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Quick spreading of the exotic amphipod *Laticorophium baconi* (Shoemaker, 1934): another small stowaway overlooked?

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Abstract

Studies of non-indigenous species (NIS) often tend to focus on medium and large-sized taxa with potential for remarkable ecological and/or economic impact, whereas the early detection of small invertebrates is often delayed due to taxonomic challenge, lack of consistent, standardised monitoring efforts and limited funding. This study represents the first records of the marine amphipod *Laticorophium baconi* (Shoemaker, 1934) in Morocco, Tunisia, Corsica (France), Italy, Greece, Egypt, Saudi Arabia and New Caledonia (France). Furthermore, it reports an expansion of its known distribution in Portugal (earliest and northernmost record for the country and first record for Macaronesia), Spain (earliest record for Atlantic and Mediterranean European waters), and Australia (first record for Indian Ocean). Recreational boating and commercial shipping, mainly through hull fouling and secondarily ballast waters, are proposed as vectors for introduction and secondary spread of *L. baconi*. The following traits, analysed during the present study, could contribute to its invasive potential: (i) quick and extensive spread of the species worldwide, (ii) high densities in marinas, harbours, hull fouling and other artificial habitats, including aquaculture facilities and floating debris, (iii) high ability for short-term colonisation of empty artificial niches, (iv) diet based on detritus suggesting an opportunistic feeding behaviour, and (v) population survival during seasonal fluctuations in different regions. Taxonomic expertise and scientific collaboration, based on multidisciplinary networks of experts, are crucial for the early detection, distribution updates, and risk assessment of small and overlooked stowaways in marine environments.

Keywords: early detection; non-indigenous; Amphipoda; taxonomic expertise; scientific collaboration; anthropogenic dispersal.

Introduction

The introduction of non-indigenous species (NIS) is one of the main threats to global biodiversity (Bax *et al.*, 2003; Pyšek *et al.*, 2020; Ruiz *et al.*, 2020; IPBES, 2023; Ros *et al.*, 2023). To better understand the role of NIS in structuring marine communities and to develop effective management strategies, it is crucial to have a comprehensive and accurate understanding of the global distribution of these species (Marchini & Cardeccia, 2017). Unfortunately, NIS knowledge in marine environments is limited by several factors, including the lack of historical records, few long-term monitoring efforts, funding, long time-lags in detection and reporting, uncertain biogeographical information, and scarcity of specialist taxonomists (Coleman, 2015; Ojaveer *et al.*, 2015; Galil *et al.*, 2018; Zenetos *et al.*, 2017, 2019). Managing NIS becomes particularly difficult once a species is established, underscoring the importance of prevention and early detection (Bergstrom *et al.*, 2018; Carvalho *et al.*, 2023). Therefore, rigorous baseline surveys and collaborative monitoring programmes are required for detecting NIS (Lehtiniemi *et al.*, 2015; Tsiamis *et al.*, 2021; Galanidi *et al.*, 2023). However, most efforts usually focus on conspicuous or medium and large-sized species with clear economic and/or ecological impacts, while overlooking smaller vagile invertebrates (Martínez-Laiz *et al.*, 2020; Cuthbert *et al.*, 2021).

Among vagile fauna, peracarid crustaceans are widely used as environmental indicators (Navarro-Barranco *et al.*, 2020), and have been proposed as a target group for assessing the level of biocontamination (Saenz-Arias *et al.*, 2022a, b). Within peracarids, amphipods are considered as a model group to explore biological invasions in marine ecosystems (Cabezas, 2022). Amphipods are of special concern since: (i) they constitute one of the dominant taxa in shallow-water marine ecosystems, with important ecological roles (Bell, 1991); (ii) they lack pelagic planktonic larval stages and so large dispersal movements can hardly be explained by natural causes (Arfianti & Costello, 2020); (iii) some species are prone to inhabit fouling communities and are particularly well-suited for transport on vessel hulls as biofouling (Martínez-Laiz *et al.*, 2022); and (iv) there is a large availability of taxonomic reports and faunistic inventories including marine amphipods from all world regions (Horton *et al.*, 2023). However, it is likely that the actual number of non-indigenous amphipods is underestimated mainly due to the presence of cryptogenic species, unresolved taxonomy of cryptic species complexes and overlooked introductions (Marchini & Cardeccia, 2017; Martínez-Laiz *et al.*, 2020).

The early detection of certain non-indigenous amphipods in the Mediterranean region, such as the caprellids *Caprella scaura* Templeton, 1836 or *Paracaprella pusilla* Mayer, 1890, has been achieved through distinctive and easily recognizable characteristics (e.g., Ros *et al.*, 2014a), which are strikingly different from those exhibited by related Mediterranean species (e.g., Krapp-Schickel, 1993). However, the time lag between an introduction and its first detection can be significantly delayed in taxonomically challenging non-indigenous amphipods (e.g., *Jassa slatteryi* Conlan, 1990 or *Stenothoe georgiana* Bynum & Fox, 1977), which could be largely overlooked due to misidentifications with morphologically similar native species (Bonifazi *et al.*, 2018; Beermann *et al.*, 2020; Martínez-Laiz *et al.*, 2020). Indeed, Zenetos *et al.* (2019) refer to a significant time lag between detection and publication due to lack of taxonomic expertise. *Stenothoe georgiana* stood out as a primary example of how combining taxonomic expertise, scientific cooperation based on a research network, and efficient monitoring programmes can result in the successful detection of NIS (Martínez-Laiz *et al.*, 2020).

In 2018, *Laticorophium baconi* (Shoemaker, 1934) (Amphipoda: Corophiidae), a small amphipod likely native to the Pacific coast of North and Central America (Shoemaker, 1934, 1949; Bousfield & Hoover, 1997; Fofonoff *et al.*, 2018), was found inhabiting fouling communities on mooring buoys of the marina Sant Carles de la Ràpita, Tarragona, on the Spanish Mediterranean coast (Gouillieux & Sauriau, 2019) (Table 1). This was the first record for this species in European waters. Fifty years ago, in 1967, the species was first found outside its native range in Hawaiian Islands, in Kaneohe Bay, Oahu, and Coconut Island Inlet, Hawaii (Barnard, 1970). Later, in 1973 it was reported in Pearl Harbor, Oahu (Coles *et al.*, 1999) and the species was also cited from other harbours of Oahu Island, and at Allen, on Kauai (Fofonoff *et al.*, 2018). The earliest record of *L. baconi* in the Northwest Atlantic corresponds to the Laguna Madre, Texas (McKinney, 1977; LeCroy, 2004) and the species is currently distributed in South Carolina, Florida and Gulf of Mexico (LeCroy, 2004; Winfield *et al.*, 2015). In 1985, *L. baconi* was also collected in Hong Kong, China and considered established there (Hirayama, 1990; Lowry, 2000; Fofonoff *et al.*, 2018; Rahim *et al.*, 2022). In 1990 it was found at Bass Point, New South Wales, Australia (Storey, 1996; Hayes *et al.*, 2005; Ahyong & Wilkens, 2011; Fofonoff *et al.*, 2018). Navarro-Barranco *et al.* (2022) confirmed an established population of the species in New South Wales, reaching very high densities in Chowder Bay, Sydney. In 2001, *L. baconi* was recorded from Rio de Janeiro, Brazil (Valério-Berardo & de Souza, 2009; Serejo & Siquiera, 2018). In 2006, it was collected from the hull of a boat at Opua, New Zealand (McFadden *et al.*, 2007; Ahyong & Wilkens, 2011). In 2007-2009, live specimens of *L. baconi* were found in hull fouling associated to commercial transoceanic vessels in Halifax harbour, Nova Scotia (Sylvester *et al.*, 2011). Although the establishment of the species in the area is not confirmed, this citation represents the northernmost record in the West Atlantic Ocean.

The presence of *L. baconi* in marinas from the Iberian Peninsula (Gouillieux & Sauriau, 2019; Saenz-Arias *et al.*, 2022a,b; Revanales *et al.*, 2023; Ruiz-Velasco *et al.*, 2023) drew attention to the possibility that the species could have been overlooked and/or potentially confused with other Corophiidae species, such as *Apocorophium acutum* (Chevreux, 1908). Early and rapid dissemination of information among colleagues encouraged the re-examination of old samples and the collection of new ones to investigate whether the species was present in the Mediterranean Sea and other world locations. Based on this collaboration, the main objectives of the present study were to: (i) update the worldwide distribution of *L. baconi*, including new records, and taxonomic and ecological remarks; (ii) characterise its population density, short-term colonisation ability, and diet (as a proxy of feeding habits); and (iii) discuss the invasion dynamics and potential vectors of its introduction.

