributed to the form "*typica*" while its absence to the form "*scaura*" (see Krapp *et al.*, 2006). The degree of tuberculation in females was also used to differentiate between the two forms, with the "extremely spinous" females belonging to the form *C. s. typica* (Martinez & Adarraga, 2008). As we found that these characters vary within the same population, both in the specimens collected from the study area and in the specimens examined from Mauritius and Brazil, we consider that this feature is not a good and stable taxonomical character to differentiate subspecies. Based on this premise, both *C. scaura typica* and *C. scaura scaura* match quite well with the material collected and may correspond to the same subspecies, the subspecies which is spreading in the Mediterranean and the eastern Atlantic coastal area. This also suggests that the remaining subspecies, with a different morphology and a restricted distribution range (Fig. 4, Table 2), could correspond to different valid species, as has already happened with other "forms" described by Mayer (i.e. Cabezas *et al.*, 2013; Takeuchi & Oyamada, 2012). The form "*typica*" has also been reported as the variety introduced along the east and west coast of North America (Marelli, 1981; Foster *et al.*, 2004) and Hawaii (Edmonson & Mansfield, 1948). However, a molecular approach is necessary to confirm if there is only one form that is spreading by human-mediated transport between different areas in the world and if the remaining forms correspond to different species with restricted distribution.

### *Invasion pattern of C. scaura and worldwide distribution*

Taking into account that specimens collected in the study area match quite well with *C. scaura typica* and *C. scaura scaura*, in order to understand the invasion pattern of *C. scaura* it is necessary to analyze the worldwide distribution of both subspecies (Fig. 4, Table 3). The origin of *Caprella scaura* is unknown (Carlton & Eldredge,

