Research Article

Mediterranean Marine Science
Indexed in WoS (Web of Science, ISI Thomson) and SCOPUS
www.hcmr.gr
DOI: https://doi.org/10.12681/mms.41784

The spread of *Aoroides longimerus* Ren & Zheng, 1996 across the Mediterranean and the Atlantic: genetic diversity, anthropogenic transport, and ecological implications

José Manuel GUERRA-GARCÍA[1], Andrea DESIDERATO[2], Serena MUCCIOLO[2], Carlos NAVARRO-BARRANCO[1], Macarena ROS[1], Jasmine FERRARIO[3], Paula MORETTI[3,4], Agnese MARCHINI[3], Nawfel MOSBAHI[5], Sofía RUIZ-VELASCO[1], Ignacio GESTOSO[6,7,8], Patrício RAMALHOSA[7,9], João CANNING-CLODE[7,8,9], Celia OLABARRIA[10], Eva CACABELOS[7,11], Jesús S. TRONCOSO[10], Jean-Philippe PEZY[12], Aurore RAOUX[12], Jean-Claude DAUVIN[12], Mathilde CHARBONNELLE[12], Ferdinand SCHLICKLIN[12], Hiroyuki ARIYAMA[13], Emanuele MANCINI[14,15,36], Andrea BONIFAZI[16], Vincent LE GARREC[17], Thomas BUREL[18], Benoit GOUILLIEUX[19], Cristina ESPÍRITO SANTO[20], Paula CHAINHO[21], Romeu S. RIBEIRO[21,22,23], Inês AFONSO[21], Yanrong WANG[24], Jean-Charles LECLERC[25], Marine MOAL[25], Céline HOUBIN[26], Frédérique VIARD[27], Eric THIÉBAUT[25, 26], Victoria FERNANDEZ-GONZALEZ[28], Sandra NAVARRO-MAYORAL[29], Sonia DÍAZ-VERGARA[29], Arjan GITTENBERGER[30], Lauren Elizabeth HUGHES[31], Maria LAMPA[32,33], Giorgos CHATZIGEORGIOU[34], Wanda PLAITIS[34], Francesco TIRALONGO[35,36], Gemma MARTÍNEZ-LAIZ[1], M. Pilar CABEZAS[37,38], Sofia DUARTE[37,38], João P. R. PINHEIRO[37,38], Giovanna O. REIS[2,39], Triana REVANALES[40], Juan SEMPERE-VALVERDE[1,41,42], Eva AYLAGAS[41], Angelo POLISENO[41], Sahar CHEBAANE[7,41,42], Susana CARVALHO[41], Vasilis GEROVASILEIOU[34,43], Inmaculada FRUTOS[2,44] and Pablo SAENZ-ARIAS[1]

[1]Laboratorio de Biología Marina, Department of Zoology, Faculty of Biology, University of Seville, Spain
[2]Department of Invertebrate Zoology and Hydrobiology, University of Lodz, Banacha 12/16, 90-237 Lodz, Poland
[3]Department of Earth and Environmental Sciences, University of Pavia, 27100 Pavia, Italy
[4]Departamento de Biologia Animal (Laboratório de Interações entre Comunidades Marinhas), Instituto de Biologia,
Universidade Estadual de Campinas, Campinas, São Paulo, Brasil
[5]Laboratoire de Biodiversité Marine et Environment, Faculté des Sciences de Sfax, Université de Sfax, BP 1171, 3038, Sfax, Tunisia
[6]Marine Research Institute (INMAR), Department of Biology, Faculty of Marine and Environmental Sciences,
University of Cádiz, Puerto Real, Cádiz, Spain
[7]MARE – Marine and Environmental Sciences Centre / ARNET - Aquatic Research Network,
Agência Regional para o Desenvolvimento da Investigação Tecnologia e Inovação, Funchal, Madeira, Portugal
[8]Smithsonian Environmental Research Centre, Edgewater, MD, USA
[9]Faculty of Life Sciences, University of Madeira, Funchal, Madeira Island, Portugal
[10]CIM - Centro de Investigación Mariña and Departamento de Ecoloxía e Bioloxía Animal, Facultade de Ciencias do Mar,
Universidade de Vigo, Spain
[11]Centro Oceanográfico de Vigo, Instituto Español de Oceanografía, CSIC, Subida a Radio Faro, 50, 36390 Vigo, Spain
[12]UNICAEN, Laboratoire Morphodynamique Continentale et Côtière, CNRS UMR 6143 M2C,
Normandie Univer., 24 rue des Tilleuls, 14000 Caen, France
[13]Osaka Museum of Natural History, Nagai Park, Higashi-Sumiyoshi, Osaka 546-0034 Japan
[14]Dipartimento di Scienze e Tecnologie Biologiche ed Ambientali, DiSTeBA, University of Salento, 73100, Lecce, Italy
[15]National Biodiversity Future Center, 90100 Palermo, Italy
[16]Dipartimento Stato dell' Ambiente, ARPA Lazio, 00173 Rome, Italy
[17]Univ Brest, CNRS, IRD, Observatoire, IUEM, F-29280 Plouzané, France
[18]Univ Brest, CNRS, IRD, Ifremer, LEMAR, IUEM, F-29280 Plouzané, France
[19]Université de Bordeaux, CNRS, Bordeaux INP, EPOC, UMR 5805, 33600 Pessac, France
[20]MARE - Marine and Environmental Sciences Centre, Aquatic Research Network, Laboratório de Ciências do Mar,
Escola de Ciências e Tecnologia, Universidade de Évora, 7521-903 Sines, Portugal
[21]MARE - Marine and Environmental Sciences Centre, Aquatic Research Network, Faculdade de Ciências,
Universidade de Lisboa Campo Grande, 1749-016 Lisboa, Portugal
[22]Escola Superior de Tecnologia de Setúbal, Instituto Politécnico de Setúbal, Estefanilha, 2910-761 Setúbal, Portugal
[23]MARE - Marine and Environmental Sciences Center, Aquatic Research Network,
Polytechnic Institute of Setúbal. IPS Campus - Estefanilha. 2910-761 Setúbal, Portugal
[24]Laboratory of Marine Organism Taxonomy and Phylogeny,
Institute of Oceanology, Chinese Academy of Sciences, Qingdao 266071, China
[25]Sorbonne Université, CNRS, Station Biologique de Roscoff, UMR7144, Place Georges Teissier, 29680 Roscoff, France
[26]Sorbonne Université, CNRS, OSU STAMAR, UAR 2017, Station Biologique de Roscoff,
Place Georges Teissier, 29680 Roscoff, France

