Scientific collaboration for early detection of invaders results in a significant update on estimated range: lessons from Stenothoe georgiana Bynum & Fox 1977

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Abstract

Detection of new non-indigenous species is often delayed when taxa are taxonomically challenging, such as small-sized marine organisms. The present study highlights the relevance of scientific cooperation in the early detection of the invader amphipod *Stenothoe georgiana*. Originally described from North Carolina (USA), the species was recently found in Chile and the Western Mediterranean. Here, we provide the first record of the species in Macaronesia, Atlantic coasts of continental Europe, North Africa and Australia, and extend its known distribution along the Mediterranean coast. Just like other small crustaceans, shipping (both ballast water and recreational boating) and aquaculture are probably the main vectors of introduction and secondary spread for this amphipod species. This case of *S. georgiana* sheds light on the importance of promoting taxonomical knowledge, and building multidisciplinary networks of experts that ensure an effective dissemination of alien species information. We also encourage the implementation of standardized monitoring methodologies to facilitate early detection of small mobile invaders.

Keywords: early detection; bioinvasions; Amphipoda; scientific cooperation; taxonomy promotion; knowledge transfer.

Introduction

It is well understood that in the marine realm, prevention and early detection represent the only viable and cost-effective strategies in managing biological invasions (IUCN 2009, Roy *et al.*, 2014). Managing vectors of invasion may limit new arrivals and, in case of alien incursions, early detection allows a rapid eradication response prior to spreading and establishment (see Genovesi, 2011; Bergstrom *et al.*, 2018). In order to ensure early detection of introductions, rigorous baseline surveys are required, along with surveillance and monitoring programs (Lehtiniemi *et al.*, 2015). Unfortunately, such missions are hampered by issues such as incomplete and inaccurate data availability on species distributions; scattered information across different unstandardized datasets; and cumulative time-lags in detection, acknowledgment and reporting of invaders (Gatto *et al.*, 2013; Ojaveer *et al.*, 2015; Marchini & Cardeccia, 2017; Gallil *et al.*, 2018; Zenetos *et al.*, 2019). This is especially relevant for the so-called “hidden invaders”, including unicellular taxa like benthic foraminifera (Guastella *et al.*, 2019) or small invertebrates with cryptic behaviour. Hence, special attention should be paid to detecting invasions of small or taxonomically challenging species (see Xavier *et al.*, 2009; Carlton, 2011; Marchini *et al.*, 2016). For
example, when conducting monitoring campaigns in harbours and marinas, rapid assessment surveys may suffice for larger-sized taxa or sessile invertebrates. Contrarily, *in situ* detection of numerous epifaunal species is often impossible; usually due to their small sizes and cryptic within their arborescent substrate. In these cases, it is crucial to also sample the fouling substrate inhabiting the surface of artificial structures, which have a tendency to harbor non-native species (DaForn *et al.*, 2012; Airoldi *et al.*, 2015; Foster *et al.*, 2016). Despite their small size, small invertebrates have a crucial role in marine food webs, nutrient cycling, habitat structuring and ecosystem functioning (e.g. Ieno *et al.*, 2006; Merrifild-Blondin & Rosenberg, 2006). In many cases, managing newly detected alien species is neither efficient nor affordable, often due to time-lags in the timing of records and uncertainty about potential impacts. Consequently, there is a great need of taxonomic expertise focusing on smaller organisms, a better understanding of their functional role in ecosystems, and sustained cooperation among the scientific community through open communication and knowledge dissemination.

Comprising almost ten thousand species, the Amphipoda are one of largest groups of crustaceans and rank among the least well described taxa, even taking into account the increasing description rate of species within the last decades (Coleman, 2015; Arfianti *et al.*, 2018). Amphipods are highly abundant and species rich in most marine habitats, and frequently dominate the mobile macrofauna associated with fouling communities. The sessile invertebrates and macroalgae that foul marine surfaces are frequently transported by anthropic vectors, such as aquaculture and recreational boating (Ashton *et al.*, 2007; Martínez-Laiz *et al.*, 2019). While there are some well-documented invasions of amphipods, the number of introduced species is almost certainly underestimated due to the presence of cryptogenic species, unresolved taxonomy and overlooked introductions (see Marchini & Cardecia, 2017). To tackle this difficult group, a strong and active cooperation between senior, experienced taxonomists, early-career taxonomists or parataxonomists, and those involved in processing large numbers of samples from monitoring surveys, are key factors that need to be encouraged.

The amphipod species *Stenothoe georgiana* Bynum & Fox, 1977 stands out as a primary example of how the combination of taxonomical expertise and scientific cooperation can result in the early detection of small marine invaders. Indeed, the genus *Stenothoe* stands out as one of the most taxonomically challenging amphipod genera, due to smaller than average sizes and minute differences among species in the relevant characters for identification (Krapp-Schickel, 2015). *Stenothoe georgiana* recently emerged as a new non-indigenous species (NIS) in the Mediterranean Sea (Fernández-González & Sanchez-Jerez, 2017; Ulman *et al.*, 2017; Servello *et al.* 2019) and Southeastern Pacific (Pérez-Schultheiss & Ibarra, 2017). It was first described from North Carolina (USA) by Bynum & Fox (1977) and all of its records in the subsequent decades were limited to the Atlantic coast of USA (e.g. Fox & Ruppert, 1985; Nelson & Demetriades, 1992). In 2017, one of the co-authors of the present study, Victoria Fernández-González (hereafter VF-G), found the species across the Atlantic in 2010 from the Spanish Mediterranean coast. An early and rapid exchange of information amongst several amphipod experts aided other researchers working with NIS in fouling communities to detect the new invader in other Mediterranean regions (Ferrario *et al.*, 2017, 2018; Ulman *et al.*, 2017, 2019; Servello *et al.*, 2019). As a further advancement of the above-mentioned collaboration, we present here an updated worldwide distribution of the species, including new records, along with a discussion about invasion dynamics and *S. georgiana*’s new status as a neo-cosmopolitan species (*sensu* Darling & Carlton, 2018). Using this case study, we highlight the need for scientific cooperation to properly address early detections and better manage invasive species.

