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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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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; Galil *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 crypsis 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 (Dafforn *et al.*, 2012; Airoidi *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; Mermillod-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 & Cardeccia, 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 (Fernandez-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 (thereafter 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 of 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 Chiaje, 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.

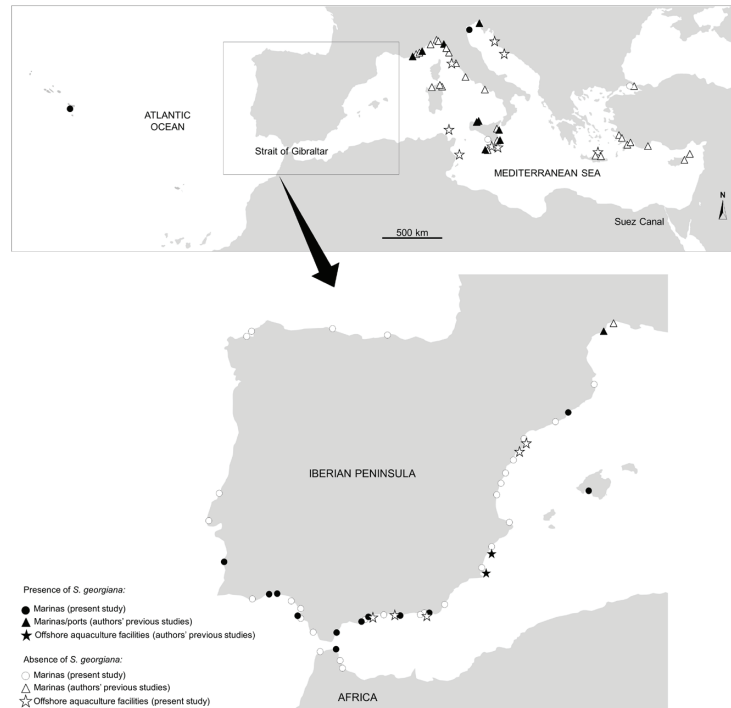


Fig. 1: Presence/absence of *Stenothoe georgiana* in localities studied by the authors. Previous records are taken from Fernández-González & Sánchez-Jerez, 2017; Ferrario *et al.* 2017, 2018; Ulman *et al.*, 2017, 2019; Lo Brutto *et al.*, 2018. See also Table 2 for presence records and Supplementary material for absence records.

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 Fernández-González & Sánchez-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; Fernández-González *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*. Similarly, from April 2014 until November 2015, marinas across the northern rim of the Mediterranean Sea were

sampled for their biofouling compositions focusing on alien species in Malta, Greece and Turkey. A hand-held rigid net with one sharpened edge was used 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 the Lagoon of Venice (Italy, North Adriatic Sea), a sampling survey was conducted in July 2017 along the estuarine gradient of the River Dese, within the northern part of the lagoon; using a hand-held net, eight stations were sampled focusing on the subtidal portion of wooden piles, which mark the navigable canals. Temperature and salinity were measured during both low and high tidal conditions. Additionally, samples were obtained from an offshore platform located in the North Adriatic Sea, at 7.8 nautical miles from the coast. Located just in front of the Lagoon of Venice, this platform is a stop-over site for cruise and commercial ships, while they are waiting for access permission into the Lagoon, and is one of the sites where the Regional Agency for Environmental Protection and Prevention of the Veneto (ARPAV) regularly conducts monitoring surveys. In March and September 2019, 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.

Azores (Macaronesia)

In spring of 2013, 2014 and 2015, surveys of the fouling communities associated with boat hulls and pontoons

were conducted in Ponta Delgada (Azores), as a part of 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.