[27]ISEM, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France
[28]Department of Marine Science and Applied Biology, University of Alicante,
Carretera San Vicente del Raspeig s/n, 03690, Alicante, Spain
[29]Universidad de Las Palmas de Gran Canaria, IU-ECOAQUA, Biodiversidad y Conservación,
Parque Científico Tecnológico Marino, 35200 Telde, Las Palmas, Spain
[30]GiMaRIS, Rijksstraatweg 75, 2171 AK Sassenheim, The Netherlands
[31]Life Science Department, Natural History Museum, London, Cromwell Road, South Kensington, United Kingdom
[32]Hellenic Center for Marine Research, Institute of Oceanography, Thalassocosmos, Gournes, Heraklion, Crete, Greece
[33]Marine Ecology Laboratory, Department of Biology, University of Crete, 70013 Heraklion, Greece
[34]Hellenic Center for Marine Research, Institute of Marine Biology Biotechnology and Aquaculture, Thalassocosmos,
Gournes, Heraklion, Crete, Greece
[35]Department of Biological, Geological, and Environmental Sciences, University of Catania, Catania, Italy
[36]Ente Fauna Marina Mediterranea, Avola, Italy
[37]Centre of Molecular and Environmental Biology and Aquatic Research Network, Department of Biology,
University of Minho, Campus de Gualtar, Braga, Portugal
[38]Institute of Science and Innovation for Bio-Sustainability, University of Minho, Campus de Gualtar, Braga, Portugal
[39]Programa de Pós-Graduação em Biologia Animal, Laboratório de Carcinologia,
Universidade Federal do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brasil
[40]Departamento de Biología, Instituto Universitario de Investigación Marina,
Universidad de Cádiz, Campus Universitario de Puerto Real, 11510, Puerto Real, Cádiz, Spain
[41]Biological and Environmental Sciences and Engineering Division, King Abdullah University of Science and Technology,
Thuwal 23955-6900, Saudi Arabia
[42]Notre Grand Bleu, Résidence Kairouan Cap marina Monastir, Monastir 5000, Tunisia
[43]Department of Environment, Faculty of Environment, Ionian University, Zakynthos, Greece
[44]Institut de Systématique, Évolution, Biodiversité ISYEB - UMR 7205 - Muséum national d'Histoire naturelle CNRS, MNHN, UPMC,
EPHE, Sorbonne Université, 57 rue Cuvier, CP 26, 75005 Paris, France

Corresponding author: José Manuel GUERRA-GARCÍA; jmguerra@us.es

Contributing Editor: Argyro ZENETOS

Received: 12 June 2025; Accepted: 18 September 2025; Published online: 17 October 2025

Abstract

Accurate knowledge of the global distribution of non-indigenous species (NIS) is essential for understanding their invasion dynamics and for implementing timely management measures. This study reports the first records of the marine amphipod *Aoroides longimerus*, putatively native to the East Asian coast, in Italy (2018), Spain (2019) and Tunisia (2022) and provides the earliest documented record of the species in its introduced European range (Portugal, 2011). Furthermore, it expands the species' known distribution in mainland Portugal (including the northernmost record), Macaronesia (with first records in the Canary Islands and Madeira), and confirms its presence along the Atlantic coasts of France and the Netherlands. Aquaculture facilities, particularly those associated with oyster farming, are probably the primary vector of introduction, while recreational boating may have contributed significantly to secondary dispersal. In comparison to other exotic amphipods, *A. longimerus* remains absent from many marinas, ports and/or aquaculture facilities in the Mediterranean Sea and adjacent regions, such as the Red Sea. This suggests that the species may still be in the early stages of expansion, or that its dispersal ability across marinas and ports is more limited than that of other amphipods. The present study, however, highlights several key ecological traits of *A. longimerus*: (i) it can survive year-round despite seasonal fluctuations, and reach high local densities, (ii) it exhibits strong colonisation capacity, as shown by its rapid establishment on settlement plates, and (iii) it displays opportunistic feeding behaviour, primarily consuming detritus. These characteristics underscore the importance of continuous surveillance and effective communication with stakeholders to prevent further expansion of this species.

Keywords: early detection; non-indigenous; Amphipoda; taxonomic expertise; scientific collaboration; aquaculture; recreational boating.