**Material and Methods**

**Collection of samples**

Samples for this study were collected during several sampling surveys between 2010 to 2017 in Portugal, Spain, Morocco, Italy, Tunisia, Malta, Croatia, Greece, Turkey and Australia (Fig. 1).

**Iberian Peninsula, Balearic Islands and North Africa**

A total of 42 marinas were surveyed along the whole Iberian Peninsula and North Africa during the late spring-summer of 2011 (see Ros *et al.*, 2014 for details). In each marina, three colonies of the bryozoan *Bugula neritina* (Linnaeus 1758) were hand-collected from the submerged portion of pontoons close to the surface (see Ros *et al.*, 2015 for details). Out of these, twelve marinas of the Andalusian coasts (Iberian Peninsula) were sampled a second time in 2017 using the same methodology. Additionally, extra samples from fouling communities growing on artificial hard substrate including pontoons, ropes, wheels, buoys and ship hulls were inspected in these marinas. These included red and green algae, hydroids, bryozoans, ascidians and molluscs and their associated mobile epifauna. Finally, the Marina de Ceuta (North Africa) was sampled in 2015 and 2016 as part of an experimental field study (Ros *et al.*, 2020). In this case, a survey of the floating pontoons was carried out by scraping the artificial substrate. To explore seasonal fluctuations of *S. georgiana*, we also analysed data from two monitoring programs in 2012, aimed to assess the peracarid community associated with fouling substrates. In Puerto América marina (Cádiz), three replicates of the hydroid *Eudendrium racemosum* (Cavolini, 1785) and the bryozoan *Amathia verticillata* (delle Chiaie, 1822) were sampled monthly from floating pontoons. In Palma Marina (Balearic Islands), three replicates of the hydroid *E. racemosum* were collected monthly for the same purpose.
Between 2010 and 2013, a total of 10 offshore aquaculture facilities were sampled around the Spanish border of the western Mediterranean coast and Tunisia (see Fernandez-Gonzalez & Sanchez-Jerez, 2017 for details). In each facility, samples were collected from mooring ropes by scraping all fouling organisms from 20 cm of rope. Between 2010 and 2011, two of these fish farms (located in Alicante) were additionally sampled to study seasonal fluctuations in different fouling substrates (i.e. mussels, hydroids and algae) using an air-lift device to ensure a quantitative sampling method. In 2014, as part of an integrated multi-trophic aquaculture study, artificial collectors were deployed around two fish farms in Málaga and Almería (Andalusian coast).

In all surveys, samples were preserved (in ethanol 70%, formalin or frozen until examined) and checked for the presence of *S. georgiana* (see Ros et al., 2015; Fernandez-Gonzalez et al., 2018 for details).

Italian Peninsula, Croatia, Malta, Greece and Turkey

Between 2010 and 2013, as part of the offshore aquaculture study, seven facilities were sampled in the coasts of Italy, Croatia, Malta and Greece, using the same methods described above. In all surveys, the biota collected off the substrates (both natural and artificial) were preserved in ethanol or formalin and sorted later at the laboratory to check for the presence of *S. georgiana* (see Ros et al., 2015; Fernandez-Gonzalez et al., 2018 for details).

Azores (Macaronesia)

In spring of 2013, 2014 and 2015, surveys of the fouling communities associated with boat hulls and pontoons were conducted on the Azores (Macaronesia). In 2013 and 2014, surveys were conducted using a hand-held rigid net with one sharpened edge to scrape the submerged portion of pontoons; and a paint scraper was used to sample buoys and ladders. The samples were preserved in 96% ethanol, sorted and identified to species level. In 2015, the fouling community was collected by scuba divers by scraping the surface of 33 x 33 cm quadrats from a zinc-coated iron pillar, at both 6 m and 14 m depths.

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were conducted in Ponta Delgada (Azores), as a part of a general study aimed at identifying alien species in the area. The marina in Ponta Delgada had been expanded in 2008 to allow the simultaneous mooring of 600 recreational boats plus a transatlantic cruise pontoon. Fouling organisms (mainly bryozoans) growing on artificial hard substrata were hand-collected by snorkeling and immediately placed into zip-lock plastic bags. Samples were subsequently cleaned in seawater and Amphipoda were sorted, preserved in 96% ethanol, and identified to species level.

New South Wales (Australia)

In 2017, artificial collectors made of several small branches of frayed polypropylene rope were deployed in Chowder Bay (Sydney, Australia) during one month, as part of an experimental recolonization study for peracarid crustaceans (Navarro-Barranco et al., unpublished data). Samples were preserved in 70% ethanol, and the associated fauna was sorted and examined for the presence of *S. georgiana*.

**Dissemination of records information**

In 2012, VF-G observed an unusual species of the genus *Stenothoe* in samples collected in 2010 from the Spanish Mediterranean coast. The identity of the specimens remained unknown until a key publication was published which included a taxonomical revision of the *Stenothoe* genus by a senior taxonomist (Krapp-Schickel, 2015), providing a comprehensive key to global species. The same year, VF-G performed a thorough taxonomic analysis, and personally communicated with Traudl Krapp-Schickel which confirmed the identity as *S. georgiana*. When it was clear that the finding represented a new record for the Mediterranean Sea, prior to the publication of the record, the author personally communicated her finding with some previous Spanish collaborators and co-authors of the present work. In parallel work, Italian co-authors found additional specimens of “unknown” *Stenothoe* sp. in fouling samples from multiple Mediterranean marinas in 2016, and reported these findings to the same amphipod team to help determine the identity.

**Fig. 2:** *Stenothoe georgiana* Bynum & Fox, 1977. Lateral view, gnathopod 1 (Gn1), gnathopod 2 (Gn2) with propodus detail, uropods 1, 2 and 3 (U1, U2, U3) of males from Southern Iberian Peninsula. Gnathopod 2 with propodus detail (Gn2 Aust) of male from Sydney, Australia.
This early exchange of information enabled researchers working with NIS to detect *S. georgiana* in further Mediterranean regions. It is worth mentioning that these and multiple other researcher’s scientific networks were born from participating in the International Colloquium of Amphipoda (ICA), a biannual specialist international conference on this group taxa. All teams raised the flag on the presence of a new invader among the Amphipod network’s experts working with fouling communities; and engaged researchers from 12 institutions from different countries to coordinate the present work.