Material and Methods

Sampling surveys to update the known worldwide distribution of L. baconi

Specimens of Corophiidae were collected during several sampling surveys carried out by different research teams between 1996 and 2023 (Fig. 1, Table 2, Text S1). The geographic coverage of samples spanned from the Atlantic Ocean (Portugal, including Macaronesian Islands, and Spain) to the Mediterranean Sea (Spain, Morocco, Tunisia, France, Italy, Greece and Egypt), Red Sea (Saudi Arabia) and Indo-Pacific Ocean (Australia and New Caledonia, France). Samples were mainly collected from artificial substrates in marinas, ports and aquaculture facilities, and occasionally in natural habitats. Different sampling techniques were used, including: sampling of biogenic substrates (basibionts), scrapings of fouling communities, deployment of different artificial collectors (e.g., PVC plates, experimental ropes or fish nets), Rapid Assessment Surveys (RAS) or collection of floating marine debris. After collection, most of the samples were fixed with 70-96% ethanol (occasionally with 4% formalin seawater solution), sieved with a mesh size between 0.5 and 1 mm, sorted and checked for the presence of *L. baconi*. In the case of Saudi Arabia, specimens were not collected but detected with eDNA (see the detailed description of all sampling techniques by country/area in Text S1).

Voucher material of the species is deposited in Museo Nacional de Ciencias Naturales (MNCN, Madrid, Spain), Muséum national d'Histoire naturelle (MNHN, Paris, France), Museo di Storia Naturale dell'Università di Pavia (MSNPV, Pavia, Italy), Museum of Zoology of the University of Palermo (MZPA, Palermo, Italy), Museo di Biologia Marina "Pietro Parenzan", University of Salento (MBMCA, Salento, Italy) and Western Australia Museum (WAM, Perth, Australia) (see Table S1 for a detailed information on the voucher specimens deposited in museums including Museum Catalogue numbers, sampling locations, coordinates, collection date, substrates, and numbers of specimens deposited).

Population density, gut content analyses, colonisation ability and temporal analysis in Spain

Five marinas from southern Spain (Chipiona, Puerto América, La Línea, Fuengirola, and Almería) were selected to characterise population density, dietary contents, and colonisation success of *L. baconi*. Details of marinas (surface area, berths number and density of human population) are included in Guerra-García *et al.* (2021a). The region where the marinas are located (Strait of Gibraltar and surrounding areas) is very important for commercial and recreational maritime traffic, and a hot spot for biological invasions (Drake & Lodge, 2004). Indeed, Puerto América marina has been suggested as an excellent location for studying fouling communities on artificial substrates and an appropriate scenario for monitoring NIS settlement (Ros *et al.*, 2013; Gavira-O'Neill *et al.*, 2018).

For population density estimation, sampling was conducted in June-July 2017 across the five marinas. Three random floating pontoons were haphazardly surveyed at each marina. On each pontoon, three random grids (15 × 15 cm) were set on the submerged portion of pontoons close to the surface and the fouling community

Table 1. Previously known records of *Laticorophium baconi* worldwide. Records from its putative introduced range are shaded. Asterisk indicates the type locality and dash data not available.

Date	Country	Localities	Habitat/substrates	References
1890	USA/Rusia	Bering Sea (Albatross St. 3253)	-	Shoemaker, 1934
1926*	Peru	off coast of Peru, north of Paita	-	Shoemaker, 1934
-	USA	Venice and Santa Monica, southern California	-	Shoemaker, 1934
1935	USA	Newport Bay, California	-	Shoemaker, 1949
-	USA	La Jolla, Corona Del Mar, San Pedro, California	-	Shoemaker, 1949
-	Costa Rica	Salinas Bay	-	Shoemaker, 1949
1962-1964	Ecuador	Galapagos Islands	Intertidal and shallow waters	Barnard, 1979
1962-1964	Mexico	Gulf of California (Puerto Peñasco, Bahía Kino, Bahía de Los Angeles, Topolobampo, Isla Espiritu Santo, Bahía San Evaristo)	Intertidal and shallow waters	Barnard, 1979; García-Madrigal, 2007
1964	Canada	Pidwell Reef, North-Central mainland coast; off Brady's Beach, Southern mainland coast	-	Bousfield & Hoover, 1997
1965	Canada	Hecate Strait, Queen Charlotte Islands	-	Bousfield & Hoover, 1997
1966	USA	Juan de Fuca Strait, Washington	-	Bousfield & Hoover, 1997
1967	USA	Hawaiian Islands (Kaneohe Bay, Oahu and Coconut Island Inlet, Hawaii)	Harbour, alga *Dictyospora* and coral head	Barnard, 1970, 1971
1969	USA	Alaska (Unimak and IzeMbek lagoon, Aleutian Islands)	-	Bousfield & Hoover, 1997
1975	Canada	Gooding Cove, Vancouver Island	-	Bousfield & Hoover, 1997
1976-1978	Canada	Burrard Inlet, Southern mainland coast	-	Bousfield & Hoover, 1997
-	USA	Laguna Madre and Boca Chica Beach, Texas	-	McKinney, 1977; LeCroy, 2004
1985	China	Hong Kong, Daya Bay and adjacent waters	-	Hirayama, 1990; Lowry, 2000; Rahim *et al.*, 2022
1990	Australia	Bass Point, New South Wales	30 m	Storey, 1996; Hayes *et al.*, 2005; Ahyong & Wilkens, 2011; Fofonoff *et al.*, 2018; Australian Museum, 2021

Continued

Table 1 continued

Date	Country	Localities	Habitat/substrates	References
1998-2002	USA	St. Andrew Bay, Florida	Algae and hydroids from jetties	Foster *et al.*, 2004
2001	Brazil	22.91917º S, 43.83472º W, Rio de Janeiro	Intertidal	Valério-Berardo & De Souza, 2009
-	Brazil	Laguna de Itaipú, Rio de Janeiro	-	Serejo & Siqueira, 2018
-	USA	Murrells Inlet, South Carolina	-	LeCroy, 2004
-	USA	Horn Island, Mississippi, Gulf of Mexico	-	LeCroy, 2004
-	USA	Titusville and Hutchinson Island, Florida	-	LeCroy, 2004
-	USA	between Cape Sable and Cape Romano, St. Petersburg and St. Andrew Bay, Florida	-	LeCroy, 2004
2005	Mexico	San Quintin Bay, Baja California	Seagrass *Zostera marina*	Quiroz-Vázquez *et al.*, 2005
2006	New Zealand	Opua, Bay of Islands	Hull fouling (keel of a boat)	McFadden *et al.*, 2007; Ahyong & Wilkens, 2011
2006	USA	Saint Joseph Bay, Florida	Sponge *Amphimedon viridis*	Huang *et al.*, 2008
2007-2009	Canada	Vancouver port	Hull fouling (commercial transoceanic vessels)	Sylvester *et al.*, 2011
2007-2009	Canada	Halifax port	Hull fouling (commercial transoceanic vessels)	Sylvester *et al.*, 2011
2011-2021	Spain	Marinas of Southern Spain: Chipiona, Puerto América, Barbate, La Línea, Fuengirola and Almería	Fouling communities of pontoons	Saenz-Arias *et al.*, 2022a,b
2012	Mexico	Puerto Progreso	Macroalgae from piles and buoys	Martín *et al.*, 2013; Winfield *et al.*, 2015
2017	Australia	Chowder Bay, Sydney	Ropes (artificial habitat units)	Navarro-Barranco *et al.*, 2022
2017	Spain	Marinas of Southern Spain: Chipiona, Rota, Puerto América, Sancti Petri, Conil, Barbate and La Línea	Fouling communities of pontoons	Revanales *et al.*, 2023
2018	Spain	Marina Sant Carles de la Ràpita, Tarragona	Fouling communities on mooring buoy	Gouillieux & Sauriau, 2019
2019	Portugal and Spain	Marinas of Southern Portugal: Albufeira and Faro Marinas of Southern Spain: Isla Canela, Isla Cristina, El Rompido, Rota, Puerto América, Sancti Petri, Málaga and Almería	Fouling communities associated to the polychaete *Sabella spallanzanii*	Ruiz-Velasco *et al.*, 2023