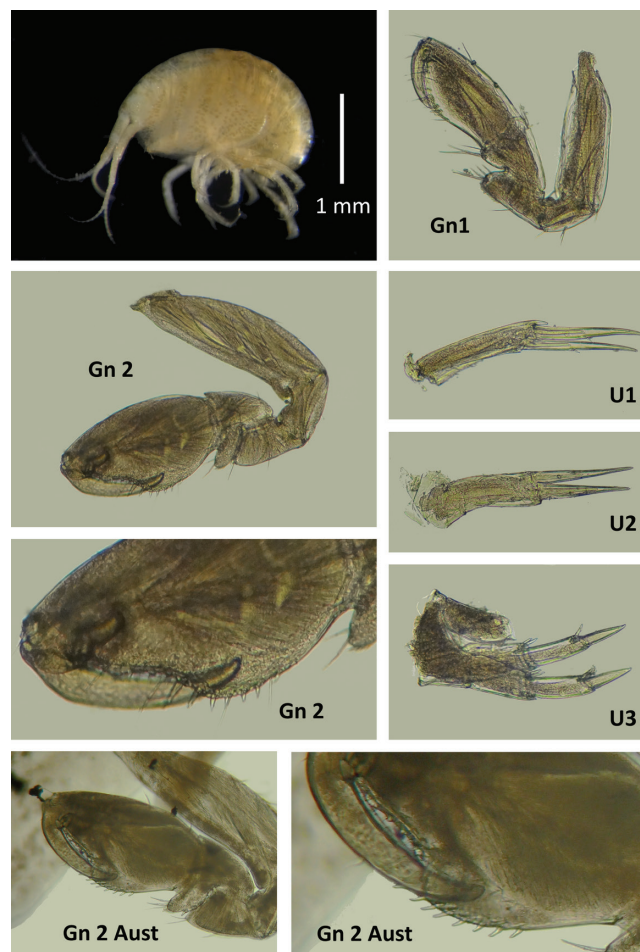


Fig. 2: *Stenothoe georgiana* Bynum & Fox, 1977. Lateral view, gnathopod 1 (Gn1), gnathopod 2 (Gn2) with propodus detail, uropods 1, 2 and 3 (U1, U2, U3) of males from Southern Iberian Peninsula. Gnathopod 2 with propodus detail (Gn2 Aust) of male from Sydney, Australia.

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 specialistic 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 convex, palm defining angle bearing 4 spines and dactyl fitting palm; U1 peduncle slightly longer than rami, 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 cusps (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 Almería, 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⁻²).

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.

Date	Country	Localities	Collected from	Vector	Author of record
1935	USA	Sapelo Island (Georgia)	Offshore, 11 miles off-coast	-	Identified by Mr. Clarence R. Shoemaker GBIF.org (2019) ¹
-	USA	Chesapeake Bay and Norfolk (Virginia); New River, Shackelford Bank and Beaufort (North Carolina); St. Catherine Sound (Georgia); Sarasota Bay, Tampa Bay and Loggerhead Key (Florida)	-	-	Mr. Clarence R. Shoemaker, unpublished data in Bynum & Fox (1977)
-	Brazil	Rio de Janeiro and Sacco São	-	-	Mr. Clarence R. Shoemaker, unpublished data in Bynum & Fox (1977)
1957-1966	USA	Institute of Marine Science pier station, Drum Inlet station, Lockwoods Folly Inlet station (North Carolina), North Carolina,	Nocturnal surface macroplankton in estuaries	-	Williams & Bynum (1972) in Bynum & Fox (1977) (as ' <i>Stenothoe</i> sp.' and ' <i>S. minuta</i> ')
1971	USA	Chesapeake Bay (Virginia), Tybee Inlet and Sebastian Inlet (Florida) *	Fouling community on a pier	-	Bynum & Fox, (1977)
1975	USA	North Carolina estuaries	Fouling community and shelly bottom	-	Fox & Bynum (1975)
1980-1981	USA	Charleston (South Carolina), Sapelo Island (Georgia), Jacksonville (Florida)	Stomach contents of <i>Archosargus probatocephalus</i> at offshore reef habitats	-	Sedberry (1987)
1981-1985	USA	South Carolina, shallow waters	Pilings and Seawalls, creeks and sounds	-	Fox & Ruppert (1985)
1982	USA	St. Catherine's Island (Georgia)	Sponges and corals at hard-bottom area	-	Wendt <i>et al.</i> (1985)
April 1984 - March 1985	USA	Sebastian Inlet (Florida)	Sabellariid worm <i>Phragmatopoma lapidosa</i> at rock jetties	-	Nelson & Demetriades (1992)
1985-1987	USA	South Carolina	Stomach contents of <i>Chaetodipterus faber</i> in shallow nearshore habitats (sponges, soft corals); estuarine habitats; and artificial reefs and jetties	-	Hayse (1990)
2004	USA	Tampa Bay (Florida)	Artificial reefs dominated by mussels and oysters	-	Dix <i>et al.</i> (2005)
2010	Spain	Alicante and Murcia, off-coast sea bass-sea bream aquaculture facilities	Fouling dominated by algae, hydroids and mussels	AQ	Fernandez-Gonzalez & Sanchez-Jerez (2017)
2011	Spain	Alicante, off-coast sea bass-sea bream and oyster aquaculture facilities	Fouling dominated by algae, mussels and anemones	AQ	Fernandez-Gonzalez & Sanchez-Jerez (2017)
2012	Chile	Los Lagos and Atacama	Salmonid farms	AQ*	Pérez-Schultheiss & Ibarra (2017)
2013	Italy	Lerici marina	Fouling communities on dock walls and floating pontoons	SF (rb)	Ferrario <i>et al.</i> (2017)
2014	Italy	Porto Torres harbour	Fouling communities on the subtidal level of dock walls	SF	Ferrario <i>et al.</i> (2017)
2015	Mexico	Puerto Progreso (Yucatan)	Macroalgae associated to buoys, chains, pilings and seawalls	SF*	Winfield <i>et al.</i> (2015)