**Identification remarks**

Detailed morphological descriptions of *S. georgiana* are provided by Bynum & Fox (1977) and Pérez-Schultheiss & Ibarra (2017). The species is distinguishable by the following characters for males (Fig. 2): palmar corner of gnathopod 2 defined by a semicircular rounded spinose hump; large coxa, rounded anteroventrally and straight posteriorly; gnathopod 1 article 6 with posterior border convave, palm defining angle bearing 4 spines and dactyl fitting palm; U1 peduncle slightly longer than ramus with small distal tooth; U2 peduncle and rami subequal, rami with longitudinal rows of fine serrations; U3 peduncle shorter than entire ramus, article 2 of ramus shorter than article 1; telson apex acute, lateral margins bearing two spines. These and other authors (e.g. Krapp-Schickel, 2006) highlighted the morphological similarities between *S. georgiana* and *S. estacola* J.L. Barnard 1962, the latter described from the Pacific coast of USA (Barnard, 1962). *Stenothoe* *georgiana* and *S. estacola* were also grouped with the Hawaiian species *Stenothoe* *haleloke* J.L. Barnard 1970, within the key to all *Stenothoe* species provided by Krapp-Schickel (2006). Males of *S. haleloke* were not available at that time but the later synonymization between *S. haleloke* and *Stenothoe* *qingtaoensis* Ren, 1992 contributed to the establishment of distinguishable characters (e.g. unlike *S. estacola* and *S. georgiana*, gnathopod 2 propodus in males and females of *S. haleloke* lack a clear palmar corner; Krapp-Schickel et al., 2015, Krapp-Schickel, 2015).

Males of both *S. georgiana* and *S. estacola* are characterized by a defining palmar hump on the propodus of gnathopod 2. However, only *S. georgiana* bears robust spines on the hump. Other noticeable differences are: a narrow palmar carpal lobe of *S. estacola* gnathopod 2 (broader in *S. georgiana*), the presence of several additional small palmar blunt cups (absent in *S. georgiana*), a clearly longer antenna 2 in comparison with antenna 1 in *S. estacola* (antenna 1 is a slightly longer in *S. georgiana*), and the number of dorsal setae on peduncle of the uropod 3 (1 in *S. georgiana* vs 3 in *S. estacola*) (Bynum & Fox, 1977; Pérez-Schultheiss & Ibarra, 2017). However, after examination of additional material (also collected in the California coast and presumably attributed to *S. estacola*) and type series specimens of *S. estacola*, Barnard (1969) reported contrasting characters with those described in the holotype which included the presence of spines on the surface of the palmar hump, a less noticeable cusp, a broader carpal lobe, a slightly longer antenna 1 and differing number of spines on uropod 3. At that time, Barnard (1969) suggested that the differences could be attributable to ontogenetic changes, but this hypothesis was not later confirmed. Likewise, the specimens examined by Barnard (1969) more closely resemble *S. georgiana* (that would be described eight years later) than the *S. estacola* holotype described by Barnard (1962). Unfortunately, Bynum & Fox (1977) did not mention the particularity of this material on the original description of *S. georgiana*. Under this scenario, further molecular and morphologic phylogenetic studies would be helpful to help clarify the relationship between *S. estacola* and *S. georgiana*.

**Results**

**Previous records and habitat use of *S. georgiana***

The known distribution records of *S. georgiana* prior to the present study (from 1935 to 2017 in both putative native and introduced ranges) are listed in Table 1. Fifty-four percent of those locations represented records of its putative native range. Of those, 31% of records correspond to natural habitats (offshore hard-bottom areas, nearshore habitats including mud, sand, patches of sponges, and soft corals), 46% to artificial habitats (piling and seawalls, rock jetties, artificial reefs, and piers) and 23% to anthropized sounds and estuaries. In contrast, all records from the putative introduced range are from artificial habitats (75% in harbours and marinas; and 25% in aquaculture facilities).

**New records and spreading of *S. georgiana***

**A - New regions**

The present study provides new records of *S. georgiana* in Portugal, North Africa (Ceuta) and Australia, as well as new locality records in countries where the species had already been detected: Spain and Italy (Table 2, Figs. 1, 2).

In the marinas of the Iberian Peninsula, the species is mainly distributed in the southern region, from Sines to Almeria, but is also present in Barcelona (North - Western Mediterranean Sea) and Palma (Balearic Islands). In Venice Lagoon (Northeastern Italy, Adriatic Sea), where salinity varies with tidal conditions, *S. georgiana* was found in the higher salinity portion of the estuarine gradient, up to a station where salinity dropped to about 25 PSU under low tide conditions. Two years later (2019), it was also observed outside the lagoon (at an offshore platform) in rather high abundances (up to 2420 ind. m$^{-3}$).
Table 1. Previously known *Stenothoe georgiana* records worldwide. Records from its putative introduced range are shaded. Likely vectors: ‘SF’ = ship fouling; ‘SF (rb) = recreational boating; ‘BW’ = ballast water; ‘AQ’ = aquaculture. * in vectors represents assumptions made by the authors. '-' = data not available.