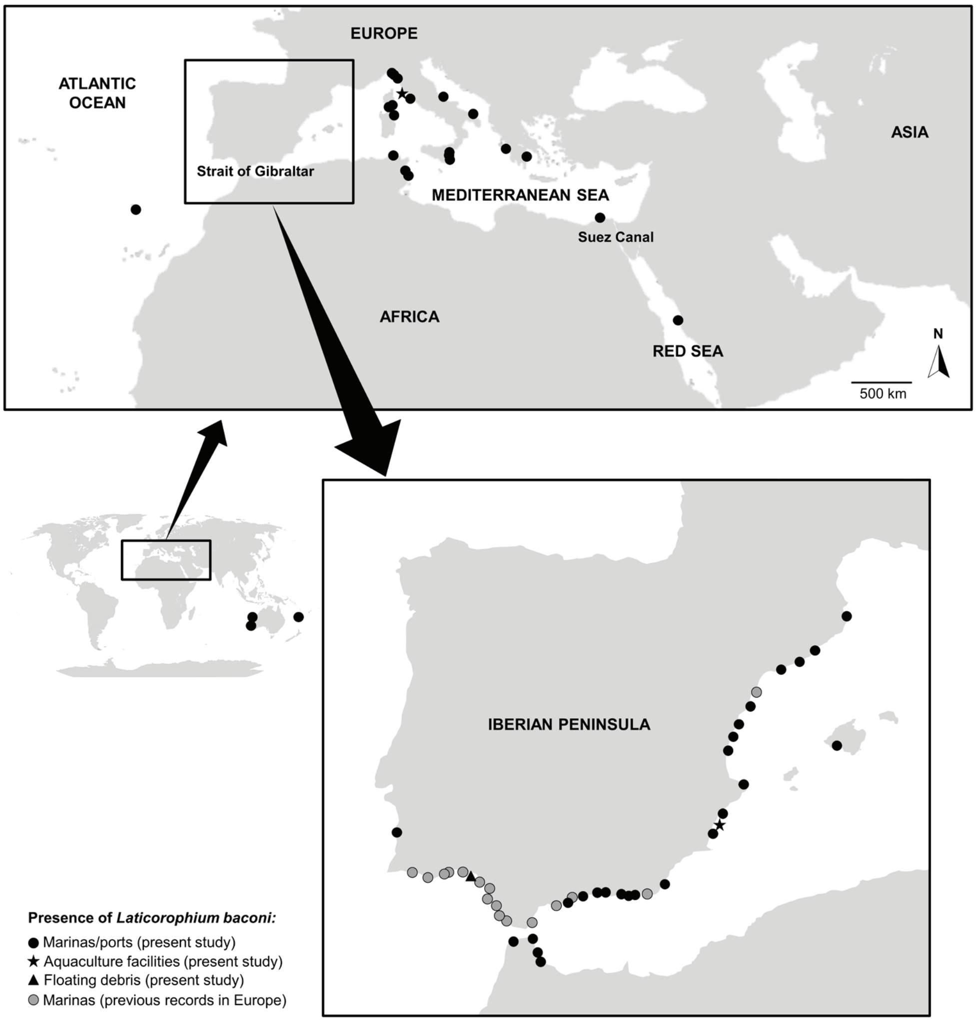

Fig. 1: New records for *Laticorophium baconi* worldwide, with detail on its distribution along the Iberian Peninsula. Previous records of the species in European waters provided by Gouillieux & Sauriau (2019), Saenz-Arias *et al.* (2022a), Revanales *et al.* (2023) and Ruiz-Velasco *et al.* (2023) are also indicated.Although all the records included in the map correspond to ports, marinas, aquaculture facilities and floating debris, one juvenile was found in natural habitats of the Grand récif de Koumac, New Caledonia (see Table 2).

was scraped (Saenz-Arias *et al*., 2022b). Samples were washed through a mesh sieve of 0.5 mm, and the retained fraction was fixed in 96% ethanol. In the laboratory, invertebrate vagile macrofauna was sorted and specimens identified as *L. baconi* separated and counted. Abundances were expressed as individuals per m^2.

To characterise the diet of *L. baconi*, a total of 125 specimens collected during this population density study (25 specimens per marina) were examined. Individuals were analysed following the methodology proposed by Bello & Cabrera (1999), which has been used for dietary characterisation of amphipods (see details in Guerra-García *et al*., 2014; Ros *et al*., 2014b).

To assess the colonisation and recruitment ability of *L. baconi* in artificial substrates, three-dimensionally folded plastic extendable meshes (30 x 50 cm, and 50 ml volume) were randomly placed in each marina (three replicates per marina) submerged at a depth of 1 m. These collectors can recruit a high abundance and diversity of species, including NIS, and constitute a standardised methodology for the study of motile macroinvertebrates in marinas (Ros *et al*., 2019, 2020; Scribano *et al*., 2021; Revanales *et al*., 2022). Collectors were deployed for one-month period (August 2021). At the end of this period, they were carefully retrieved and meshes were enclosed in a plastic pot before breaking the rope-tie (Ros *et al*., 2020). Collectors were repeatedly washed with freshwater to release the vagile fauna. The freshwater with the released fauna was filtered through a 0.5 mm mesh-sized sieve and preserved in 96% ethanol. In the lab, the retained biological material was sorted and *L. baconi* specimens counted. Abundance was expressed as individuals per collector.

To explore the presence of *L. baconi* throughout the year, data from two monitoring programs carried out in 2012, one located in Puerto América marina, Cádiz, and the other one in Palma marina, Balearic Islands, were analysed. In Puerto América marina, three replicates of the hydroid *Eudendrium racemosum* (Cavolini, 1785) and the bryozoan *Amathia verticillata* (delle Chiaje, 1822) were sampled monthly from the submerged portion of pontoons close to the surface. In Palma marina, three replicates of the hydroid *E. racemosum* were collected monthly for the same purpose. Samples were fixed in ethanol 96%, sieved using a mesh size of 0.5 mm and checked for the presence of *L. baconi*.

Table 2. New records for *Laticorophium baconi*. Substrates: *Av=Amathia verticillata*, *Bn=Bugula neritina*, *Ee=Ellisolandia elongata*, *Er=Eudendrium racemosum*, *Mg= Mytilus galloprovincialis*, *Ss=Sabella spallanzanii*, *Ti=Tricellaria inopinata*, Fc=Fouling communities. RAS: Rapid Assessment Survey. *Although the presence of *L. baconi* had been already documented in these marinas (see Saenz-Arias *et al*., 2022a,b; Revanales *et al*., 2023; Ruiz-Velasco *et al*., 2023), the present study provides additional records, including the earliest one for each marina.

Country/Locality	Date	Coordinates	Substrates
PORTUGAL:			
Sines marina	9 May 2011, Apr 2019	37.95053º N, 8.86511º W	*Bn* (pontoons)
Albufeira marina*	10 May 2011	37.08487º N, 8.26617º W	*Bn* (pontoons)
Faro marina*	11 May 2011	37.01497º N, 7.93669º W	*Bn* (pontoons)
Calheta marina, Madeira	Jan 2022	32.71792º N, 17.17247º W	Fc (plates)
SPAIN:			
Marinas:			
Isla Canela*	16 May 2011	37.18650º N, 7.34000º W	*Bn* (pontoons)
El Rompido*	25 Nov 2010, 16 May 2011, 5 Sep 2021	37.21617º N, 7.12872º W	*Bn* (pontoons)
Chipiona*	17 May 2011, 6 Sep 2021	36.74486º N, 6.43033º W	*Av*, *Bn* (pontoons, buoys, mooring ropes, hull fouling)
Puerto América*	9 Jul 2010, 2012 (see Table S2)	36.54144º N, 6.28400º W	*Av*, *Bn*, *Er*, Fc, *Ti* (pontoons, buoys, mooring ropes, hull fouling)
La Línea (Puerto Chico)*	17 Jul 2010	36.15989º N, 5.35756º W	*Bn* (pontoons, buoys, mooring ropes, hull fouling)
Fuengirola*	15 May 2011, Apr 2019, 8 Sep 2021	36.54161º N, 4.61719º W	*Bn*, *Ee*, *Ss* (pontoons, buoys, mooring ropes, hull fouling)
Benalmádena	15 May 2011, Apr 2019	36.59597º N, 4.51231º W	*Bn* (pontoons)
Málaga*	3 Jul 2011	36.70824º N, 4.41282º W	*Bn*, *Ss* (pontoons)
Caleta Vélez	3 Jul 2011, Apr 2019, 8 Sep 2021	36.74883º N, 4.06731º W	*Bn* (pontoons)
Marina del Este	9 Sep 2021	36.72533º N, 3.72597º W	Fc (pontoons)
Motril	2 Jul 2011, Apr 2019	36.72417º N, 3.52875º W	*Bn*, *Ss* (pontoons)
Adra	Apr 2019, 9 Sep 2021	36.74703º N, 3.02042º W	*Bn* (pontoons)
Almerimar	1 Jul 2011	36.69700º N, 2.79178º W	*Bn*, Fc (pontoons)
Roquetas	1 Jul 2011	36.75653º N, 2.60644º W	*Bn* (pontoons)