Introduction

To properly understand how non-indigenous species (NIS) affect marine ecosystems, comprehensive knowledge of their global distribution is essential (Marchini & Cardeccia, 2017; Sun *et al.*, 2017). Unfortunately, the lack of biogeographical information and historical records, funding constraints, long detection and reporting time lags (Zenetos *et al.*, 2019), limited long-term monitoring programmes, and scarcity of taxonomy experts prevent adequate NIS management (Guerra-García *et al*., 2023 and references therein). Although most efforts have been focused on conspicuous or medium and large-sized organisms with evident economic and/or ecological impacts (Cuthbert *et al*., 2021), interest in updating the distribution of smaller vagile invertebrates, such as amphipods, has increased in recent years.

Among vagile fauna, peracarid crustaceans represent an ecologically highly relevant group due to their widespread occurrence and sensitivity to environmental changes. For instance, they have been proposed as a target group for assessing levels of biocontamination (Saenz-Arias *et al*., 2022a). Within peracarids, amphipods stand out as one of the most interesting taxa due to their dominance in marine habitats, their ability to inhabit fouling communities, and their potential to be transported on vessel hulls (Bell, 1991; Arfianti & Costello, 2020; Martínez-Laiz *et al*., 2022; Saenz-Arias *et al*., 2022b). Recent collaborative efforts have been undertaken to update the distribution of these small, often overlooked amphipods which have been quickly spreading throughout their introduced range (e.g., Beermann *et al*., 2020; Martínez-Laiz *et al*., 2020; Guerra-García *et al*., 2023).

Aoroides longimerus was originally described by Ren & Zheng (1996) from the coast of China. Later, Ariyama (2004) recorded this species along the Japanese coast. Since all species within the genus *Aoroides* have been described from coastal regions of the Pacific Ocean (WoRMS Editorial Board, 2025), this region can be considered its native distribution range. Furthermore, Ariyama (2004) proposed that *Aoroides* may have originated from the genus *Aora* Krøyer, 1845 in the Southwest Pacific and then dispersed northward before spreading into the East Pacific. To our knowledge, *A. longimerus* has only been recorded in China and Japan within its native range.

Outside this putative native range, Gouillieux *et al.* (2015) found specimens of *A. longimerus* from subtidal slipper limpet *Crepidula fornicata* Linnaeus, 1753 beds and *Zostera marina* Linnaeus, 1753 meadows in Arcachon Bay, as well as from floating pontoons in the Bay of Brest, western France, in 2013 and 2014. They also reported two other *Aoroides* species in European waters, namely *A. semicurvatus* Ariyama, 2004 and *A. curvipes* Ariyama, 2004 in Arcachon Bay, located in the southern Bay of Biscay. This was the first record of the genus *Aoroides* in European marine waters. *Aoroides longimerus* was also detected in the Azores in 2013 (Castro *et al*., 2022) and was first recorded in the Mediterranean in 2015, inhabiting hull fouling in Port Camargue marina, France (Ulman *et al*., 2017). More recent records in the NE Atlantic include mainland Portugal in 2019 (CIEMAR, 2021) and the eastern English Channel, France (Dauvin *et al*., 2020). In 2020 and 2021, several specimens were also found inhabiting fouling communities in Delta marina and in Geersdijk harbour in the southern Netherlands (Faasse & Gittenberger, 2021). These scattered reports of *A. longimerus* in Europe outside the native range, covering extensive parts of Europe, have raised important questions about the true extent of its distribution in the Atlantic Ocean and the Mediterranean Sea, as well as the invasion dynamics that might be occurring in other regions. The exchange of information on the occurrence of *A. longimerus* among researchers has encouraged the re-examination of previously collected samples and motivated new sampling efforts, to better understand whether the species is spreading across the Mediterranean, the East Atlantic and elsewhere globally.

Building upon this collaborative approach, the present study specifically aims to: (i) update the global distribution of *A. longimerus*, including new records, (ii) provide taxonomic and ecological knowledge, including morphological and genetic data, from both native and introduced populations; (iii) characterise its diet (as a proxy for feeding habits); and (iv) discuss its invasion dynamics, potential introduction and spreading vectors.

Material and Methods

Sampling surveys and species identification

Several sampling surveys were carried out by different research teams between 1964 and 2024 (Table 1, Table S1). The geographic coverage of these surveys spanned across the Atlantic Ocean (Netherlands, France, Portugal and Spain, including the Macaronesian Islands), the Mediterranean Sea (Spain, Morocco, France, Tunisia, Italy, Croatia and Greece), the Red Sea (Saudi Arabia), and the Indo-Pacific Ocean (Saudi Arabia, Japan and Australia). Samples were mostly collected from artificial substrates in marinas (mainly pontoons, ropes and buoys), but also in ports, on boat hulls, in aquaculture facilities, and occasionally from natural habitats, such as subtidal or shingle beaches and coral reefs. Different sampling techniques were used, including the collection of biogenic substrates (basibionts), scrapings of fouling communities, deployment of PVC settlement plates, and Rapid Assessment Surveys (RAS) among others. After collection, most 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 examined for the presence of *A. longimerus*. In some cases, DNA metabarcoding approach was used to screen for the presence of *A. longimerus* from environmental samples including biofouling and water samples (see Text S1 for a detailed description of all sampling techniques by country/area).

Morphological identification of *Aoroides* specimens was based on key characters established by Barnard & Karaman (1991): (i) accessory flagellum of antenna 1 absent or vestigial, (ii) mandibular palp article 3 rectilinear (except for *A. palfreyensis* Myers, 2009 and *A. vitiosus* Myers, 1995, which lack a mandibular palp), (iii) gnathopod 1 of males merochelate, (iv) gnathopod 2 not carpochelate, and (v) uropod 3 biramous (see Gouillieux *et al*., 2015). The diagnostic characters for the species *A. longimerus* were based on Ren & Zheng (1996) and Ariyama (2004) (see also taxonomic remarks in the discussion section). It is important to note that the keys for identifying *Aoroides* species are currently proposed for

Table 1. Global distribution records of *Aoroides longimerus* Ren & Zheng, 1996. Records from its putative introduced range are shaded. The earliest record for the country is marked in bold. Asterisk (*) indicates the presence of at least one DNA sequence in this study. Atl: Atlantic coast; Med: Mediterranean coast.