<table>
<thead>
<tr>
<th>Date</th>
<th>Country</th>
<th>Localities</th>
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<td>1935 USA</td>
<td>USA</td>
<td>Sapelo Island (Georgia) Offshore, 11 miles off-coast</td>
<td>Identified by Mr. Clarence R. Shoemaker GBIF.org (2019)</td>
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<td>-</td>
<td>USA</td>
<td>Chesapeake Bay and Norfolk (Virginia); New River, Shackleford Bank and Beaufort (North Carolina); St. Catherine Sound (Georgia); Sarasota Bay, Tampa Bay and Loggerhead Key (Florida)</td>
<td>-</td>
<td>Mr. Clarence R. Shoemaker, unpublished data in Bynum &amp; Fox (1977)</td>
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<td>-</td>
<td>Brazil</td>
<td>Rio de Janeiro and Sacco Sáo</td>
<td>-</td>
<td>Mr. Clarence R. Shoemaker, unpublished data in Bynum &amp; Fox (1977)</td>
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<td>1957-1966</td>
<td>USA</td>
<td>Institute of Marine Science pier station, Drum Inlet station, Lockwoods Folly Inlet station (North Carolina)</td>
<td>Nocturnal surface macroplankton in estuaries</td>
<td>Williams &amp; Bynum (1972) in Bynum &amp; Fox (1977) (as ‘<em>Stenothoe sp.</em>’ and ‘<em>S. minuta</em>’)</td>
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<td>1971 USA</td>
<td>USA</td>
<td>Chesapeake Bay (Virginia), Tybee Inlet and Sebastian Inlet (Florida)</td>
<td>Fouling community on a pier</td>
<td>Bynum &amp; Fox, (1977)</td>
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<td>1975 USA</td>
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<td>North Carolina estuaries</td>
<td>Fouling community and shelly bottom</td>
<td>Fox &amp; Bynum (1975)</td>
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<td>1980-1981</td>
<td>USA</td>
<td>Charleston (South Carolina), Sapelo Island (Georgia), Jacksonville (Florida)</td>
<td>Stomach contents of <em>Archeacanthella probatocephala</em> at offshore reef habitats</td>
<td>Sedberry (1987)</td>
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<td>1981-1985</td>
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<td>Piling and Seawalls, creeks and sounds</td>
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<td>1982 USA</td>
<td>USA</td>
<td>St. Catherine’s Island (Georgia)</td>
<td>Sponges and corals at hard-bottom area</td>
<td>Wendi et al. (1985)</td>
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<td>April 1984 - March 1985 USA</td>
<td>Sebastian Inlet (Florida)</td>
<td>Sabellariid worm <em>Phragmatopoma lagidosoides</em> at rock jetties</td>
<td></td>
<td>Nelson &amp; Demetriades (1992)</td>
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<td>1985-1987</td>
<td>USA</td>
<td>South Carolina</td>
<td>Stomach contents of <em>Chaetodipterus faber</em> in shallow nearshore habitats (sponges, soft corals); estuarine habitats; and artificial reefs and jetties</td>
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<td>2004 USA</td>
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<td>2012 Chile</td>
<td>Los Lagos and Atacama</td>
<td>Salmonid farms</td>
<td>AQ*</td>
<td>Pérez-Schultheiss &amp; Ibarra (2017)</td>
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<td>2013 Italy</td>
<td>Lerici marina</td>
<td>Fouling communities on dock walls and floating pontoons</td>
<td>SF (rb)</td>
<td>Ferrario et al. (2017)</td>
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<td>2014 Italy</td>
<td>Porto Torres harbour</td>
<td>Fouling communities on the subtidal level of dock walls</td>
<td>SF</td>
<td>Ferrario et al. (2017)</td>
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<td>2015 Mexico</td>
<td>Puerto Progreso (Yucatan)</td>
<td>Macroalgae associated to buoys, chains, pilings and seawalls</td>
<td>SF*</td>
<td>Winfield et al. (2015)</td>
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*continued*
In Sines (Portugal, Iberian Peninsula), three specimens were collected in 2011; and in Azores (Portugal, Macaronesian region) another three specimens were found in Ponta Delgada marina in 2013, 2014 and 2015. These findings represent the first record of the presence of S. georgiana in the Central-East Atlantic coast. In North Africa coast, S. georgiana (ca. 10 specimens) was found for the first time in September 2015 (late summer); and later in January 2016 (winter); in association with fouling substrata attached to floating pontoons, including *Eudendrium sp.*, *Ellisolandia elongata* (J.Ellis & Solander) K.R. Hind & G.W. Saunders, *Mytilus sp.*, *B. neritina*, *Dictyota dichotoma* (Hudson) J.V. Lamouroux, and plumularid hydroids. Finally, S. georgiana was recorded for the first time in Australian waters (ca. 15 specimens), on piers from Chowder Bay (Sydney). Localities sampled by the authors where S. georgiana was not detected are included in the supplementary material (Table 1. Supplementary).

### B - New locations (within regions previously sampled)

In the Southern Iberian Peninsula, *Stenothoe georgia* was recorded in four marinas in 2011 [Puerto América (Atlantic Ocean), La Línea, Málaga and Motril (Mediterranean Ocean)]; and six years later, it was found in eight marinas from the same region: the previous ones plus Isla Canela and El Rompido in the Atlantic Ocean, and Fuengirola and Almería in the Mediterranean Sea. It should be noted that in the last three marinas, the species was found in samples collected using a slightly different methodology than in 2011. Finally, S. georgiana was not present in Ceuta in 2011, but was found there in 2015 and 2016 (Table 2).

### C - Evidence for seasonal patterns (establishment at new locations)

The presence of *S. georgiana* in all months sampled confirm the existence of established populations in the new localities in Spain and Italy. The monitoring studies also reveal that *S. georgiana* populations are present throughout the entire year. In Palma Marina, a total of ca. 100 specimens were collected from *E. racemosum*, being present in all sampled months, with higher densities found in February and December. In Puerto América, Cádiz, the species was also found most of the year associated to the substrates *E. racemosum* (ca. 90 specimens collected) and the alien bryozoan *A. verticillata* (ca. 110 specimens collected) (Table 2).

### Taxonomical remarks

Although Pérez-Schultheiss & Ibarra (2017) reported some minute morphological differences in the propodus of gnathopod 2 of introduced Chilean populations of *S. georgiana* and the original description by Bynum & Fox (1977) (see Pérez-Schultheiss & Ibarra, 2017), we did not find constant differences within the rest of introduced populations [Mediterranean, East Atlantic coast, Chile, Australia] (Fernandez-Gonzalez & Sanchez-Jerez, 2017, Ulman et al., 2017). Furthermore, preliminary molecular analysis indicates that populations from the Iberian Peninsula and Australia belong to the same species (Cabaza et al. unpublished data). Further molecular studies are advised to confirm *S. georgiana* as a neo-cosmopolitan species—an introduced species having achieved a widespread