continued

Table 1 continued

Date	Country	Localities	Collected from	Vector	Author of record
2015	France	Port du plaisance du Port Camargue (Le Grau-du-Roi), Port Principal du Cad d'Agde (Agde) and Port Vauban (Antibes)	Marina fouling at Port Camargue; recreational vessel hull-fouling at Cap d'Agde and Port Vauban	SF (rb)	Ulman <i>et al.</i> (2017)
2015	Italy	Porto Turistico Marina Piccola di Sorrento (Sorrento, Campania)	Marina fouling and vessel hull-fouling	SF(rb)	Ulman <i>et al.</i> (2017)
2016	USA	Tampa Bay (Florida)	Artificial reefs dominated by barnacles, sponges ascidians and bryozoans		Karlen <i>et al.</i> (2017)
2016	Italy	Marina Villa Igica (Palermo), Porto Grande (Siracusa), Porto dell'Etna (Riposto), Marina di Cala del Sole (Licata) (Sicily)	Marina fouling and vessel hull-fouling at Palermo and Licata; marina fouling at Siracusa; hull-fouling at Riposto	SF(rb)	Ulman <i>et al.</i> (2017)
2016	France	St. Tropez marina (Cote d'Azur)	Sailing boat hull-fouling	SF(rb)	Ulman <i>et al.</i> (2017)
2016	Malta	Valletta	Marina fouling at Grand Harbour Marina	SF(rb)	Ulman <i>et al.</i> (2017)
2017	Slovenia	Harbour of Piran	Dock fouling	SF	Ferrario <i>et al.</i> (2018)
2017	Italy	Porto di Palermo (Palermo, Sicily)	Rope fouling	SF	Lo Brutto <i>et al.</i> (2018)

¹The 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.

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 georgiana* 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, Pérez-Schultheiss & Ibarra, 2017 and present study). Furthermore, preliminary molecular analysis indicates that populations from the Iberian Peninsula and Australia belong to the same species (Cabezas *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

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.