Date	Country	Localities	Habitat/substrates	References
Aug 1979-Aug 1980	**Japan**	Kodomari, Takahama Town, Fukui Prefecture	Alga *Sargassum* sp.	Ariyama, 2022; present study
Jul 1981-Mar 2021	Japan	Hannan City, Osaka Bay, Osaka Prefecture	Algae, pontoon, artificial seaweed	Ariyama, 2022; present study
Apr 1982-Mar 2000	Japan	Misaki Town, Osaka Bay, Osaka Prefecture	Algae, sponges, bryozoans, hydrozoans, experimental blocks, artificial seaweed, sandy-mud bottom	Ariyama, 2022; present study
9 Jul 1988	Japan	Off Tanigawa in Misaki, Osaka Prefecture (34.31667º N, 135.11667º E)	Bryozoans, 7 m depth	Ariyama, 2004
10 May 1989	Japan	Off Tanigawa in Misaki, Osaka Prefecture	Brown alga *Sargassum filicinum*	Ariyama, 2004
28 Apr 1991	Japan	Outside of the mouth of the Onosato River in Han 'nan, Osaka Prefecture	Pebble beach	Ariyama, 2004
1 Jul 1992	**China**	Dayawan, Guangdong province (TYPE LOCALITY)	Fouling communities	Ren & Zheng, 1996; Ren, 2006
18 Mar 1994	Japan	Off Tanigawa in Misaki, Osaka Prefecture	Ascidian *Halocynthia dumosa*, 5 m depth	Ariyama, 2004
28 Aug 1995	Japan	Off Tanigawa in Misaki, Osaka Prefecture	Hydroid *Aglaophenia whiteleggei*, 2 m depth	Ariyama, 2004
May 1996-April 2006	Japan	Sennan City, Osaka Bay, Osaka Prefecture	Sponges, algae, experimental blocks, buoys	Ariyama, 2022; present study
10 Jul 1996	Japan	Tanigawa in Misaki, Osaka Prefecture	Experimental board for fouling organisms, l m depth	Ariyama, 2004
Apr 1997, Aug 2010	Japan	Shirahama Town, Wakayama Prefecture	Algae, experimental blocks	Ariyama, 2022; present study
Dec 1998-Jun 2009	Japan	Izumisano City, Osaka Bay, Osaka Prefecture	Algae	Ariyama, 2022; present study
Aug 2001	Japan	Himagajima Is. and Nezumijima Is., Mikawa Bay, Aichi Prefecture	Algae, sandy-mud bottom, shell bottom	Ariyama, 2022; present study
Aug 2008	Japan	Ena, Yura Town, Wakayama Prefecture	Sponges	Ariyama, 2022; present study
May 2020	Japan	Mihogaseki, Matsue City, Shimane Prefecture	Bryozoan	Ariyama, 2022; present study
9 May 2011	**Portugal**	Cascais marina (38.69094º N, 9.41855º W), Sines marina (37.95053º N, 8.86511º W)	Bryozoan *Bugula neritina*, floating pontoons	Present study
2013	Portugal	São Miguel, Azores	Hull fouling	ICES, 2018, DQEM, 2020, Castro *et al*., 2022
Jul 2013	**France** (Atl)	Courbey, Arcachon Bay (44.66667º N, 1.20000º W)	*Zostera marina* meadow, 2 m depth	Gouillieux *et al*., 2015
Jun-Jul 2014	France (Atl)	Thiers, Arcachon Bay (44.65000º N, 1.16667º W)	Slipper limpet bed, 5 m depth	Gouillieux *et al*., 2015
Aug 2014, 2 Jun 2022, 24 Sep 2024	France (Atl)	Château marina, Bay of Brest (48.36667º N, 4.48333º W; 48.37908º N, 4.48950º W) *	Fouling communities on floating pontoons, 1 m depth, among *B. neritina*	Gouillieux *et al*., 2015; present study
Oct 2014	France (Atl)	Arguin, Arcachon Bay (44.56667º N, 1.23333º W)	Pacific oyster reef, 0.1 m depth	Gouillieux *et al*., 2015