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**Table 1 continued**

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<td>Port du plaisance du Port Camargue (Le Grau-du-Roi), Port Principal du Cad d’Aigde (Aigde) and Port Vauban (Antibes)</td>
<td>Marina fouling at Port Camargue; recreational vessel hull-fouling at Port Vauban</td>
<td>SF (rb)</td>
<td>Ulman et al. (2017)</td>
</tr>
<tr>
<td>2015</td>
<td>Italy</td>
<td>Porto Turistico Marina Piccola di Sorrento (Sorrento, Campania)</td>
<td>Marina fouling and vessel hull-fouling</td>
<td>SF (rb)</td>
<td>Ulman et al. (2017)</td>
</tr>
<tr>
<td>2016</td>
<td>USA</td>
<td>Tampa Bay (Florida)</td>
<td>Artificial reefs dominated by barnacles, sponges ascidians and bryozoans</td>
<td></td>
<td>Karlen et al (2017)</td>
</tr>
<tr>
<td>2016</td>
<td>Italy</td>
<td>Marina Villa Iglesia (Palermo), Porto Grande (Sicily), Porto dell’Etna (Riposto), Marina di Cala del Sole (Licata) (Sicily)</td>
<td>Marina fouling and vessel hull-fouling at Palermo and Licata; marina fouling at Siracusa; hull-fouling at Riposto</td>
<td>SF (rb)</td>
<td>Ulman et al. (2017)</td>
</tr>
<tr>
<td>2016</td>
<td>France</td>
<td>St. Tropez marina (Cote d’Azur)</td>
<td>Sailing boat hull-fouling</td>
<td>SF (rb)</td>
<td>Ulman et al. (2017)</td>
</tr>
<tr>
<td>2017</td>
<td>Slovenia</td>
<td>Harbour of Piran</td>
<td>Dock fouling</td>
<td>SF</td>
<td>Ferrario et al. (2018)</td>
</tr>
<tr>
<td>2017</td>
<td>Italy</td>
<td>Porto di Palermo (Palermo, Sicily)</td>
<td>Rope fouling</td>
<td>SF</td>
<td>Lo Brutto et al. (2018)</td>
</tr>
</tbody>
</table>

*The earliest record of the species are some specimens collected by M.C.R. Shoemaker from Sapelo Island (Georgia) and deposited in 1935 in the National Museum of Natural History, Smithsonian Institution.*
The voucher materials have been deposited in Museo Nacional de Ciencias Naturales de Madrid (MNCN, Madrid, Spain), Museo di Storia Naturale di Venezia (MSN-VE, Venice, Italy), and Museo di Storia Naturale dell’Università di Pavia (MSNPV, Pavia, Italy). In MNCN: 7 males collected from Puerto América Marina, Cádiz, Spain, 36.54° N; 6.28° W, associated to *Eudendrium racemosum* colonizing floating pontoons, August 15, 2012 (MNCN 20.04/12009) were deposited; 9 males collected from Palma Marina, Spain, 39.57° N; 2.63° E, associated to *E. racemosum* colonizing floating pontoons, February 18, 2012 (MNCN 20.04/12010); 5 males collected from Barcelona Marina, Barcelona, Spain, 41.38° N; 2.18° E; associated to *Bugula neritina* colonizing floating pontoons, June 16, 2011 (MNCN 20.04/12011); 2 males collected from Chowder Bay, Sydney, Australia, 33.84° S; 151.25° E, associated to artificial collectors deployed in piers, December 3, 2017 (MNCN 20.04/12012). In MSNVE: 25 specimens (10 males, 8 females, 7 juveniles) collected from an offshore platform located in front of the Venice Lagoon.

**Table 2.** New records for *Stenothoe georgiana*. Monthly presence/absence of the species in Cádiz (2012) and Palma (2012) is also included. PT=Portugal, ES=Spain, IT=Italy, AU=Australia.

<table>
<thead>
<tr>
<th>Country</th>
<th>Locality</th>
<th>Date</th>
<th>Coordinates</th>
<th>Substrates</th>
</tr>
</thead>
<tbody>
<tr>
<td>PT</td>
<td>Sines marina, Alentejo</td>
<td>9 May 2011</td>
<td>37.95° N; 8.87° W</td>
<td>Pontoons (Bagula neritina)</td>
</tr>
<tr>
<td></td>
<td>Ponta Delgada marina, São Miguel, Azores</td>
<td>22 May 2013, 2 April 2014, 10 March 2015</td>
<td>37.73° N; 25.65° E</td>
<td>Boat hulls, pontoons</td>
</tr>
<tr>
<td></td>
<td>Isla Canela marina, Huelva</td>
<td>26 June 2017 (Absent in 2011)</td>
<td>37.19° N; 7.34° W</td>
<td>Pontoons (Bagula neritina)</td>
</tr>
<tr>
<td></td>
<td>El Rompido marina, Huelva</td>
<td>26 June 2017 (Absent in 2011)</td>
<td>37.22° N; 7.13° W</td>
<td>Pontoons (fouling communities)</td>
</tr>
<tr>
<td></td>
<td>Puerto América marina, Cádiz</td>
<td>17 May 2011, 2 July 2017</td>
<td>36.54° N; 6.28° W</td>
<td>Pontoons (fouling communities)</td>
</tr>
<tr>
<td></td>
<td>La Línea marina, Cádiz</td>
<td>15 May 2011, 30 June 2017</td>
<td>36.16° N; 5.36° W</td>
<td>Pontoons (fouling communities)</td>
</tr>
<tr>
<td></td>
<td>Fuengirola marina, Málaga</td>
<td>29 June 2017 (Absent in 2011)</td>
<td>36.54° N; 4.62° W</td>
<td>Pontoons (fouling communities)</td>
</tr>
<tr>
<td></td>
<td>Málaga marina, Málaga</td>
<td>3 July 2011, 29 June 2017</td>
<td>36.72° N; 4.41° W</td>
<td>Pontoons (Bagula neritina)</td>
</tr>
<tr>
<td></td>
<td>Motril marina, Granada</td>
<td>2 July 2011, 28 June 2017</td>
<td>36.72° N; 3.53° W</td>
<td>Pontoons (Bagula neritina)</td>
</tr>
<tr>
<td></td>
<td>Almería marina, Almería</td>
<td>27 June 2017 (Absent in 2011)</td>
<td>36.83° N; 2.46° W</td>
<td>Pontoons (fouling communities)</td>
</tr>
<tr>
<td></td>
<td>Barcelona marina, Barcelona</td>
<td>26 June 2011</td>
<td>41.38° N; 2.18° E</td>
<td>Pontoons (Bagula neritina)</td>
</tr>
<tr>
<td></td>
<td>Palma marina, Baleares</td>
<td>18 December 2011</td>
<td>39.57° N; 2.63° E</td>
<td>Pontoons (Eudendrium racemosum)</td>
</tr>
<tr>
<td></td>
<td>Ceuta, North Africa</td>
<td>September 2015, January 2016 (Absent in 2011)</td>
<td>35.89° N; 5.31° W</td>
<td>Pontoons (see Results)</td>
</tr>
<tr>
<td>ES</td>
<td>Venice lagoon</td>
<td>12 June 2017</td>
<td>45.47° N; 12.41° E</td>
<td>Wooden piles</td>
</tr>
<tr>
<td></td>
<td>Adriatic Sea (off the Venice Lagoon)</td>
<td>12 March 2019; 16 September 2019</td>
<td>45.31° N; 12.51° E</td>
<td>Offshore platform pillar</td>
</tr>
<tr>
<td>IT</td>
<td>Chowder Bay, Sydney</td>
<td>3 December 2017</td>
<td>33.84° S; 151.25° E</td>
<td>Piers (Artificial collectors)</td>
</tr>
</tbody>
</table>