Country	Locality	Date	Coordinates	Substrates
PT	Sines marina, Alentejo	9 May 2011	37.95° N; 8.87° W	Pontoons (<i>Bugula neritina</i>)
	Ponta Delgada marina, São Miguel, Azores	22 May 2013, 21 April 2014, 10 March 2015	37.73° N; 25.65° E	Boat hulls, pontoons
ES	Isla Canela marina, Huelva	26 June 2017 (Absent in 2011)	37.19° N; 7.34° W	Pontoons (<i>Bugula neritina</i>)
	El Rompido marina, Huelva	26 June 2017 (Absent in 2011)	37.22° N; 7.13° W	Pontoons (fouling communities)
	Puerto América marina, Cádiz	17 May 2011, 2 July 2017	36.54° N; 6.28° W	Pontoons (fouling communities)
	La Línea marina, Cádiz	15 May 2011, 30 June 2017	36.16° N; 5.36° W	Pontoons (fouling communities)
	Fuengirola marina, Málaga	29 June 2017 (Absent in 2011)	36.54° N; 4.62° W	Pontoons (fouling communities)
	Málaga marina, Málaga	3 July 2011, 29 June 2017	36.72° N; 4.41° W	Pontoons (<i>Bugula neritina</i>)
ES	Motril marina, Granada	2 July 2011, 28 June 2017	36.72° N; 3.53° W	Pontoons (<i>Bugula neritina</i>)
	Almería marina, Almería	27 June 2017 (Absent in 2011)	36.83° N; 2.46° W	Pontoons (fouling communities)
	Barcelona marina, Barcelona	26 June 2011	41.38° N; 2.18° E	Pontoons (<i>Bugula neritina</i>)
	Palma marina, Baleares	18 December 2011	39.57° N; 2.63° E	Pontoons (<i>Eudendrium racemosum</i>)
	Ceuta, North Africa	September 2015, January 2016 (Absent in 2011)	35.89° N; 5.31° W	Pontoons (see Results)
IT	Venice lagoon	12 June 2017	45.47° N; 12.41° E	Wooden piles
	Adriatic Sea (off the Venice Lagoon)	12 March 2019; 16 September 2019	45.31° N; 12.51° E	Offshore platform pillar
AU	Chowder Bay, Sydney	3 December 2017	33.84° S; 151.25° E	Piers (Artificial collectors)

Locality: Puerto América marina, Cádiz, SPAIN (36° 32' 29.2" N; 6° 17' 02.4" W)	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Noe	Dec
Substrates: <i>Eudendrium racemosum</i> <i>Amathia verticillata</i>	✓			✓	✓	✓	✓	✓	✓	✓	✓	✓

Locality: Palma marina, Baleares, SPAIN (39° 34' 2" N; 2° 37' 56" E)	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Noe	Dec
Substrate: <i>Eudendrium racemosum</i>	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓

distribution through anthropogenic dispersal (Darling & Carlton, 2018).

The voucher materials have been deposited in Museo Nacional de Ciencias Naturales de Madrid (MNCN, Madrid, Spain), Museo di Storia Naturale di Venezia (MSNVE, 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 *E. 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 *B. 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

(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 macrofouling 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 Saco São 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