Continued

Table 1 continued

Date	Country	Localities	Habitat/substrates	References
May 2015	Japan	Takasu, Kurashiki City, Seto Inland Sea, Okayama Prefecture	Seagrass *Zostera*	Ariyama, 2022; present study
May 2015	Japan	Izu-ōshima Island,Tokyo Prefecture	Sponges	Ariyama, 2022; present study
16-28 May 2015	France (Med)	Le Grau-du-Roi, Port du Plaisance du Port Camargue marina (43.51500º N, 4.13200º E)	Hull fouling	Ulman *et al*., 2017
Jul 2018-Jul 2022	**Italy**	Santa Teresa marina (44.08167º N, 9.881978º E)	Fouling communities on PVC plates	Present study
30 Jan 2019, 25 Jun 2024	Portugal	Quinta do Lorde marina (32.74169º N, 16.71191º W), Madeira *	Fouling communities on PVC plates and artificial structures, 1-1.5 m depth	Present study
12 Feb 2019, Jun 2021-Oct 2022	France (Atl)	Granville marina, Normandy (48.83339º N, 1.60020º W)	Fouling communities on pontoons, piles and PVC plates	Dauvin *et al*., 2020; present study
25 Feb 2019	France (Atl)	Bassin Vauban marina, Le Havre, Normandy (49.49004º N, 0.12375º E)	Fouling communities on pontoons, piles and PVC plates	Dauvin *et al*., 2020; present study
1 Mar 2019, Jun 2021-Oct 2022	France (Atl)	Cherbourg marina, Normandy (49.64782º N, 1.62171º W) *	Fouling communities on pontoons, piles and PVC plates	Dauvin *et al*., 2020; present study
16 Apr 2019	France (Atl)	Saint-Vaast-La-Hougue (49.57298ºN, 1.27139º W)	Brown alga *Sargassum muticum*	Dauvin *et al*., 2020
Apr-Aug 2019*	**Spain** (Atl)	Ría de Vigo: Cangas marina (42.26089º N, 8.78379º W), Davila marina (42.23362º N, 8.74283º W), Moaña port (42.27610º N, 8.73481º W), Museo del Mar harbour (42.22482º N, 8,76865º W), Naútico port (42.24225º N, 8.72229º W), Toralla harbour (42.20196º N, 8.79850º W), Cíes floating pier (42.22632º N, 8.89959º W)	Fouling communities on PVC plates	Present study
2019, 2021, 2022, 2023	Portugal	Porto de Sines (marina and commercial port terminals) (37.95198º N, 8.88690º W; 37.95040º N, 8.86672º W; 37.93850º N, 8.86415º W; 37.93697º N, 8.84805º W)	Fouling communities on PVC plates	CIEMAR, 2021, 2025; present study
9, 23 Oct 2020, 5 Sep 2024	**Netherlands**	Kortgene, Delta marina, Lake Veere (51.55192º N, 3.81062º E; 51.552183º N, 3.81172º E)	Pontoons	Faasse & Gittenberger, 2021; present study
28 May 2021	Netherlands	Geersdijk jetty of port, Lake Veere (51.55468ºN, 3.76229º E)	Fouling communities	Faasse & Gittenberger, 2021
Jul 2021-Jul 2022	Italy	Le Grazie marina (44.06751º N, 9.83570º E), Fezzano marina (44.08022º N, 9.82732º E), Portovenere (44.050961º N, 9.834921º E)	Fouling communities on PVC plates	Present study
Sep 2021	Portugal	Costa Nova marina, Sailing Club (40.61989º N, 8.74832º W), Aveiro	Fouling communities on pontoons	Present study
Oct 2021	Portugal	Setúbal Fishing Port (38.51969º N, 8.89999º W), Sado estuary	Fouling communities on pontoons	Present study

Continued

Table 1 continued

Date	Country	Localities	Habitat/substrates	References
Dec 2021, Jan 2022	Spain (Atl)	Mussel farm, Ría de Vigo (42.27556º N, 8.72495º W)	Fouling communities on aquaculture facilities	Present study
9 May 2022, 12 Jun 2023, 13 Sep 2023, 18 Oct 2024	France (Atl)	Roscoff marina (48.71596º N, 3.96635º W; 48.71523º N, 3.96705º W) *	Fouling communities on pontoons and ropes	Present study
May-Jun 2022	France (Atl)	Trébeurden marina (48.77032º N, 3.58702º W) *, Saint Quay marina (48.64712º N, 2.82010º W), Saint Malo marina (48.63889º N, 2.02592º W) *, Concarneau marina (47.87008º N, 3.91421º W), Le Havre marina (49.48847º N, 0.09561º W), Piriac marina (47.38256º N, 2.54365º W) *	Fouling communities on pontoons	Present study
Sep 2022	Portugal	Alcantara marina (38.70141º N, 9.17107º W), Tagus estuary	Fouling communities on pontoons	Present study
Oct 2022	France (Atl)	Dieppe marina, Normandy (49.92797º N, 1.08197º W)	Fouling communities on pontoons, piles and PVC plates	Present study
Oct 2022	**Tunisia**	Sfax fishing port (34.72083º N, 10.76264º E)	Alga *Ulva* sp. on muddy sediments 2-6 m depth	Present study
27 Jan 2023	Spain (Atl)	Garachico marina (28.37359º N, 16.75579º W), Tenerife, Canary Islands *	Fouling communities on pontoons, ropes and buoys	Present study
28 Jan 2023, 19 Jun 2023	Spain (Atl)	Las Galletas marina (28.00715º N, 16.66107º W), Tenerife, Canary Islands	Fouling communities on pontoons, ropes and buoys, including the bryozoan *Vírididentula dentata*	Present study
Mar-Nov 2023	Tunisia	Skhira fishing port (34.28728º N, 10.09555º E)	Algae *Ulva* spp. on muddy sediments, 3-5 m depth	Present study
28 Jun 2023	Spain (Atl)	Gran Tarajal marina (28.20616º N, 14.02637º W), Fuerteventura, Canary Islands	Bryozoan *Vírididentula dentata*	Present study
14 Aug 2023	France (Med)	Barcares, Gulf of Lion (42.81000º N, 3.01900º E)	Fouling communities on pontoons	Present study
28 Sep 2023	France (Med)	Leucate harbour, Gulf of Lion (42.87000º N, 3.04660º E)	Fouling communities on pontoons	Present study
Mar-Apr 2024	Tunisia	Kneiss Islands (34.37438º N, 10.29865º E)	Intertidal meadows of *Zostera noltii* and *Halophila stipulacea*	Present study
25 Jun 2024	Japan	Hakotsukuri, Hannan City, Osaka Prefecture (34.34305º N, 135.20250º E) *	Algae	Present study
Jun-Jul 2024	France (Atl)	Dinard, Brittany (48.63830º N, 2.02660º W)	Fouling communities	Present study
6 Aug 2024	France (Atl)	Arcachon harbour, Arcachon Bay (44.65970º N, 1.15190º W)	Fouling communities on pontoons	Present study

adult males. Females and juveniles of different *Aoroides* species can exhibit significant morphological similarity, making identification difficult in the absence of males.