Continued

Table 2 continued

Country/Locality	Date	Coordinates	Substrates
Almería*	1 Jul 2011, 9 Sep 2021	36.83150º N, 2.46167º W	*Bn* (pontoons, buoys, mooring ropes, hull fouling)
Carboneras	30 Jun 2011	36.99106º N, 1.89633º W	*Bn* (pontoons)
Torrevieja	29 Jun 2011	37.97472º N, 0.68322º W	*Bn* (pontoons)
Alicante	29 Jun 2011	38.33964º N, 0.48631º W	*Bn* (pontoons)
Dénia	28 Jun 2011	38.84551º N, 0.11161º E	*Av*, *Bn* (pontoons)
Valencia	28 Jun 2011	39.42811º N, 0.33239º W	*Av*, *Bn* (pontoons)
Burriana	28 Jun 2011	39.86081º N, 0.07275º W	*Bn* (pontoons)
Oropesa del Mar	28 Jun 2011	40.07533º N, 0.13331º E	*Bn* (pontoons)
Benicarló	27 Jun 2011	40.41536º N, 0.43367º E	*Av*, *Bn* (pontoons)
Tarragona	27 Jun 2011	41.10861º N, 1.25194º E	*Bn* (pontoons)
Vilanova Geltrú	27 Jun 2011	41.21358º N, 1.72906º E	*Av*, *Bn* (pontoons)
Barcelona	26 Jun 2011	41.37725º N, 2.18292º E	*Av*, *Bn* (pontoons)
L'Estartit	25 Jun 2011	42.05400º N, 3.20603º E	*Av*, *Bn* (pontoons)
Palma, Balearic Islands	2012 (see Table S2)	39.56272º N, 2.62836º E	*Er* (pontoons)
Ceuta, North Africa	29 May 2011	35.88958º N, 5.31619º W	*Av*, *Bn* (pontoons)
Offshore aquaculture facilities:			
Guardamar del Segura	Jul 2010, Jul 2011	38.09608º N, 0.60439º W	Fc (Fish farm)
Guardamar del Segura	Jul 2011	38.10600º N, 0.59525º W; 38.06678º N, 0.60986º W	Artificial collector
Guardamar del Segura	Jul 2011	38.06678º N, 0.60986º W	Nocturnal plankton haul
Floating debris:			
Mazagón marina	19 Mar 2023, 12-16 Apr 2023, 14 Jun 2023	37.13172ºN, 6.82850º W	Detached floating ropes
MOROCCO:			
Tanger marina	31 May 2011	35.78731º N, 5.80594º W	*Bn* (pontoons)
Kabila marina	30 May 2011	35.71986º N, 5.33550º W	*Av*, *Bn* (pontoons)
M'Diq marina	30 May 2011	35.68269º N, 5.31364º W	*Av*, *Bn* (pontoons)

Continued

Table 2 continued

Country/Locality	Date	Coordinates	Substrates
TUNISIA:			
Bizerte marina	Aug 2021	37.27456º N, 9.88156º E	Fc (RAS: pontoons, buoys, mooring ropes, etc)
El Kantaoui marina	Aug 2021	35.89392º N, 10.59797º E	Fc (RAS: pontoons, buoys, mooring ropes, etc)
Monastir marina	Aug 2021	35.77969º N, 10.83325º E	Fc (RAS: pontoons, buoys, mooring ropes, etc)
FRANCE:			
Bonifacio marina, Corsica	20 Oct 2020	41.38945º N, 9.15988º E	Fc (Hydrozoa, hand collection)
Porto-Vecchio marina, Corsica	15 Oct 2020, 27 Oct 2020	41.58788º N, 9.29034º E, 41.58794º N, 9.28983º E	Fc (brushing technique)
ITALY:			
Olbia port, Sardinia	24 May 2010	40.92167º N, 9.50500º E	Fc (concrete docks)
La Spezia port and marina	4 Jun 2010, Jul 2013, Oct 2018	44.10417º N, 9.83417º E	Fc (concrete docks and plates)
Fezzano marina	Aug 2021, Feb 2022	44.08028º N, 9.82806º E	Fc (plates)
Le Grazie marina	Aug 2021, Feb 2022	44.06769º N, 9.83569º E	Fc (plates)
Port of Livorno (touristic harbour)	Jun 2019, Mar-Apr 2023	43.54753º N, 10.30847º E	Fc (concrete docks and artificial substrates)
Orbetello lagoon (fish farm)	2 Mar 2023	42.43200º N, 11.16306º E	Fc (floating dock)
Civitavecchia port (marina)	15 May 2023	42.09400º N, 11.78919º E	Fc, *Mg*, ascidians (mooring ropes and buoys)
Civitavecchia port (fishing dock)	25 Jun 2023	42.09561º N, 11.78836º E	Fc (mooring ropes)
Riposto port (marina), Sicily	8 Jul 2023	37.72906º N, 15.20917º E	Fc (mooring ropes)
Catania port, Sicily	Jul 2022	37.49906º N, 15.09853º E	Fc (plates)
Siracusa harbour (marina), Sicily	15 Jul 2023	37.06622º N, 15.29094º E	Fc (mooring ropes)
Port of Brindisi	7 Aug 2023	40.65967º N, 17.96383º E	*Av*
Port of Ortona	19 Nov 2023	42.34667º N, 14.41533º E	Fc (mooring ropes)

Continued

Table 2 continued

Country/Locality	Date	Coordinates	Substrates
GREECE:			
Zakynthos harbour	Nov 2022	37.78406° N, 20.90233° E	Fc (RAS: pontoons, buoys, mooring ropes, etc)
Nafplio port marina	Nov 2022	37.56686° N, 22.79481° E	Fc (RAS: pontoons, buoys, mooring ropes, etc)
EGYPT:			
Abu-Qir military port	3 Sep 2022	31.32067° N, 30.07544° E	Fc (RAS: pontoons, buoys, mooring ropes, etc)
SAUDI ARABIA:			
Jeddah Islamic Port	Mar-Jul 2011	21.46597° N, 39.16661° E	Fc (plates) Samples identified by eDNA
AUSTRALIA:			
Dampier, WA	27 Mar 2011, 4 Jul 2011	20.66199° S, 116.70087° E; 20.58333° S, 116.63333° E	Fc (hull fouling)
Fremantle (Inner harbour, North Mole, Rous Head and Rocky Bay), WA	Apr-May 1999, 12 Sep 2011	32.04836° S, 115.74322° E; 32.05000° S, 115.73330° E; 32.05000° S, 115.75000° E; 32.03019° S, 115.75978° E	Fc (scraping)
Cockburn Sound (Henderson, Kwinana Grain Terminal), WA	25 Apr 1999, Sep-Oct 2011, Feb-Mar 2012	32.25411° S, 115.74272° E; 32.15509° S, 115.76319° E	Fc (hull fouling)
Bunbury (Inner Harbour), WA	Mar 1996	33.32000° S, 115.66000° E	Fc (pylons)
NEW CALEDONIA (FRANCE):			
Marina de Koumac	18-19 Nov 2019	20.57994° S, 164.27481° E; 20.58086° S, 164.27469° E; 20.58136° S, 164.27383° E	Fc
Grand récif de Koumac	18 Nov 2019	20.83092° S, 164.27808° E	Natural habitats on the reef (only one juvenile)

Results

New records and spreading of L. baconi

The known distribution records of *L. baconi* prior to the present study are listed in Table 1, including citations of its putative native range (throughout the whole eastern North Pacific from Bering Sea to north Peru), and records from artificial structures or human impacted habitats (mainly port environments) within the introduced range. Comprehensive data regarding habitat and substrate suitability remains limited.

The present study provides the first records of *L. baconi* in Morocco, Tunisia, Corsica (France), Italy, Greece, Egypt, Saudi Arabia and New Caledonia (France) in the South Pacific, showing the worldwide spreading of the species (Table 2; Figs. 1, 2). Specimens from Saudi Arabia were identified based on eDNA, and no specimens were available for morphological confirmation. Additionally, new locality records are provided for countries where the species had previously been identified, such as Portugal, Spain and Australia. This study represents the earliest and northernmost record for mainland Portugal (2011) and the first record for Macaronesia. Furthermore, it also allows for backdating the earliest records for Atlantic and Mediterranean European waters, since the species was confirmed to be already present in 2010 in Atlantic marinas of El Rompido and Puerto América, the Mediterranean marina of La Línea, the aquaculture facilities of Guardamar del Segura, Alicante, and the ports of Olbia and La Spezia, Italy. Therefore, the species has been inhabiting the Mediterranean and nearby Atlantic regions for over a decade, being repeatedly misidentified. Within Australian waters, the species had been documented only from the southeast coast of New South Wales (1990) (Table 1), and here we confirm its presence in temperate Western Australia since 1996 (Table 2), making it the official first record of the species in the Indian Ocean, with records from tropical Western Australia being made more recently (2011). New records from New Caledonia (2019), Tunisia (2021), Saudi Arabia (2021), Greece (2022), and Egypt (2022) are more recent. To our knowledge, specimens from New Caledonia also represent the first record of the Corophiini tribe in this region.

Within the Iberian Peninsula, the species is mainly distributed in the southern region, spanning from Sines (SW Portugal) to Almería (SE Spain). However, its presence was also documented along the Mediterranean coast, from marinas in Alicante (Torrevieja) to Gerona (L'Estartit), including the Balearic Islands (Palma) (Fig. 1; Tables 1, 2). In those marinas that were frequently sampled from 2010/2011 to 2021/2022 during this or previous studies in Spain (Isla Canela, El Rompido, Chipiona, Puerto América, Barbate, La Línea, Fuengirola, Caleta de Vélez and Almería) and Italy (Gulf of La Spezia: locality of La Spezia, Fezzano and Le Grazie) (see Tables 1, 2 and Saenz-Arias *et al.*, 2022a,b; Revanales *et al.*, 2023; Ruiz-Velasco *et al.*, 2023), the occurrence of the species was consistent throughout the entire 10-year period, thus confirming its successful establishment in Mediterranean and Atlantic waters.