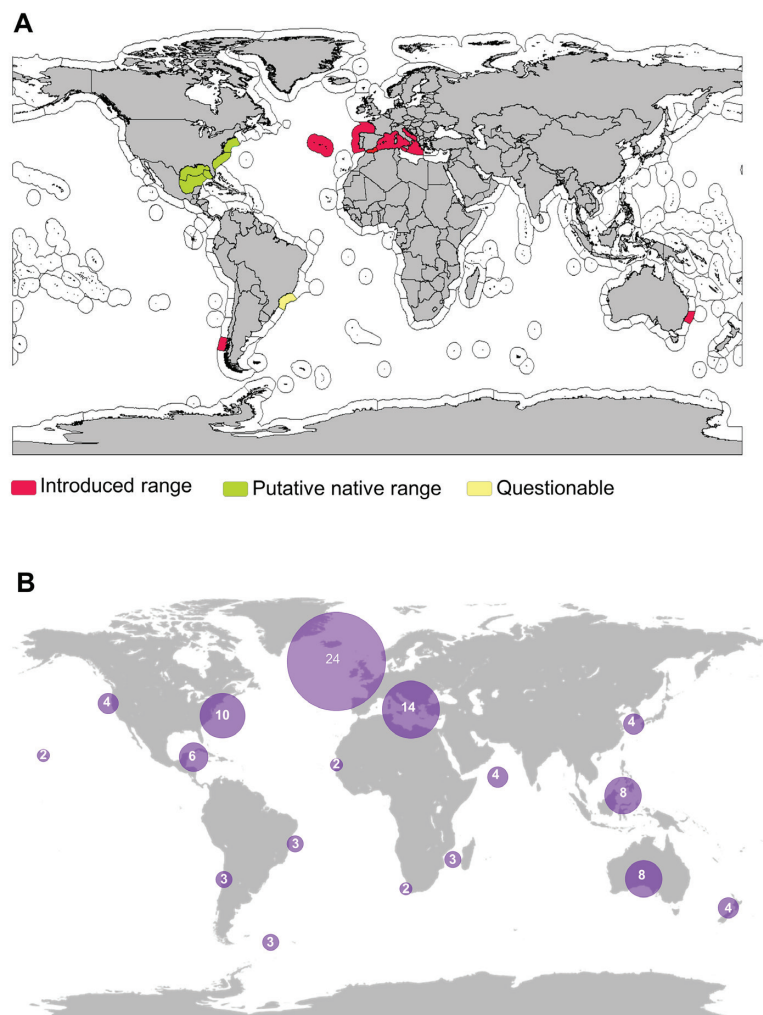


Fig. 3: a) Updated worldwide distribution of *Stenothoe georgiana* including its introduced range (in red) and its putative native range (in green). Records from Brazil are considered questionable (in yellow). Information based on data showed in Tables 1 and 2. b) Number of *Stenothoe* spp. recorded 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 Lejeune *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 (Fofonoff *et al.*, 2009 –NEMESIS). Another example is the case of the *Stenothoe gallensis* 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-García *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 taxonomy 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/infrastrutture-di-ricerca-per-le-risorse-biologiche-marine/piattaforme-tecnologiche/tassonomia-classica-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. specialistic 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/aquanis/>) 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-Schickel (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, Atlanto-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 management (see Crooks *et al.*, 2005, 2011). This temporal window could be reduced by enhanced cooperation and communication amongst the scientific community. Sometimes, academic publishing requirements and hyper-competition push researchers to avoid disseminating their new alien records prior to publication. Instead, we highly recommend participation with integrative and collective 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 identities of doubtful specimens. Secondly, the willingness of exchanging opinions and sharing knowledge among colleagues raised the flag on the presence of this invader in several distinct regions. And lastly, open communication within the amphipodologist group allowed the acceleration of its identification and revealed its introduced distribution 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 its 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 collection 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 difficulty 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 quantitative monitoring methodology for fouling communities. This methodology should: i) facilitate sampling processing and identification at both the morphological and molecular levels, ii) allow comparisons across spatio-temporal scales and different habitats (e.g. artificial and natural), and iii) reduce sampling bias when absence records are provided. We thus strongly encourage scientific 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 bioinvasion 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) implementing efficient standardized monitoring methodologies to facilitate early detection of introduced species.

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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.

Country	Locality	Date	Coordinates	Source
PORTUGAL	Nazaré, Marina, Eastern Atlantic	9 May 2011	39.59° N; 9.07° W	Present study
	Cascais Marina, Eastern Atlantic	9 May 2011	38.69° N; 9.42° W	Present study
	Faro Marina, Gulf of Cádiz	11 May 2011; 26 Jun 2017	37.01° N; 7.94° W	Present study
MOROCCO	Tanger, Eastern Atlantic	31 May 2011	35.79° N; 5.81° W	Present study
	Marina Smir, Alboran Sea	30 May 2011	35.75° N; 5.34° W	Present study
	M-Diq, Alboran Sea	30 May 2011	35.68° N; 5.31° W	Present study
	Santander Marina, Bay of Biscay	2 May 2011	43.45° N; 3.82° W	Present study
	Gijón Marina, Bay of Biscay	3 May 2011	43.54° N; 5.67° W	Present study
	A Graña Marina, Eastern Atlantic	7 May 2011	43.48° N; 8.26° W	Present study
	A Coruña Marina, Eastern Atlantic	4 May 2011	43.37° N; 8.39° W	Present study
	Chipiona Marina, Gulf of Cádiz	17 May 2011; 1 Jun 2017	36.74° N; 6.43° W	Present study
	Rota Marina, Gulf of Cádiz	17 May 2011	36.62° N; 6.35° W	Present study
	Sancti Petri Marina, Gulf of Cádiz	17 May 2011	36.40° N; 6.21° W	Present study
SPAIN	Barbate harbour, Gulf of Cádiz	17 May 2011; 1 Jun 2017	36.19° N; 5.93° W	Present study
	BenaImádena Marina, Alboran Sea	15 May 2011	36.43° N; 4.51° W	Present study
	Málaga, Alboran Sea (aquaculture facilities)	May 2010; Nov 2012; Sep 2014	36.71° N; 4.36° W	Present study
	La Caleta Marina, Alboran Sea	3 Jul 2011; 28 Jun 2017	36.75° N; 4.07° W	Present study
	Salobreña, Alboran Sea (aquaculture facilities)	May 2010	36.74° N; 3.61° W	Present study
	Almerimar Marina, Alboran Sea	1 Jul 2011	36.70° N; 2.79° W	Present study
	Roquetas de Mar Marina, Alboran Sea	1 Jul 2011	36.76° N; 2.61° W	Present study
	Almería, Alboran Sea (aquaculture facilities)	Sep 2014	36.83° N; 2.46° W	Present study
	Carboneras harbour, Western Mediterranean	30 Jun 2011	36.99° N; 1.90° W	Present study
	Marina Salinas, Torrevecija, Western Mediterranean	29 Jun 2011	37.97° N; 0.68° W	Present study
	Alicante Marina, Western Mediterranean	29 Jun 2011; 14 Nov 2016	38.34° N; 0.49 W	Present study
	Dénia Marina, Western Mediterranean	28 Jun 2011	38.85° N; 0.11° W	Present study
	Valencia Marina, Western Mediterranean	28 Jun 2011	39.43° N; 0.33° W	Present study