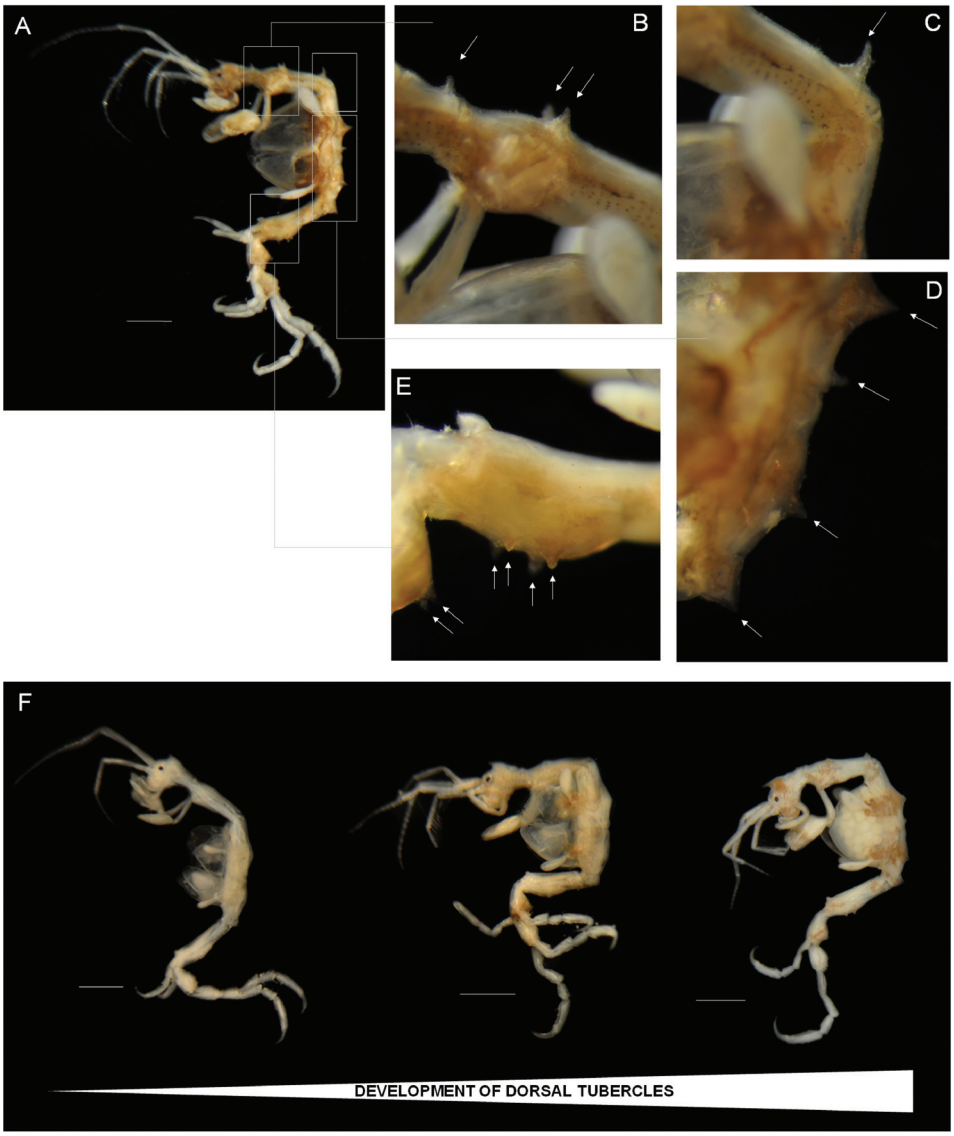


***Fig. 3**:* Intraspecific variations found in the dorsal tubercles of *C. scaura* females. A) Female with a marked dorsal protuberance pattern. B-E) Detail of tubercles of pereonites 1-6. F) Variations in the development of the dorsal protuberance pattern. All individuals belong to the same locality: Cádiz, Spain. Scale bars: 1mm.

2009), as it occurs with other non-native species associated with fouling communities of artificial structures such as harbours and marinas. Records on geographically disjunct occurrences of *C. scaura* date back to when the species was described for the first time in Mauritius. Only two years later, the species was found in Brazil and a short time later in the Caribbean Sea, Australia and Japan (references in Table 3). Thus, we consider that the species cannot be demonstrably classified as native or non-native in these regions, and it must be referred to as cryptogenic (Carlton, 1996). Therefore, the potential native range for *C. scaura* may include, at least, the regions of Mauritius, Brazil, Caribbean Sea, Australia and Japan. In the early twentieth century, the species was introduced into Pearl Harbour, Hawaii, by ship fouling and/or ballast water (Carlton, 2009). At the end of the twentieth century the species was found on the west coast of USA and a short time later on the east coast of this country. On both occasions, *C. scaura* was found associated with fouling communities in harbours, thus supporting the human-mediated introduction of the species. In 1994, it was found for the first time in the Mediterranean Sea, in Italy. Since then, *C. scaura* has spread very fast to several regions of the Mediterranean Sea and the east Atlantic Ocean. According to our results, *C. scaura* is now widely distributed along the Mediterranean coast of the Iberian Peninsula and along the Portuguese coast, with Cascais on the south coast of Portugal being its northernmost distribution limit. So far its occurrence in the study area has only reported by Martínez & Adarraga (2008) on the northeastern coast of Spain, and by Guerra-García *et al.* (2011) in southern Spain and the Canary Islands. As regards the