Identification remarks

The morphology of the studied specimens of *L. baconi* (Figs. 3 and 4) agrees with the original description of Shoemaker (1934) based on material from its putative native range, as well as with the redescription provided by Gouillieux & Sauriau (2019) using the specimens

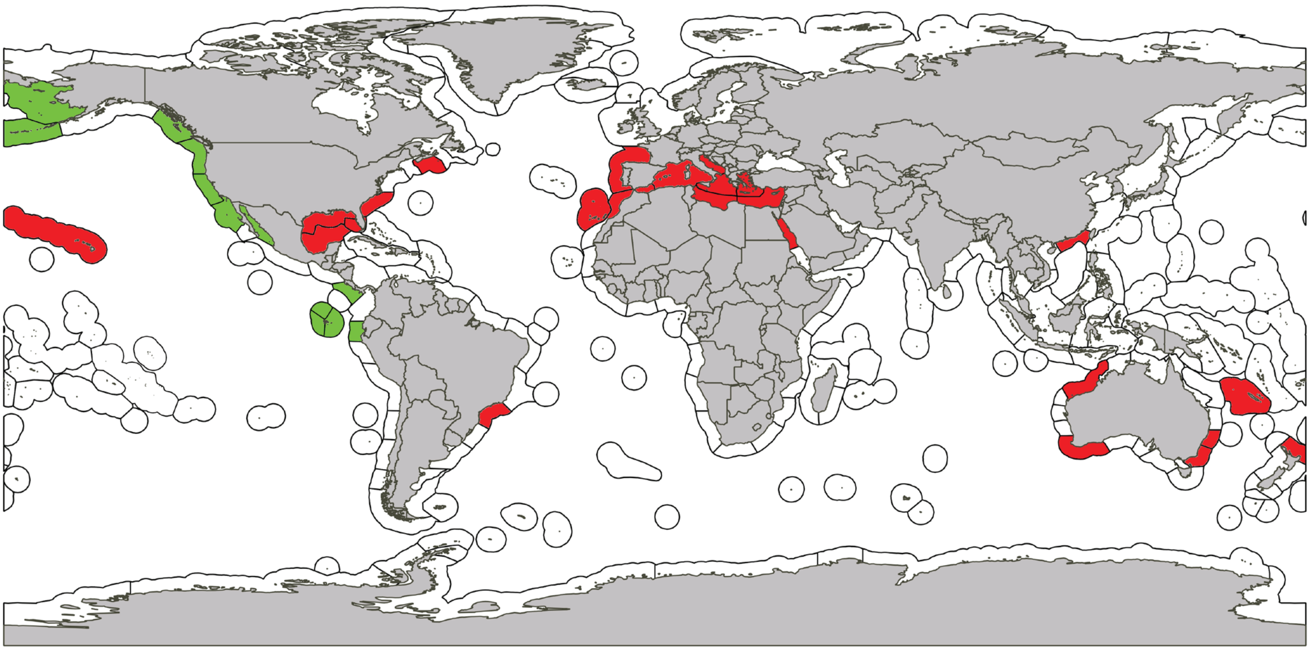

Fig. 2: Updated worldwide distribution of *Laticorophium baconi* including its introduced range (in red) and its putative native range (in green). Information based on data showed in Tables 1 and 2. Presence of the species in the Red Sea requires further validation based on morphological identification.

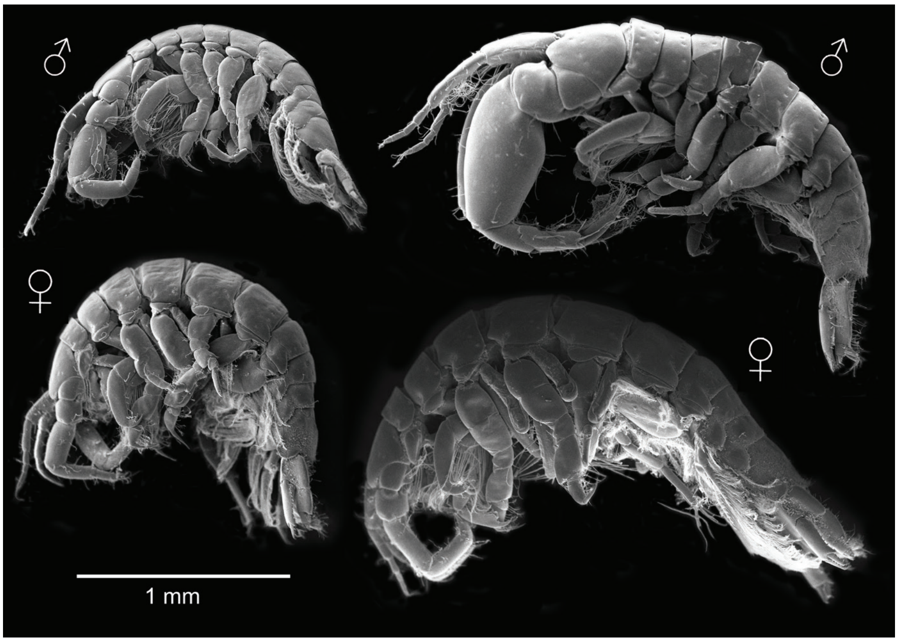

Fig. 3: SEM micrographs of males and females in lateral view of *Laticorophium baconi* from La Línea (Puerto Chico marina), Cádiz, September 2021.

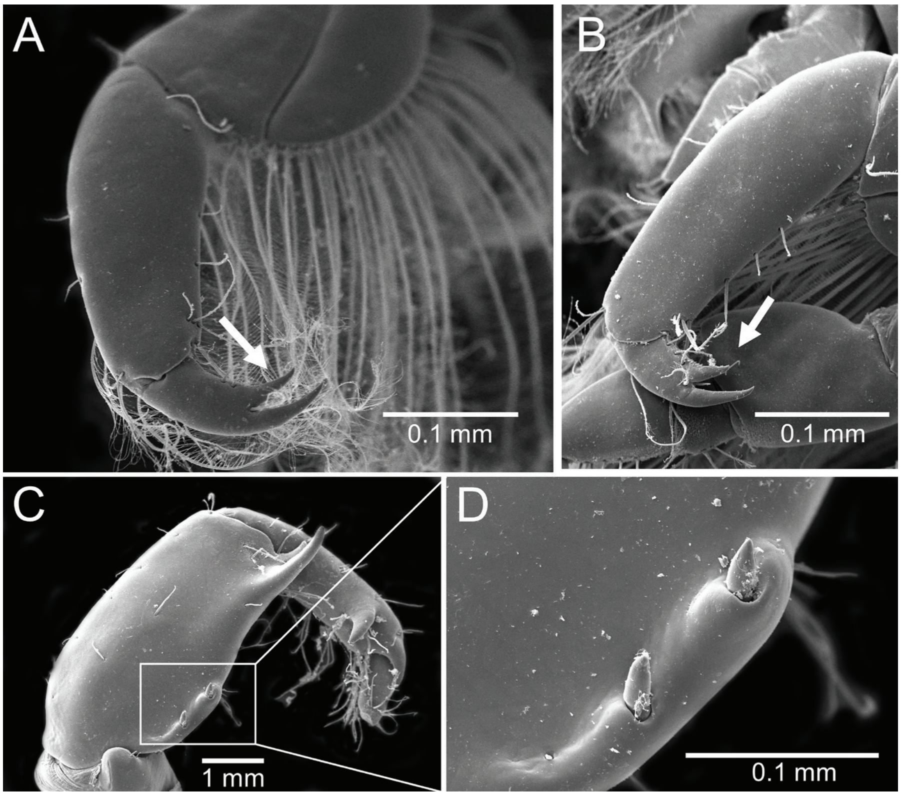

Fig. 4: SEM micrographs of *Laticorophium baconi* from La Línea (Puerto Chico marina), Cádiz, September 2021. Gnathopod 2 of male (A) and female (B) showing the detail of dactylus. Male antenna 2 (C) showing detail of two robust setae on article 4 (D).

from the introduced range. The species closely resembles the cosmopolitan *Apocorophium acutum*, with urosome segments fused, uropod 1 inserted ventrally and male antenna 2 processes. However, both species can be mainly differentiated by the dactylus of gnathopod 2, with one tooth on flexor margin in *L. baconi* (Fig. 4 A, B) and 2-3 teeth in *A. acutum*. Genus *Hirayacorophium* Myers*,* 2022 (previously known as *Hirayamaia*) is also provided with a single tooth, but the urosome lateral margin is smooth (*Hirayacorophium*) instead of notched (*Laticorophium*) (see Gouillieux & Sauriau, 2019 for details). The main difference between *L. baconi* and the other single species of the genus, *Laticorophium bifurcatum* Myers & Nithyanandan, 2016, is the presence of robust setae in ventral margin of the article 4 of antenna 2 in males of *L. baconi* (Fig. 4 C, D) and absence in *L. bifurcatum* (Myers & Nithyanandan, 2016; Gouillieux & Sauriau, 2019). Although most of the studied specimens were provided by 2 robust setae in article 4 of antenna 2 (Fig. 4 C, D), some specimens from the Spanish coast and Western Australia had only a single robust seta.