continued

Table 1 continued

Country	Locality	Date	Coordinates	Source
SPAIN	Burriana Marina, Western Mediterranean	28 Jun 2011	39.86° N; 0.07° W	Present study
	Oropesa Marina, Western Mediterranean	28 Jun 2011	40.08° N; 0.13° E	Present study
	Benicarló Marina, Castellón Western Mediterranean	27 Jun 2011	40.42° N; 0.43° E	Present study
	Tarragona Marina, North Western Mediterranean	27 Jun 2011	41.1° N; 1.25° E	Present study
	Tarragona A, North Western Mediterranean (aquaculture facilities)	Oct 2010	40.88° N; 0.81° E	Present study
	Tarragona B, North Western Mediterranean (aquaculture facilities)	Oct 2010	40.53° N; 0.59° E	Present study
	L'Estartit Marina, North Western Mediterranean	25 Jun 2011	42.05° N; 3.21° E	Present study
	Port de la Grande-Motte, North Western Mediterranean	2 Nov 2016	43° 33' N; 4° 5' E	Ulman <i>et al.</i> , 2017
	Cogolin Marina, North Western Mediterranean	1 Apr 2016	43.55° N; 4.08° E	Ulman <i>et al.</i> , 2017
	Sainte-Maxime Marina, North Western Mediterranean	1 Apr 2016	43.3° N; 6.63° E	Ulman <i>et al.</i> , 2017
FRANCE	Cannes Le Vieux Port, North Western Mediterranean	19 Apr 2015	43.53° N; 7.03° E	Ulman <i>et al.</i> , 2017
	Port de Villefranche, North Western Mediterranean	22 Nov 2016	43.7° N; 7.3° E	Ulman <i>et al.</i> , 2017
ITALY	Alassio Marina, North-Western Mediterranean	27 May 2016	44.02° N; 8.18° E	Ulman <i>et al.</i> , 2019
	Genoa harbour, North-Western Mediterranean	29 Jul 2013	44.4° N; 8.93° E	Ferrario <i>et al.</i> , 2017
	Santa Margherita Ligure Marina, North-Western Mediterranean	6 Jul 2013	44.33° N; 9.22° E	Ferrario <i>et al.</i> , 2017
	La Spezia harbour, Ionian Sea	11 Jul 2013	44.02° N; 9.83° E	Ferrario <i>et al.</i> , 2017
	Leghorn harbour, Ionian Sea	28 Jun 2013	43.55° N; 10.3° E	Ferrario <i>et al.</i> , 2017
	Viareggio harbour, Ionian Sea	27 Jun 2013	43.87° N; 10.25° E	Ferrario <i>et al.</i> , 2017
	Follonica, Ionian Sea (aquaculture facilities)	Apr 2011	42.91° N; 10.64° E	Present study
	Terre Rosse Marina, Ionian Sea	26 Jul 2016	42.95° N; 10.55° E	Ulman <i>et al.</i> , 2019
	Scarlino Marina, Ionian Sea	27 Jul 2016	42.88° N; 10.78° E	Ulman <i>et al.</i> , 2019
	Punta Ala Marina, Ionian Sea	27 Jul 2016	42.80° N; 10.73° E	Ulman <i>et al.</i> , 2019
Castelsardo harbour, North-Western Mediterranean	Olbia harbour, Ionian Sea	10 Jun 2014	40.92° N; 9.52° E	Ferrario <i>et al.</i> , 2017
	Porto Rotondo Marina, Ionian Sea	11 Jun 2014	40.92° N; 8.7° E	Ferrario <i>et al.</i> , 2017
	Porto Turistico di Roma, Ionian Sea	9 Jun 2014	41.03° N; 9.55° E	Ferrario <i>et al.</i> , 2017
	Porto Turistico di Roma, Ionian Sea	12 Jul 2015	41.73° N; 12.25° E	Ulman <i>et al.</i> , 2017
	Casamicciola Marina, Ionian Sea	1 Aug 2015	37.75° N; 15.9° E	Ulman <i>et al.</i> , 2017