Voucher specimens of *A. longimerus* are deposited in the Museo Nacional de Ciencias Naturales, Madrid (MNCN) and Muséum national d'Histoire Naturelle Paris (MNHN) (see Table S2 for detailed information on the voucher specimens, including Museum Catalogue numbers, sampling locations, coordinates, collection dates, substrates, and numbers of specimens deposited).

Individual specimens barcoding: DNA isolation, amplification and alignment

Total DNA was extracted from two pleopods per specimen (or the whole pleosome for specimens smaller than 3 mm), adapting the protocol from Casquet *et al.* (2012). Out of 107 specimens planned to be sequenced, DNA was successfully extracted and amplified only from 25 (Table S3). Many of the specimens were indeed old or not properly preserved for subsequent DNA analyses. All specimens are available at the University of Lodz in the invertebrate collection of the Department of Invertebrate Zoology and Hydrobiology. Amplifications of both the mitochondrial DNA cytochrome c oxidase subunit 1 (CO1) and 16S rRNA genes were carried out using the primers sets LoboF1 and LoboR1 (Lobo *et al.*, 2013), and 16STf (Macdonald *et al.*, 2005) and 16Sbr (Palumbi, 1996), respectively. Amplifications were performed in a 15 µl reaction volume mix containing 7.5 µl DreamTaq Green PCR Master Mix (2X), 1.2 µl forward and reverse primers (5 µM), 1 µl template DNA, and nuclease-free water to a final volume of 15 µl, using the polymerase chain reaction (PCR) program described in Hou *et al.* (2007). PCR products were sequenced bidirectionally using the same primers sets used for amplification by Macrogen Europe (Amsterdam, The Netherlands). Raw sequences were trimmed using Geneious R11.0 (https://www.geneious.com), and consensus sequences were aligned using ClustalW (Larkin *et al.*, 2007) with default parameters. CO1 sequences were then visually inspected for stop codons and/or indels to avoid including pseudogenes in the analyses. All the obtained sequences were deposited in the BOLD project and dataset: ALONG and DS-AORLONG respectively (www.boldsystems.org, Ratnasingham *et al.*, 2024; Table S3).

Phylogenetic analyses

To determine the phylogenetic placement of the collected specimens and ascertain their membership to the target species, CO1 and 16S datasets were analysed independently. The sequences of other *Aoroides* species retrieved from public repositories, were used as outgroups: three CO1 sequences of *Aoroides intermedius* Conlan & Bousfield, 1982 from BOLD (BCAMP255-08, BCAMP102-08, NJCGS736-10), three CO1 of *Aoroides columbiae* Walker, 1898 species complex from GenBank (MG936292.1, MG317304.1, JX545451.1) (Clark *et al.*, 2016), and two 16S of *A. columbiae* from GenBank (JX545420.1, JX545421.1) (only sequences available). The final alignments consisted of 660 bp for CO1 and 425 bp for 16S. These alignments were used to calculate intra- and interspecific pairwise genetic distances (Kimura 2 parameters- K2P- with 999 bootstrap replicates) in MEGA 11 (Tamura *et al.*, 2021) and run a maximum likelihood phylogenetic analysis through PhyML (1000 bootstrap replicates; Guindon *et al.*, 2010). The best substitution models (HKY85 + G for CO1 and HKY85 + I for 16S) were tested with the Smart Model Selection (SMS) routine in PhyML using Bayesian information criteria (BIC) as optimality criteria (Lefort *et al.*, 2017). To better investigate the molecular variation among the specimens sequenced, a median-joining haplotype network was built using the PopART v1.7 software. For building the network, the sequences were further trimmed (i.e., 564 and 300 bp for CO1 and 16S, respectively) to exclude missing bases at both ends.

Gut contents analysis

To characterise the diet of *A. longimerus*, a total of 125 specimens collected from marinas of the Iberian Peninsula were examined: Sines (May 2011, n = 3 specimens), Cascais (May 2011, n = 20), Cangas (April 2019, n = 15; August 2019, n = 15), Davila (April 2019, n = 12; August 2019, n = 20), and Moaña (April 2019, n = 20; August 2019, n = 20). Dietary analysis followed the methodology proposed by Bello & Cabrera (1999), previously used for amphipod gut content characterisation (see details in Guerra-García *et al.*, 2014).

Results

New records of **Aoroides longimerus** *in its introduced range*

Examination of old specimens in the collections enabled us to provide the earliest known record of the species in its introduction range, namely 2011 in Portugal (Cascais and Sines marinas) (Table 1). The present work also provides the first records of *Aoroides longimerus* in Italy (2018), Spain (2019) (Fig. 1) and Tunisia (2022), and reports an expansion of its known distribution in mainland Portugal (including the northernmost record) and Macaronesia (with first records for the Canary Islands and Madeira). Additionally, it also confirms the presence of the species in the Atlantic coasts of France and the Netherlands. Therefore, to date, the introduced range of *A. longimerus* encompasses five ecoregions (North Sea, Celtic Sea, South European Atlantic Shelf, Azores Canaries Madeira and Western Mediterranean) of three biogeographical provinces (Northern European Seas, Lusitanian and Mediterranean Sea), according to Spalding *et al.* (2007).