The body length of adult specimens of *L. baconi* ranged from 1.2 to 4.1 mm. Data per country revealed similar sizes in all populations worldwide; Portugal: 1.6-3.1 (n=10); Spain: 1.3-3.8 (n=122); Morocco: 1.4-3.5 (n=20); Tunisia: 1.2-3.2 (n=15); Italy: 1.6-4.0 (n=109); Greece: 1.4-3.3 (n=14); Egypt: 1.4-2.1 (n=12), Australia: 1.4-4.1 (n=60); New Caledonia: 1.7-3.2 (n=14). The larger sizes corresponded to ovigerous females.

Habitat use

The majority of records provided in this study correspond to port environments. *Laticorophium baconi* was found inhabiting fouling communities attached to artificial substrates such as pontoons, concrete docks, mooring ropes or buoys. This amphipod was often associated with the bryozoans *Bugula neritina* (Linnaeus, 1758), *Amathia verticillata* and *Tricellaria inopinata* d'Hondt & Occhipinti Ambrogi, 1985, the hydroid *Eudendrium racemosum*, the mussel *Mytilus galloprovincialis* Lamarck, 1819, the tubes of the polychaete *Sabella spallanzanii* (Gmelin, 1791) and the rhodophyte *Ellisolandia elongata* (J.Ellis & Solander) K.R.Hind & G.W.Saunders (Table 2). Moreover, *L. baconi* specimens were collected from PVC settlement plates or artificial collectors (e.g., Madeira, Spain, Italy and Saudi Arabia) and vessel hulls (e.g., Spanish coast or Western Australia). Although the sampling efforts of this study were focused on marinas, *L. baconi* was also recorded in fouling communities of aquaculture facilities, plankton samples, and floating debris (detached ropes) (Table 2). Only some specimens were found in the offshore aquaculture facilities of Guardamar del Segura, Spain while *L. baconi* strongly dominated the fouling community in the fish farm of Orbetello, Italy. Of the nine floating ropes collected in Mazagón marina (Huelva), *L. baconi* was present in eight of them, showing high abundances (more than 1,000 specimens including ovigerous females).

Population density, feeding habits, colonisation ability and temporal analysis in Spain

High densities of *L. baconi* were recorded in floating pontoons on marinas from both the Atlantic and Mediterranean coasts of Southern Spain (Chipiona: 894±320 individuals/m^2, Puerto América: 5388±1979, La Línea: 760±289, Fuengirola: 10844±5034, Almería: 222±141, mean±SE).

This amphipod clearly showed a detritivorous diet. Digestive contents were found in 123 of the 125 analysed specimens and consisted almost exclusively of detritus in all specimens. The total area occupied by content (detritus) in the whole digestive tract ranged from 51% in Chipiona to 69.2% in Fuengirola. In two specimens, some microalgae were found in the gut (probably ingested together with the detritus).

Laticorophium baconi showed a high colonisation ability according to the results of the experimental colonisation of artificial substrates in the five marinas of southern Spain. All collectors were colonised by the species after one month of deployment. Densities ranged from 8 to 880 specimens per collector (Chipiona: 543±229, Puerto América: 25±13, La Línea: 211±33, Fuengirola: 91±42, Almería: 49±9, mean±SE).

Regarding the temporal analysis of the presence of *L. baconi*, the species was registered throughout the whole year in Puerto América marina (Table S2), as long as substrates were present. Similarly, in Palma marina, the species was detected in most of the months sampled, except during the coldest months (January and February).

Discussion

Invasion patterns and worldwide distribution of L. baconi

The amphipod *Laticorophium baconi* has been reported as introduced in Hawaii, China, Australia, New Zealand, the East coast of USA and Canada, the Gulf of Mexico, Brazil, Portugal and Spain (Table 1 and references herein, Fig. 2). This study represents its first record in Morocco, Tunisia, Corsica (France), Italy, Greece, Egypt, Saudi Arabia and New Caledonia (France). Furthermore, it reports an expansion of its known distribution in Portugal, Spain and Australia. In the case of Spain, it provides the earliest record for Atlantic and Mediterranean European waters, confirming that the species was already present since, at least, 2010. In Australia, its presence on artificial substrates and hull fouling in Western Australia since, at least, 1996 enlarges the distribution of the species to the Indian Ocean (Table 2, Fig. 2). This study also indicates that *L. baconi* is already present in the Red Sea, which is known as a passing route connecting the Indian Ocean and the Mediterranean Sea. Nevertheless, considering that data of Saudi Arabia was based on molecular data alone, targeted collections are needed in the region to allow for a morphological confirmation.

Along its introduced range, *L. baconi* mainly inhabits bryozoans and hydroids attached to pontoons, rocky jetties, piers, concrete docks, seawalls, offshore platforms, buoys, mooring ropes, aquaculture facilities and floating debris (McKinney, 1977; LeCroy, 2004; present study). In fact, all records of the present study in the introduced range were registered in artificial structures and human impacted habitats, except for a juvenile which was found in the Grand Récif de Koumac, outside the marina, New Caledonia. As this juvenile was collected from a fish net placed in the water for a year, the specimen probably arrived dragged by the currents from the Koumac marina, where the species is established. Thus, throughout its introduced range, *L. baconi* is more abundant in artificial habitats, mainly occurring as a fouling organism in commercial ports and marinas, where it can be one of the dominant peracarid species (Saenz-Arias *et al*., 2022a). Based on this, we suggest recreational boating and commercial shipping, mainly through hull fouling and secondarily ballast waters, as the likely vectors for introduction and secondary spread of *L. baconi.* Indeed, the species was collected from vessel hulls in different locations along the Spanish and Western Australian coasts. Similarly, Carlton & Eldredge (2009) proposed ballast water or hull fouling as vectors involved in the transport of this amphipod to Hawaiian Islands, and LeCroy (2004) and Fofonoff *et al.* (2018) suggested hull fouling and ballast water respectively for its transport through the Panama Canal. Within artificial habitats, the association of *L. baconi* with widely distributed fouling basibionts, such as *B. neritina*, *A. verticillata*, *T. inopinata* or *S. spallanzanii*, could have facilitated its spread via hull fouling and subsequent establishment in these habitats. For example, Martínez-Laiz *et al.* (2022) found that sessile fouling basibionts provided refugia and boosted the probability of the exotic amphipod *Caprella mutica* Schurin, 1935 remaining attached under flow exposure trials. Besides this, our finding of several specimens in floating ropes in southern Spain also indicates, for the first time, the potential role of marine litter in the secondary spread of this species.

Despite the clear association between *L. baconi* and artificial habitats in its introduced range, the species has been occasionally found in natural habitats. Valério-Berardo & de Souza (2009) found the species in intertidal ecosystems from Rio de Janeiro, Brazil and Huang *et al.* (2008) reported *L. baconi* as one of the dominant species inhabiting the marine sponge *Amphimedon viridis* Duchassaing & Michelotti, 1864 in shallow (1-2 m depth) seagrass habitat of Saint Joseph Bay, Florida. This indicates that the species could potentially reach natural habitats in other introduced regions, as the Mediterranean, where the species is still restricted to artificial habitats. Other exotic amphipods in the Mediterranean, such as *Stenothoe georgiana*, *Caprella scaura* or *Paracaprella pusilla*, have not been established in natural environments so far, being confined to artificial habitats in the introduced range (Ros *et al*., 2014a; Cabezas *et al*., 2019; Martínez-Laiz *et al*., 2020), but it is worth noting that the level of biofouling NIS spreading in natural habitats is still poorly investigated. On the contrary, high densities of the exotic *Jassa slatteryi* have already been recorded in Mediterranean natural habitats, including marine protected areas (Navarro-Barranco *et al*., 2018, 2023). Similarly, the exotic isopod *Mesanthura* cf. *romulea* Poore & Lew Ton, 1986 has been observed in *Posidonia* seagrass meadows in Italian coasts (Stamouli *et al*., 2018). As *L. baconi* has been traditionally confused with *Apocorophium acutum*, its potential presence in natural habitats could have been overlooked due to misidentification. Indeed, well-developed populations of *A. acutum* have been recorded in seaweeds collected from natural rocky shores of the Mediterranean coast of southern Spain (Vázquez-Luis *et al*., 2008, 2009, 2013, Navarro-Barranco *et al*., 2018, 2019, 2023). Part of this material has been re-examined during the present study and the validity of the identification of *A. acutum* has been confirmed. Therefore, to our knowledge, while *A. acutum* is abundant in Mediterranean natural habitats, *L. baconi* is still restricted to artificial ones. However, continuous surveillance is recommended to detect if *L. baconi* can eventually colonise natural habitats within Mediterranean, nearby Atlantic, and other areas within its introduced range.