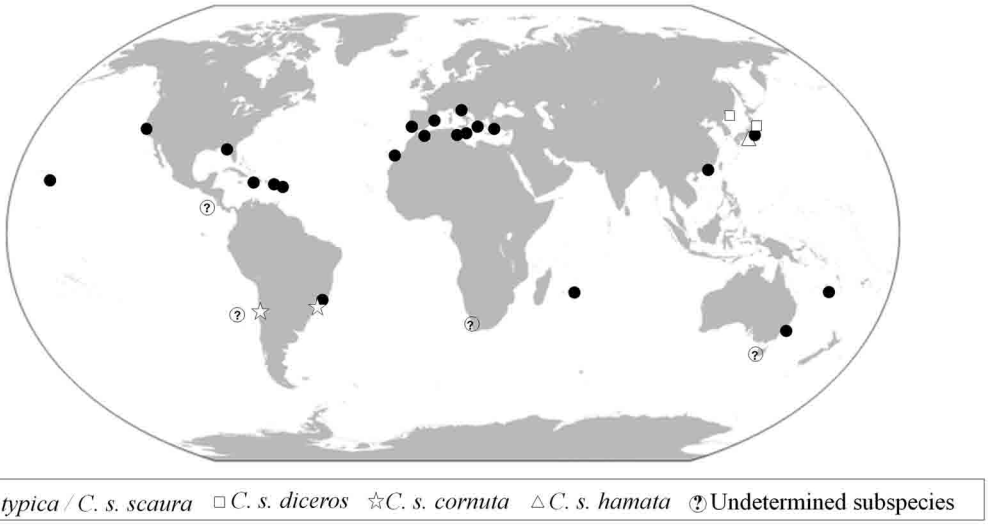


***Fig. 4:*** Distribution of the different subspecies of *C. scaura* without ventral spine in each region considered in Table 3.*Caprella s. typica* and *C. s. scaura* are considered as the same subspecies (see text). References in Tables 2 and 3.

Portuguese coast, there is a dubious record of a single female with a cephalic projection found by Marques & Bellan-Santini (1985) in Sines, which was classified as *Caprella* cf. *scaura*. However, it was found associated with algae in a natural habitat and since then, the species has not been found in Portugal until the present study. It is probable that this female corresponds with an specimen of *C. santosrosai*, a caprellid species described recently by Sánchez-Moyano *et al.* (1995) with a female morphology similar to that of the female *C. scaura.* Confirmation of this report is essential to understand the most likely entry of *C. scaura* in the Mediterranean Sea. If the species was first present on the eastern Atlantic coast of the Iberian Peninsula and then in the Mediterranean, it probably entered the Mediterranean through the Strait of Gibraltar. But if the species was first present in the eastern sector of the Mediterranean, it probably entered through the Suez Canal. The impossibility to review the material prevents clarification of this doubt. The presence of an established population in Morocco, Corsica (France), Crete (Greece) and the coastal waters of Malta (previously found by Fernandez-Gonzalez *et al.* (2011) in an offshore fish farm) confirm rapid spreading of *C. scaura* between marinas of the Mediterranean. The expansion success of this non-native caprellid may be due to the fact that it is usually associated with the bryozoan *Bugula neritina*, in which it exhibits the highest abundance (Ros *et al*., 2013b). This bryozoan is tolerant to antifouling paints (Piola & Johnston, 2006) and is able to attach easily to ship hulls, even if they are covered with fresh antifouling paint. The colonies of *B. neritina* with its associated epifaunal community are then easily transported among marinas by recreational boats, or by detached buoys or other structures (Astudillo *et al.,* 2009).

However, *C. scaura* was absent on the north coast of Portugal and the north Atlantic coast of Spain, where water temperatures are lower than in the Mediterranean Sea and the Strait of Gibraltar. An analysis of the worldwide distribution of *C. scaura typica* and *C. scaura scaura* (Fig. 4) shows that the species is also absent in the Red Sea and the northern Indian Ocean. This fact, together with the possible presence of a female of *C. scaura* on the central coast of Portugal in 1985, complicate our understanding of the introduction process of *C. scaura* in the Mediterranean Sea. Further ecological, morphological and molecular analyses are still necessary to resolve this interesting question.

In conclusion, this study reveals an important post-introduction range expansion of *C. scaura* in the Mediterranean Sea and along the South Atlantic coast of the Iberian Peninsula, representing significant improvement of the invasion dynamics of this caprellid species. Taking into account the instraspecific morphologic variations observed within populations, we also conclude that the forms *C. scaura typica* and *C. s. scaura* correspond with the same variety, thus contributing to a clarification of the *C. scaura* complex and suggesting that a single form of the complex is expanding its distribution range, while the other forms remain in a restricted distribution area.