A total of 161 specimens were collected from four Italian marinas in the Gulf of La Spezia (Le Grazie: 15, Santa Teresa: 79, Fezzano: 26, Portovenere: 41). The species was already present in Santa Teresa marina since July 2018, which represents the first record for Italy (Table 1). In the other three marinas, the species was found in 2021 and 2022 but was absent from 2018 to 2020.

In Ría de Vigo, Galicia, NW Spain, 1,841 specimens of *A. longimerus* (Fig. 1), were found among 20,872 amphipods examined from fouling PVC plates (Table 1), representing 8.82% of the total amphipod abundance (TA). This is the first record of the species in Spain. *Aoroides longimerus* was present at all locations in both sampling periods (three and nine months after deployment, corresponding to April and August 2019), but its abundance was lower in the early stages of macrofouling community

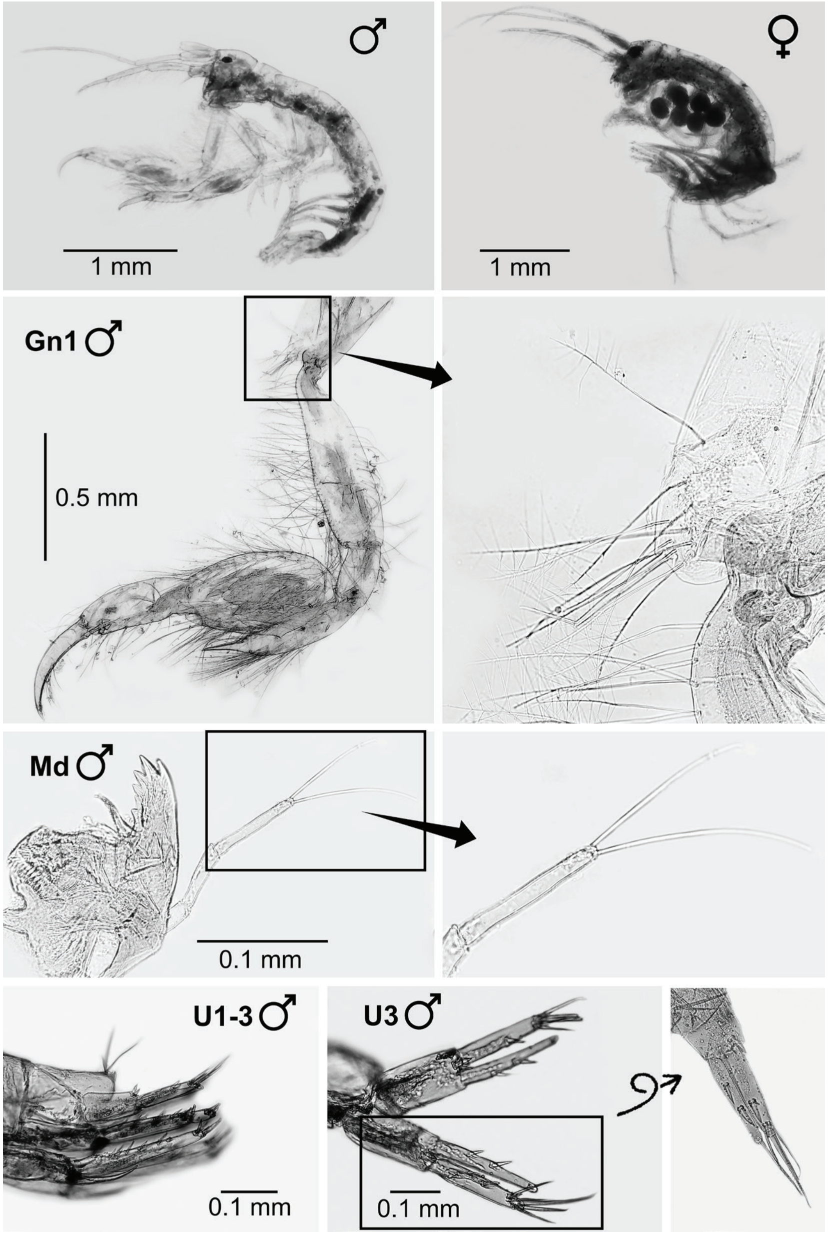

Fig. 1: Lateral view of male (Moaña marina, Galicia, NW Spain, April 2019) and female (Cíes, Galicia, NW Spain, August 2019) specimens of *Aoroides longimerus* Ren & Zheng, 1996. Details of male gnathopod 1 (Gn1) showing the plumose setae on the coxa, mandible (Md) showing the mandibular palp and uropods (U) 1-3, with a detailed view of U3.

development (April 2019: 223 individuals, 2.54% of TA) than in more mature communities (August 2019: 1,618 individuals, 13.39% of TA). These individuals were distributed as follows: 119 individuals in Cíes (23 in April, 96 in August), 197 in Cangas (22 in April, 175 in August), 330 in Davila (10 in April, 320 in August), 862 in Moaña (139 in April, 723 in August), 48 in Museo del Mar (9 in April, 39 in August), 145 in Náutico (13 in April, 132 in August) and 140 in Toralla (7 in April, 133 in August). Additionally, 40 specimens of *A. longimerus* were collected from a mussel farm in the Ría de Vigo between December 2021 and January 2022 (Table 1).