continued

Table 1 continued

Country	Locality	Date	Coordinates	Source
ITALY	Porto dell'Etma, Riposto, Central Mediterranean	18 Sep 2016	37.75° N; 15.2° E	Ulman <i>et al.</i> , 2017
	Marzamemi Marina, Central Mediterranean	8 Oct 2016	36.73° N; 15.12° E	Ulman <i>et al.</i> , 2017
	Marina di Ragusa, Sicily Channel, Central Mediterranean	15 Dec 2017	36.73° N; 14.53° E	Present study
MALTA	Qwara (aquaculture facilities)	Oct 2010	35.62° N; 14.70° E	Present study
	Il-Hofriet (aquaculture facilities)	Feb 2011	35.40° N; 14.94° E	Present study
TUNISIA	Msida Yatch Marina, Central Mediterranean	1 Jul 2016	35.9° N; 14.5° E	Ulman <i>et al.</i> , 2017
	Ghar el Melh (aquaculture facilities)	May 2013	37.32° N; 10.28° E	Present study
	Mahdia (aquaculture facilities)	May 2013	35.46° N; 11.09° E	Present study
CROATIA	Brac (aquaculture facilities)	Oct 2010	43.30° N; 16.46° E	Present study
	Ugljan (aquaculture facilities)	Oct 2010	44.03° N; 15.22° E	Present study
GREECE	Crete (aquaculture facilities)	Sep 2010	35.58° N; 25.25° E	Present study
	Old Venetian harbour, Heraklion, Aegean Sea	1 Nov 2015	35.35° N; 25.13° E	Ulman <i>et al.</i> , 2017
	Agios Nikolaos Marina, Aegean Sea	18 Nov 2015	35.18° N; 25.13° E	Ulman <i>et al.</i> , 2017
	Mandraki Port, Rhodes, Aegean Sea	2 Jun 2016	36.45° N; 28.23° E	Ulman <i>et al.</i> , 2017
	Ataköy Marina, Istanbul Marmara Sea	20 Aug 2015	41.00° N; 29.52° E	Present study
TURKEY	Setur Kalamış Marina, Istanbul, Marmara Sea	28 Aug 2015	40.98° N; 29.03° E	Ulman <i>et al.</i> , 2017
	Milta Bodrum Marina, Aegean Sea	9 Sep 2015	37.03° N; 27.43° E	Ulman <i>et al.</i> , 2017
	Data Marina, Aegean Sea	10 Oct 2015; 13 May 2016	26.72° N; 27.68° E	Ulman <i>et al.</i> , 2017
	Setur Marmaris Netsel Marina, Aegean Sea	14 Sep 2015	36.85° N; 28.28° E	Ulman <i>et al.</i> , 2017
	Eçe Marina, Fethiye, Eastern Mediterranean	19 Sep 2015	36.62° N; 29.1° E	Ulman <i>et al.</i> , 2017
CYPRUS	Setur Finike Marina, Eastern Mediterranean	18 May 2016	36.30° N; 30.15° E	Ulman <i>et al.</i> , 2017
	Karpaz Gate Marina, Eastern Mediterranean	21 Jun 2016	35.55° N; 34.23° E	Ulman <i>et al.</i> , 2017
	Famagusta harbor, Eastern Mediterranean	13 Jun 2016	35.12° N; 33.95° E	Ulman <i>et al.</i> , 2017