Regarding its native distribution range, *L. baconi* was originally described by Shoemaker (1934) from several geographically remote localities (off coast of Peru, Bering Sea and southern California) and it is considered native to the whole Northeast Pacific, from the Bering Sea to the Galapagos Islands and northern Peru (Shoemaker, 1934, 1949; Bousfield & Hoover, 1997; Fofonoff *et al*., 2018). A narrower native range cannot be ruled out, and it is possible that some of the localities included by Shoemaker (1934) and later studies (Shoemaker, 1949; Barnard, 1979; Bousfield & Hoover, 1997) are part of the introduced range. However, until further morphological or molecular evidence becomes available, we have followed the criterion of previous authors, and a wide putative native range from polar to tropical environments was assumed for the species (Fig. 2). Likewise, certain amphipods, like *Caprella irregularis* Mayer, 1890, or *Caprella laeviuscula* Mayer, 1903, also display wide-range distributions throughout the North Pacific waters of America, thriving in temperatures spanning from 5ºC to 20ºC (Laubitz, 1970). In this sense, *L. baconi* shows a wide environmental tolerance. It demonstrates an ability to tolerate a wide range of water temperatures (Bousfield & Hoover, 1997; LeCroy, 2004) and salinities (18 to 33 psu), being reported also in estuaries (Grabe *et al*., 2006). For example, we found established populations of *L. baconi* throughout a year in both the Atlantic and Mediterranean coasts of Spain, supporting its ability to survive seasonal fluctuations in locations where it is introduced. Moreover, our record for Saudi Arabia would increase its salinity tolerance range up to 42 psu. Besides this, most records of *L. baconi* within its putative native range correspond to natural habitats, such as intertidal and shallow waters, including seagrass beds. In fact, it has been reported as one of the dominant taxa of the epifaunal community associated with the seagrass *Zostera marina* Linnaeus in San Quintin Bay, Baja California (Quiroz-Vázquez *et al*., 2005). The species has also been collected from algae, and sand or muddy bottoms (McKinney, 1977; Nelson, 1995; LeCroy, 2004), at depths of 0 to 55 m (Barnard, 1979). While this evidence may support the wide native range assigned to *L. baconi*, molecular studies have revealed that species with a traditional wide latitudinal distribution in the North Pacific may, in fact, comprise species complexes. This is exemplified by the nudibranch *Aeolidia papillosa* (Linnaeus, 1761), where populations from California (southern part of its North Pacific distribution area) were recently emerged as a new pseudocryptic species known as *Aeolidia loui* Kienberger, Carmona, Pola, Padula, Gosliner & Cervera, 2016 (Kienberger *et al*., 2016). Therefore, further molecular research is essential to understand the native range of *L. baconi* and to discard the possibility of a species complex of morphologically similar species. The molecular approach has proven invaluable in exploring the native ranges and invasion patterns of other marine amphipod species, such as *Corophium volutator* (Pallas, 1766) (Einfeldt & Addison, 2015), *Caprella mutica* Schurin, 1935 (Ashton *et al*., 2008), *Caprella scaura* (Cabezas *et al*., 2014), *Paracaprella pusilla* (Cabezas *et al*., 2019) or *Jassa* spp. (Beermann *et al*., 2020) among others.

Taxonomic remarks

Shoemaker (1934, 1949) reported some slight differences among specimens from Peru, California and Bering Sea, particularly in antennae 1 and 2, and in the notch on the pleon margin. However, these dissimilarities were attributed to the state of maturity of the examined specimens. Valério-Barardo & de Souza (2009) identified material from Brazil as *L. baconi* based on the presence of the well-developed ventromedial acute process on male antenna 2, the position of medial and distal process of article 5 in the same antenna, presence of a median notch in the lateral ridge of the fused urosome, and dactylus of gnathopod 2 with one tooth in the flexor margin. However, differences emerged between the Brazilian specimens and those described by Shoemaker (1934), particularly in the number of robust setae on peduncles articles of antennae, and the absence of robust setae on ventral margin of article 4 of the antenna 2 in Brazilian specimens. In this context, Myers & Nithyanandan (2016) described a new *Laticorophium* species from Kuwait, *L. bifurcatum*, mainly based on the absence of robust setae in article 4 of the male antenna 2. Other characters considered to differentiate both species, such as the processes in article 4 and 5 of male antenna 2, can change in size, disposition, and orientation as a function of maturity (Shoemaker, 1949; Otte, 1975; Gouillieux & Sauriau, 2019). Therefore, these characters should be taken with caution. Considering that the specimens of *L. baconi* recorded by Bousfield & Hoover (1997) and Valério-Berardo & de Souza (2009) were lacking robust setae in article 4 of male antenna 2, Gouillieux & Sauriau (2019) suggested that they could correspond to *L. bifurcatum* instead of *L. baconi*. While specimens of the introduced range studied in the present work fit within the original and subsequent description of *L. baconi* from native and exotic ranges, variability in the robust setae in article 4 of antenna 2 was observed. Although most specimens displayed 2 robust setae, some specimens from Spain and Australia had only one. This adds some uncertainty in the consideration of this character as diagnostic for species identification. A molecular approach would aid to confirm *L. bifurcatum* as a different species to *L. baconi*, and to assess whether morphological variability of *L. baconi* is due to intraspecific variation or to the existence of a species complex. In any case, previous molecular and morphological works on other amphipods have revealed that, when a taxon with different ‘forms’ or ‘varieties’ within a complex rapidly spreads into an exotic range, only a single form of the complex is expanding its distribution range through anthropogenic vectors, while the other forms remain in a restricted distribution (e.g., Cabezas *et al*., 2014; Ros *et al*., 2014a). Furthermore, molecular evidence has supported that populations of all the worldwide distributed exotic amphipods investigated so far belong to single species, even when some degree of morphological variability is detected (Ashton *et al*., 2008; Cabezas *et al*., 2019; Beermann *et al*., 2020; Martínez-Laiz *et al*., 2020).

Regarding the body size, Shoemaker (1934, 1949) reported that the largest male specimen measured 3 mm, while the largest female measured 4 mm based on specimens from the putative native range. LeCroy (2004) and Fofonoff *et al.* (2018) similarly recorded adult length ranges of 2-4 mm. Measures of adult specimens obtained during the present study (1.2-4.1 mm) confirmed similar sizes for all the populations within the native and introduced ranges. Indeed, this amphipod could be easily overlooked due to, among other factors, its remarkably small size (Fofonoff *et al*., 2018).

Ecological notes and invasion success

Laticorophium baconi builds U-shaped tubes (LeCroy, 2004) and similarly to other amphipods, it has brooded embryos and direct development. Unfortunately, information on its life history is still lacking (Fofonoff *et al*., 2018). Further efforts should be focused on understanding the growth and reproduction patterns of this species (e.g., Takeuchi & Hirano, 1991; Baeza-Rojano *et al*., 2011), since this information can be relevant in management strategies. Despite this lack of knowledge, there are several traits that could explain its quick and extensive spread worldwide described above. For example, although Barnard (1970) suggested that *L. baconi* was less abundant in harbours than other corophiids because of a low tolerance to pollution, Grabe *et al*. (2006) found it on moderately contaminated sediments, and it has been described as copper tolerant (Culver *et al*., 2012; 2021). The frequent association with human impacted habitats as we found in its introduced range (see above) seems to support this tolerance. Another common feature among widely distributed species is their ability to colonise artificial structures. The greater the abundance of the species, the greater its probability of colonising anthropogenic vectors and expanding to new locations (Floerl *et al*., 2005; Ros *et al*., 2020; Revanales *et al*., 2023). Since *L. baconi* reaches high densities on pontoons (Saenz-Arias *et al*., 2022a; present study), it is to be expected that it can easily colonise the hulls of adjacent moored boats and spread by recreational boating (Martínez-Laiz *et al*., 2019). In fact, *L. baconi* was found in hull fouling during the present study. Bousfield & Hoover (1997) and LeCroy (2004) suggested that *L. baconi* could be a good coloniser because of its wide temperature tolerance and ability to colonise a wide range of habitats. The present study confirmed both its ability to survive the seasonal fluctuations along a year in the Atlantic and Mediterranean coast of Spain, and its remarkable colonisation capacity based on experimental evidence. Specifically, densities of near 1,000 specimens per collector were measured after one month of deployment in marinas of Southern Spain. Furthermore, the present study revealed that specimens of *L. baconi* also colonised plates and artificial substrates placed in marinas and ports of Madeira, Southern Spain, Italy and Saudi Arabia, and artificial collectors placed in fish farm facilities of Eastern Spain. Moreover, the species was also collected from the water column, as part of the plankton, during nocturnal migrations. The high propensity for local dispersal of this species may, therefore, increase the chances of human-vector uptake, frequency of transportation and, in turn, invasion success (Ros *et al*., 2020). Likewise, the presence of the species on a great variety of biotic substrates (Table 2) shows the great plasticity of *L. baconi* to colonise different fouling species (including macroalgae, bryozoans, hydrozoans and other sessile invertebrate species). Finally, we found that the diet of *L. baconi* was mainly based on detritus. This seems to be the general trend in the whole tribe Corophiini since Guerra-García *et al*. (2014) studied nine species of this tribe (160 specimens) and detritus was the exclusive diet item in all of them. In fact, detritus is usually the dominant component in the diet of amphipods (Guerra-García & Tierno de Figueroa, 2009; Guerra-García *et al*., 2014), especially in opportunistic species associated to anthropogenic habitats (Guerra-García *et al*., 2015; Sedano *et al*., 2020). The high availability of this feeding resource in artificial habitats could also contribute to its invasion success. Based on all this, comprehensive monitoring programmes and ecological assessments should be carried out to quantify and evaluate the expansion of *L. baconi* and its potential effects on invaded ecosystems.