**Locality: Puerto América marina, Cádiz, SPAIN**

<table>
<thead>
<tr>
<th>(36° 32’ 29.2” N; 6° 17’ 02.4” W)</th>
<th>Jan</th>
<th>Feb</th>
<th>Mar</th>
<th>Apr</th>
<th>May</th>
<th>Jun</th>
<th>Jul</th>
<th>Aug</th>
<th>Sep</th>
<th>Oct</th>
<th>Nov</th>
<th>Dec</th>
</tr>
</thead>
<tbody>
<tr>
<td>Substrates: Eudendrium racemosum Amathia verticillata</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
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<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
</tbody>
</table>

**Locality: Palma marina, Baleares, SPAIN**

<table>
<thead>
<tr>
<th>(39° 34’ 2” N; 2° 37’ 56” E)</th>
<th>Jan</th>
<th>Feb</th>
<th>Mar</th>
<th>Apr</th>
<th>May</th>
<th>Jun</th>
<th>Jul</th>
<th>Aug</th>
<th>Sep</th>
<th>Oct</th>
<th>Nov</th>
<th>Dec</th>
</tr>
</thead>
<tbody>
<tr>
<td>Substrate: Eudendrium racemosum</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
</tbody>
</table>
(45.31° N; 12.51° E); associated to mussels colonizing a zinc-coated iron pillar (MSNVE 25100). In MSNPV: 7 specimens collected from the Lagoon of Venice, Italy (45.47° N; 12.41° E); associated with a rich macrofauna community composed by mussels, sponges, tunicates and bryozoans colonising wooden piles (MSNPV-2019/8).

Discussion

*Stenothoe georgiana* has successfully extended its introduced range, now currently present in both hemispheres, both the Atlantic and the Pacific Ocean, and the Mediterranean Sea. The present case is that of a very successful colonizer on artificial structures, though easily overlooked due to its small-size and tricky identification (hidden invader). In this scenario, early detection is especially challenging; and in this particular case, it was only possible due to effective communication amongst expert groups and thorough taxonomic works (see section 4.3 below). The research conducted here becomes then of particular relevance; and it serves to point out certain challenges, and to provide suggestions to facilitate detection of hidden invaders.

On the invasion dynamics of *S. georgiana*: biogeographical patterns and vectors of introduction

*Stenothoe georgiana* was described from individuals collected from fouling communities on a pier at the University of North Carolina (type locality) by Bynum & Fox (1977). They reported *S. georgiana* as abundant in sounds and estuaries of that region. Several years before the species was described, another researcher (M.C.R. Shoemaker) was working on the description of what he called 'S. georgiana' at the time of his death. Therefore, Bynum & Fox (1977) examined his unpublished manuscript and included part of his data in their description. Shoemaker’s manuscript comprised material from Virginia, North Carolina, Georgia and Florida from the east Atlantic coast of USA, as well as Rio de Janeiro and Sacco Sào from the southeastern coast of Brazil. The earliest, but unpublished record of the species actually dates back to 1935, and belongs to specimens collected by Shoemaker from Sapelo Island, Georgia which were deposited in the National Museum of Natural History, Smithsonian Institution (*Stenothoe georgiana* Shoemaker in GBIF Secretariat, 2017; Orrell, 2019). It would be of interest to know the habitats of all the found materials, and especially to separate records from natural versus artificial habitats, in order to have hints on the possible native range of the species (when species associated to fouling communities are involved, records from an artificial habitat should be considered with caution, see Chapman & Carlton, 1991). However, such information was not provided with Shoemaker’s material, hence preventing us from knowing if the specimens from its putative native region were associated with artificial habitats or not. Analysing the global distribution records of the species (Table 1), we found that no additional records of *S. georgiana* have been reported from Brazil, which may be attributable to a lack of sampling effort or misidentifications. Instead, most records belong to the western Atlantic coast of USA and the Gulf of Mexico (included in its putative native range). Taking these facts into account, we think the record from Brazil should be considered as questionable (Fig. 3a) and we suggest further sampling in this geographical region in order to validate this.

Since its original description in 1977, and until 2017, the distribution of the species was assumed to be restricted to the Western Atlantic region. However, in 2010 and 2011, established populations of *S. georgiana* were found by Fernandez-Gonzalez & Sanchez-Jerez (2017) associated with offshore sea bass and sea bream aquaculture facilities in two Mediterranean localities. After raising the flag on the presence of *S. georgiana* amongst scientific colleagues, the species was found in additional locations in the Mediterranean Sea (published records from Italy, France, Malta and Slovenia, Table 1), and confirmed here with new Mediterranean records. This study also confirms the presence of *S. georgiana* in Macaronesia, North Africa and Australia, significantly enlarging its distributional range. Simultaneously, records of the species have also appeared from the other side of the world, Pérez-Schultheiss & Ibarra (2017) also found the species in 2012 in salmonid farms in Chile. Currently, populations of *S. georgiana* are known from both the Northern and Southern Hemispheres, specifically from: the Northwestern Atlantic coast of USA, the Gulf of Mexico, the Southwestern coast of Brazil, the Eastern Atlantic coast of Europe (including Macaronesia), the Mediterranean Sea, and the Southeastern and Southwestern Pacific coasts of Chile and Australia, respectively (Fig. 3a).