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**Table 3.** First records of *Caprella scaura typica* and *C. s. scaura* in each region including date of reporting, site of collection (if known), status in this region and possible mechanism of introduction.

| Date | Country | Localities | Collected from | Status | Vector | Author of record |
|---|---|---|---|---|---|---|
| 1836 | Mauritius | Rivière Noire | Marine Plants | C | | Templeton, 1836 |
| 1838 | Brazil | Rio de Janeiro | Seaweeds near the fort | C | | Dana, 1853 (as *C. attenuata*) |
| 1866 | Virgin Islands | Barthelemy and St. Croix | Unknown | C | | Mayer, 1903 |
| 1890 | Australia | Port Jackson (Sydney) | Unknown | C | | Mayer, 1890 |
| 1903 | Japan | Tokyo Bay | Unknown | C | | Mayer, 1903 |
| 1925* | South Africa | Malagass Island (Saldanha Bay) | Sea Urchin | Q | | Barnard, 1925 |
| 1929 | Hawaii | Pearl harbour (Honolulu), Oahu | Algae in shallow water; hull fouling organism | I | SF | Edmondson and Mansfield, 1948 |
| 1968* | Costa Rica | Cocos island | Unknown | Q | | McCain, 1968 |
| 1968 | Puerto Rico | Mayagüez | Unknown | C | | McCain, 1968 |
| 1970* | Robinson Island (Chile) | Cumberland Bay | Unknown | Q | | McCain & Steinberg, 1970 |
| 1978 | USA (weast coast) | San Francisco Bay, (California) | Electric power plant and yacth harbor | I | SF, BW | Marelli, 1981 |
| 1978* | Tasmania (Australia) | Fancy Point | *Sargassum* | Q | | Guerra-García & Takeuchi, 2004 |
| 1986 | China | Mirs Bay (Hong Kong) | Algal bed (16m deep), benthic trawl | C | | Guerra-García & Takeuchi, 2003 |
| 1989 | New Caledonia | Citrons Bay | Unknown (5m deep) | C | | Laubitz, 1991 |
| 1994 | Italy | Venice Lagoon | Wooden piles | I | SF, BW | Sconfietti & Danesi, 1996 |
| 1998 | USA (east coast) | St. Andrew Bay (Florida), Charleston harbour (South Carolina) | Fouling organisms on the jetties and channel markers | I | SF, BW | Foster *et al.,* 2004 |
| 2002 | Greece | Amvrakikos gulf | Seagrass | I | SF | Krapp *et al.* 2006 |
| 2005 | Spain | Roses Bay (Girona) | Fouling organisms: bryozoans, mussels and polychaetes | I | SF | Martinez & Adarraga, 2008 |
| 2008 | Turkey | Güllük Bay | Cages of a fish farm | I | AQ | Bakir & Katagan, 2011 |
| 2009 | Tunisia | Boughrara and Bibans | Seaweeds | I | SF | Ben Souissi *et al.,* 2010 |
| 2010 | Canary Islands (Spain) | Tenerife | Aquaculture tanks | I | AQ | Guerra-García *et al.,* 2011 |
| 2010 | Malta | | Offshore fish farm | I | AQ | Fernandez-Gonzalez *et al.*, 2011 |
| 2011 | Morocco | Marina Smir | Fouling bryozoans | I | SF | Present study |
| 2011 | Portugal | Cascais, Sines, Albufeira and Faro | Fouling bryozoans in recreational marinas | I | SF | Present study |
| 2012 | Corsica (France) | Ajaccio Marina | Fouling organisms: bryozoans and hydroids | I | SF | Present study |
| 2012 | Crete (Greece) | Heraklion Marina | Fouling bryozoans | I | SF | Present study |

Status: C- cryptogenic; I- introduced; Q– questionable. Likely vectors: SF- ship fouling; BW- ballast water; AQ-aquaculture. *Undetermided subspecies of *C. scaura* without a ventral spine.

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