When analysing global patterns of introduced amphipods, Marchini & Cardeccia (2017) pointed out that most cases belong to the family Corophiidae, followed by Aoridae, Ischyroceridae and Caprellidae. Therefore, Corophiidae can be considered a target taxon to search for non-indigenous and invasive species. In this sense, the status of the corophiid *L. baconi* is still non-indigenous in many areas and has not been treated as an invasive species so far. In New Zealand, McFadden *et al*. (2007) categorised *L. baconi* as of minor significance based on Biosecurity New Zealand's risk assessment concerning its potential establishment and associated economic and ecological implications. Recent examples of marine amphipods attaining invasive status in short periods, often leading to negative impacts on native ecosystems and marine aquaculture, highlight the importance of these assessments. For instance, *Caprella mutica* rapidly becomes invasive, potentially hampering the growth of the mussel *Mytilus* spp. on aquaculture facilities through interspecific competition for food resources (phytoplankton), in which caprellids benefit from their positioning over mussels, or by the trampling done by caprellids which causes the closing of mussels' valves, thus interrupting their feeding (Turcotte, 2010; Daneliya & Laakkonen, 2012; Almón *et al*., 2014). The high densities of *C. mutica* measured on oil platforms may also influence the degree to which these structures provide the ecological services of natural reefs by potential interaction with native species (Page *et al*., 2006). However, interactions can be complex; the potential negative effects of *C. mutica* on native vagile assemblages in oil platforms contrast with a positive effect on fish, since exotic caprellids provide food subsidy to resident microcarnivorous fish with positive effects on fish condition (Page *et al*., 2007). Similarly, Collin & Johnson (2014) provided an example of how this invasive caprellid can negatively impact the recruitment of a second invader, *Ciona intestinalis* (Linnaeus, 1767), an exotic tunicate which damages mussel aquaculture via heavy biofouling of equipment and mussels. Other example of impacts caused by an exotic amphipod on native species has been described for marinas from the Iberian Peninsula and northern Africa. Guerra-García *et al.* (2011) and Ros *et al.* (2015) suggested, based on field data, a competitive displacement of the resident *Caprella equilibra* Say, 1818 by the invasive *Caprella scaura*. In freshwater ecosystems, exotic amphipods also have an important ecological impact, especially regarding native species displacement, due to a combination of behavioural, physiological and environmental factors (Grabowski *et al*., 2007a,b). Freshwater amphipods such as *Gammarus tigrinus* Sexton, 1939 and *Chelicorophium curvispinum* (G.O. Sars, 1895), strongly affect the food web, not only horizontally (competition, swamping), but also vertically, with predators switching diets at each successful invasion (van der Velde *et al*., 2000). *Dikerogammarus villosus* (Sowinsky, 1894) is another high-impact predatory amphipod, which eliminates both native and exotic species (Dick & Platvoet, 2020). Unfortunately, the global ecological impacts of marine exotic species are insufficiently understood, and most meta-analysis focus on large or conspicuous species, while the ecological effects of small exotic invertebrates are usually overlooked or underestimated (Anton *et al*., 2019). Therefore, future experimental research is necessary to explore if *L. baconi* is displacing other native species or if it is affecting, among others, the performance of open-sea aquaculture installations.

Taxonomic expertise and scientific collaboration

The growing deficiency in taxonomic expertise impairs the ability to adequately detect and evaluate invasion risks (Ricciardi *et al*., 2021). In fact, this taxonomic impediment has resulted in underestimation of invasion occurrences (Marchini & Cardeccia, 2017; Carlton & Fowler, 2018). Achieving taxonomic resolution at the species level is necessary for the accurate identification of NIS and to properly elaborate comprehensive lists of taxa and reliable inventories and databases of biodiversity, which are essential for decision-making in bioinvasion management (Martínez-Laiz *et al*., 2020; Guerra-García *et al*., 2021b). The molecular approach is an effective tool for species identification and has contributed to better understand invasion patterns and pathways of exotic species (Cabezas *et al*., 2014; Cao *et al*., 2016; Antil *et al*., 2023). However, molecular techniques are insufficient to compensate for the taxonomic impediment, since taxonomic expertise is necessary to corroborate the correct assignment of sequences or to formally describe new taxa (Ricciardi *et al*., 2021). Unfortunately, the number of taxonomists is suffering a dramatic decline (Hopkins & Freckleton, 2012). Considering the long period necessary for training taxonomists, this decline involves a threat for bioinvasions research and management. Therefore, promoting taxonomic training and exchanging taxonomic knowledge between senior and early-career taxonomists are essential in NIS studies (Guerra-García *et al*., 2008; Coleman, 2015; Costello, 2020; Katsanevakis *et al*., 2020; Martínez-Laiz *et al*., 2020; Ragkousis *et al*., 2023). Financial support is normally biased towards larger and conspicuous species, which usually have higher social impact in the media (e.g., García-Gómez *et al*., 2021). Contrarily, taxonomic research on *non-charismatic* NIS or the so-called 'hidden invaders', which include unicellular taxa, small-sized inconspicuous, vagile invertebrates with cryptic behaviour and challenging taxonomies, are strongly undervalued and should receive a higher funding input since taxonomic expertise is pivotal in these cases (Carlton, 2011; Martínez-Laiz *et al*., 2020; Saenz-Arias *et al*., 2022b; Golo *et al*., 2023). For example, the foundational taxonomic works of Krapp-Schickel (2015) or Conlan *et al*. (2021) were essential to update the introduced range of the exotic amphipod *S. georgiana* (Martínez-Laiz *et al*., 2020) and *J. slatteryi* respectively. A fine and precise taxonomy was also crucial to detect the presence of *L. baconi* in the Mediterranean (Gouillieux & Sauriau, 2019). This significant work, based on exhaustive morphological description and detailed observations, revealed that the species could have been overlooked and/or potentially confused with other Corophiini species in previous studies. Owing to this study, the coauthors of the present study were prompted to re-identify material of old collections and to conduct new sampling programs. The willingness of exchanging opinions and sharing knowledge among colleagues allowed the detection of this exotic in several other worldwide regions. Building strong expert networks at regional, national and international levels ensure the effective transfer of knowledge among taxonomists and invasion ecologists (Martínez-Laiz *et al*., 2020). Besides taxonomic expertise, studies on natural history of exotic species, including life cycle traits, growing and reproduction patterns, feeding ecology, ability to disperse and colonise, environmental preferences, resistance to pollution, behaviour and interactions with other species, are critical to globally understand marine bioinvasions.

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Supplementary Data

The following supplementary information is available online for the article:

Text S1. Detailed information on sampling surveys.

Table S1. Detailed information on voucher material of *Laticorophium baconi* deposited in museums, including Museum Catalogue numbers, sampling locations, coordinates, collection date, substrates and numbers for the specimens. MNCN: Museo Nacional de Ciencias Naturales de Madrid, Spain; MNHN: Muséum National d'Histoire Naturelle, France; MSNPV: Museo di Storia Naturale dell'Università di Pavia, Italy; MZPA: Museum of Zoology of the University of Palermo, Italy; MBMCA: Museo di Biologia Marina "Pietro Parenzan" at the University of Salento, Italy; WAM: Western Australia Museum, Perth, Australia; *Av*=*Amathia verticillata*; *Bn*=*Bugula neritina*; *Er*=*Eudendrium racemosum*, Fc=Fouling communities. RAS: Rapid Assessment Survey.

Table S2. Monthly presence/absence of *Laticorophium baconi* in Puerto América, Cádiz and Palma, Balearic Islands throughout the year 2012. *Substrates absent.