Records of *Stenothoe georgiana* from its putative native range occur in both natural and artificial substrata. Meanwhile, records from its introduced range were exclusively associated with anthropogenically altered environments and artificial substrata (harbours, recreational marinas, aquaculture facilities). This leads to two assumptions about its native range and vectors of introduction. Firstly, although the species was described from individuals associated with artificial substrata, its presence in natural habitats along the western Atlantic coasts could support the assignment of this area as its putative native range. The Northern Atlantic Ocean represents the region with the highest diversity of *Stenothoe* species (Fig. 3b), hosting twenty-four species in the Eastern side, ten in the Western side, and six in the Gulf of Mexico and the Caribbean Sea. Although the higher number of *Stenothoe* spp. in the North-East Atlantic region could hint at the evolutionary origin of this genus in this area (Chapman & Carlton, 1991), the absence of *S. georgiana* in natural habitats, together with the lack of early records in important and comprehensive taxonomic works on Amphipoda for the area (e.g. Lincoln, 1979; Ruffo, 1993; 1998), suggests a recent introduction of the species in European waters. Molecular analysis would be necessary to confirm this assumption. Furthermore, considering the numerous records of *S. georgiana*...
in port habitats that are connected to offshore aquaculture facilities and other ports/marinas by boating activity (Sarà et al., 2007), the likely vectors of introduction of this amphipod are recreational and commercial boating. Indeed, Ulman et al. (2017) provides direct evidence of the presence of S. georgiana found on recreational boat hulls moored in France and Italy. Although no evidence has yet been found on the spreading of S. georgiana specimens through rafting on floating substrates, it is worth noting that other species of the same genus were recently reported associated with floating debris originating from the Japanese tsunami (Carlton et al., 2017).

In its putative native range S. georgiana was also found in nocturnal surface macroplankton of estuaries (Bynum & Fox, 1977). This could also imply a high ability for short-distance natural dispersal compared to other benthic amphipod species (traditionally considered poor dispersers). A high natural dispersal tendency may increase the probability of being transported by a human-mediated vector (Ros et al., 2020). This, combined with its strong affinity for artificial environments in its introduced range and its high plasticity for colonizing different biogenic substrata, may help to explain its rapid spread in European waters. Unfortunately, not enough data exists on the ecology of S. georgiana to enable a comprehensive understanding of its invasion potential. Therefore, we highlight the need for subsequent S. georgiana studies which address, among other aspects: population dynamics, trophic ecology, habitat use, behavior or tolerance to environmental stress from different areas of its distribution. In any case, this study confirms the recent presence of established populations of S. georgiana over the years (e.g. in Andalusia and Azores) as well as throughout the year (in southern Iberian Peninsula, Balearic Islands and Sicily). This may imply its rapid establishment success after its initial introduction to new region. The presence of the

![Map showing the distribution of Stenothoe georgiana](image)

**Fig. 3:** a) Updated worldwide distribution of *Stenothoe georgiana* including its introduced range (in red) and its putative native range (in green). Records from Brazil are considered questionable (in yellow). Information based on data showed in Tables 1 and 2. b) Number of *Stenothoe* spp. recorded in each region. Information based on Krapp-Schickel (2015), GBIF.org (26 June 2019) and WORMS (Horton et al. 2019).
species in very distant biogeographical areas, including tropical, subtropical and temperate regions, suggests its high adaptation capabilities to different environmental conditions. Furthermore, its occurrence in intermediate salinity conditions (25 PSU) in the Venice Lagoon suggests high salinity tolerance, a trait commonly exhibited by successful invaders (e.g. see Lejeusne et al., 2014; Hobbs et al., 2015).

*Stenothoe georgiana* is not the only *Stenothoe* species with invasion potential. For example, *Stenothoe valida* Dana, 1852 presents a cosmopolitan distribution and is considered as an introduced or cryptogenic species in the Eastern Pacific Coast of North America, Hawaii, Gulf of Mexico, New Zealand, Australia and Spain (Fotinoff et al., 2009 –NEMESIS). Another example is the case of the *Stenothoe gallennis* species complex, with some species of the complex frequently associated with fouling communities in port habitats, like *Stenothoe crenulata* Chevreux, 1908 (see Carlton & Eldredge, 2009; Carlton et al., 2017). Although morphological evidence supports the conspecificity of *S. georgiana* populations (see taxonomical remarks section), molecular evidence is needed to confirm this species as a neo-cosmopolitan species. Similarly, future molecular studies are necessary to understand the invasion pathway of *S. georgiana* in Europe and other introduced regions. For example, such studies could confirm whether *S. georgiana* entered the Mediterranean through the Strait of Gibraltar, as suggested by the current distribution of the species (i.e. from its absence in the Red Sea and the Eastern Mediterranean Sea).

**Lesson from *S. georgiana*: taxonomical expertise, scientific cooperation and efficient monitoring programs**

In marine bioinvasion science, the continuous improvement and updating of the taxonomic knowledge provide the foundation for early detection of invaders, in order to develop effective management strategies and limit their further spreading. Contrarily, insufficient taxonomical expertise and poor communication between taxonomists and researchers or professionals involved in marine alien species monitoring can lead to mistakes in species’ identification, with introduced species often being either overlooked or mistakenly identified as common native species in the area. This causes under-reporting of introduced species (see discussion in Carlton & Fowler, 2018) in technical reports, and in national inventories and databases, which are essential tools for bioinvasion management providing the basis for decision-making.

Unfortunately, invertebrate taxonomy is currently experiencing a dramatic decline. In most parts of the world, museums, research centers and academia are all suffering a loss of professional taxonomists (see Coleman, 2015), a high percentage of whom are nearing retirement, and are unlikely to be replaced due to low recruitment of emerging scientists into this discipline (Guerra-Garcia et al., 2008). Taking into account the long period necessary for training taxonomists, this decline of professional experts poses a threat for present and future marine bioinvasions research and management. Also, experts themselves sometimes fail in promoting their research to both colleagues and the general public (Hutchings, 2017); which is accentuated by the underestimation of valuable taxonomic contributions (usually relegated to lower impact journals). In fact, critical updated taxonomic advancements are sometimes ignored or not properly incorporated into alien taxa inventories (see discussion in Marchini & Cardeccia, 2017). Additionally, routine monitoring from local environmental agencies is often constrained by very tight deadlines, with little opportunity for in-depth examination of the more taxonomically challenging taxa constituting a high-risk of overlooking new alien species arrivals.

Consequently, we advocate the importance of taxonomy, and communication between taxonomists and those monitoring marine environments for improved alien species management. In order to ensure that alien species information is effectively disseminated at all levels, the following tools should be promoted:

A. increase opportunities for exchanges of knowledge between senior taxonomists and early-career taxonomists or para-taxonomists, for example by the provision of visiting fellowships/grants to universities, museums, and summer/winter schools on taxonomy;

B. establishment of local/national taxonomy networks, such as ‘SCAMIT’ in the United States (https://www.scamit.org/), and ‘MOTax’ in Italy (http://www.szn.it/index.php.it/ricerca/infrastruttur-di-ricerca-per-le-risorse-biologiche-marine/piattaforme-tecnologiche/tassonomia-clas-sica-e-molecolare-motax); these networks ensure support in cases of difficult species identifications;

C. support the participation of national experts to international events, e.g. specialist workshops/conferences on taxonomy (such as the ICA – International Colloquium of Amphipoda), and on bioinvasions, in order to establish connections and facilitate information exchanges with international colleagues;

D. increased opportunities for data/information exchanges between research scientists and environmental management agencies through workshops and stakeholders meetings, in order to cross-check advancements on knowledge of alien species;

E. more frequent updating of standardized, global alien species databases such as WRIMS (http://www.marinespecies.org/introduced/), AquaNIS (http://www.corpi.ku.lt/databases%20index.php/aquannis/) and EASIN (https://easin.jrc.ec.europa.eu/easin). Ideally, new species records being accepted for publication should immediately be forwarded to database managers, in order to ensure an early update of open-access databases.

In addition, we call attention to the number of confusing genera awaiting revision in the Amphipoda group (Navarro-Barranco, 2015; Bonifazi et al., 2018). Certainly, findings from the present study would not have been
possible without the foundational work of Krapp-Schick- 
el (2015), which provided a comprehensive key to worldwide species of Stenothoe. Owing to that work, 
specimens were successfully identified as a Stenothoe 
species previously unrecorded in the Macaronesian, At-
lanto-Mediterranean and Australian coastal areas rather 
than being erroneously attributed to congeneric species 
or remaining unidentified.

Furthermore, the time-lag between new arrivals and 
documentation of an invader is far too long to serve man-
gement (see Crooks et al., 2005, 2011). This tempo-
rnal window could be reduced by enhanced cooperation 
and communication amongst the scientific community. 
Sometimes, academic publishing requirements and hy-
per-competition push researchers to avoid disseminating 
their new alien records prior to publication. Instead, we 
highly recommend participation with integrative and col-
lective studies encompassing global records, rather than 
more local, individual publications. In the present case of 
S. georgiana, several factors notably contributed to the 
cooperative early detection of a hidden invader. Firstly, a 
key taxonomic revision drew light to the correct identi-
ties of doubtful specimens. Secondly, the willingness of 
exchanging opinions and sharing knowledge among col-
leagues raised the flag on the presence of this invader in 
several distinct regions. And lastly, open communication 
within the amphipodologist group allowed the accelera-
tion of its identification and revealed its introduced dis-
tribution range as soon as possible. If the information had 
not been circulated quickly and effectively, this NIS may 
have gone overlooked, and several publications would 
have probably been submitted without acknowledging 
it presence. This would then have had consequences on 
studies that were analysing and modelling the richness of 
NIS (e.g. Ferrario et al., 2017; Ulman et al., 2019).

Yet, a time lag of 7 years passed between the first col-
lection of samples in which S. georgiana was present (in 
2010), and the first published record in the introduced 
range (Fernandez-Gonzalez & Sanchez-Jerez, 2017), not 
surprising considering the small size and taxonomic dif-
ificulty of this taxon. In order to minimize the detection 
time-lag of small mobile epifauna, it is urgent to provide the 
scientific community with a standardized and quan-
titative monitoring methodology for fouling commu-
nities. This methodology should: i) facilitate sampling 
processing and identification at both the morphological 
and molecular levels, ii) allow comparisons across spa-
tio-temporal scales and different habitats (e.g. artificial 
and natural), and iii) reduce sampling bias when absence 
records are provided. We thus strongly encourage sci-
entific colleagues to include absence data of invaders in 
their research. This is important for properly addressing 
the propagation rate and range of introduced species, as 
well as their invasion potential.

In light of this case study, we outline the importance of: 
1) promoting the relevance of taxonomy on bioinvai-
ion research among colleagues, funding agencies and 
general public, 2) building strong expert networks at 
theregional, national and international levels; ensuring 
the effective transfer of knowledge among taxonomists,
molecular scientists and invasion ecologists, and 3) im-
plementing efficient standardized monitoring methodol-
gies to facilitate early detection of introduced species.

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-COMPETE and by National Portuguese Funds through 
FCT - Foundation for Science and Technology under the 
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### APPENDIX

Table 1. List of localities sampled by the authors where (to date) presence of *Stenothoe georgiana* Bynum & Fox, 1977 have not been detected.

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<td></td>
<td>Karpaz Gate Marina, Eastern Mediterranean</td>
<td>21 Jun 2016</td>
<td>35.55° N; 34.23° E</td>
<td>Ulman et al., 2017</td>
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<td>Famagusta harbor, Eastern Mediterranean</td>
<td>13 Jun 2016</td>
<td>35.12° N; 33.95° E</td>
<td>Ulman et al., 2017</td>
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