In 2011, *A. longimerus* was found in two (within continental Portugal) of the 42 marinas sampled along the Iberian Peninsula and North Africa, representing the earliest records of the species in its introduced range. Twenty one individuals were found in Cascais, while three were recorded in Sines (Table 1). *Aoroides longimerus* was present in the Port of Sines and its associated marina in subsequent sampling events (2019, 2021, 2022 and 2023). The species was absent from marinas in the southern Iberian Peninsula surveys in 2017 and 2019 (Table S1). However, a sizable population (69 specimens collected) was found inhabiting the Alcantara marina in the Tagus estuary, Portugal (September 2022). The present study also documents a single male specimen in the Sado estuary (Setúbal Fishing Port). The finding in Costa Nova marina, Aveiro (three specimens), represents the northernmost record for mainland Portugal.

Although *A. longimerus* had been previously reported in Macaronesia (Azores, 2013), this study provides the first records for Madeira (2019) and the Canary Islands (2023) (Table 1). In Madeira, the species (ca. 20 specimens) was collected in Quinta do Lorde marina, where it was also present during a sampling programme in June 2024 (>100 specimens identified). Five adult specimens were collected from marinas of Canary Islands (Table 1), confirming the presence of the species on two islands: Tenerife (Garachico and Las Galletas marinas) and Fuerteventura (Gran Tarajal marina).

In Tunisia, 43 specimens were collected from the fishing ports of Sfax and Skhira (Table 1). They were associated with algae (*Ulva* spp.) on muddy sediments at depths of 2-6 metres. The specimens found in Sfax (Gulf of Gabès) in October 2022 represent the first record for Tunisia and the southernmost record in the Mediterranean Sea. Between March and April 2024, 16 specimens were found inhabiting natural intertidal *Zostera noltii* Hornemann, 1832 meadows of the Kneiss Islands (Gulf of Gabès) (Table 1).

A total of 6,393 specimens of *A. longimerus* were collected from four marinas in Normandy, France (Granville, Cherbourg, Le Havre and Dieppe) between June 2021 and October 2022, representing ca. 10% of the total amphipod abundance in fouling communities. *Aoroides longimerus* was previously recorded in the region in 2019 (Table 1; Dauvin *et al*., 2020). More than 100 specimens were also collected from marinas in Brittany, France (May 2022-October 2024) (Table 1). The present study also supports the establishment of the species along the Gulf of Lion in the Mediterranean coast of France (Table 1).

In the Netherlands, the species was first recorded in Lake Veere in 2020. This study confirms its presence four years later in Delta marina, Korgene in September 2024 (Table 1).

Despite extensive sampling efforts conducted to characterise fouling communities in marinas, ports and aquaculture facilities in Morocco, Croatia, Greece, Saudi Arabia, and Australia, the species has not yet been found in these countries (Table S1).

Within the introduced area, the body length of adult specimens of *A. longimerus* ranged from 1.8 to 5.1 mm (males, n = 179) and 1.8 to 5.5 mm (females, n = 170), with the larger sizes corresponding to ovigerous females. Size data from different countries showed similar measurements across global populations. French specimens were, however, slightly larger than those from other populations; Northwestern Spain: 1.8-3.7 mm (males, n = 50) and 2.1-4.4 mm (females, n = 50), mainland Portugal: 2.6-3.6 mm (males, n = 20) and 2.2-3.9 mm (females, n = 20), Madeira: 1.9-3.4 mm (males, n = 20) and 1.9-4.3 mm (females, n = 20). France (Brittany and Normandy): 2.3-5.1 mm (males, n = 62) and 1.8-5.5 mm (females, n = 48), Tunisia: 2.8-4.3 mm (males, n = 27) and 2.9-4.4 mm (females, n = 32).

Phylogenetic analyses

The average genetic distance among *A. longimerus* sequences was 2.1% (SE: 0.4) for CO1, and 1% (SE: 0.2) for 16S. It is noteworthy than one CO1 sequence from a specimen collected in Hakotsukuri, Hannan City, Osaka Prefecture Japan (AORLON86) (Table S3) displayed a greater molecular divergence, with a maximum distance of 6.5% from the most divergent haplotype. For COI, the average distance to the specimens belonging to the congeneric species that were used as outgroups was 18.8% and 19.3% for the species complex *A. columbiae* and *A. intermedius*, respectively (Table S4). For 16S, the average distance to *A. columbiae* was 8.6% (Table S5). Phylogenetic trees clustered all *A. longimerus* sequences together, as compared to the outgroups (Figs. 2 and 3). Haplotype networks showed, for 16S, two haplotypes shared between the native (Japan) and the introduction ranges (Canary Islands and France) and one haplotype shared between two locations within the introduction range (Madeira and France) (Fig. 3). For CO1, no haplotypes were shared between the sequenced specimens, as would be expected given the high polymorphism of the marker. The haplotype network illustrates well the substantial divergence of the Japanese specimen AORLON86, as observed in the phylogenetic tree. Specimens from Madeira were more similar to each other (two to 11 mutational steps) than to specimens from other introduced populations (France and Canary Islands, min. 14 mutational steps).

Habitat use and dietary analysis

Within its introduced range, *A. longimerus* was mainly found on fouling communities of marinas during the present study (Table 1). In Portugal, it was associated to the bryozoan *Bugula neritina* (Linnaeus, 1758) on floating pontoons. In Spain, specimens were found inhabiting fouling communities on PVC plates, aquaculture facilities, and pontoons, ropes and buoys of marinas; in Canary Islands it was associated with the bryozoan *Virididentula dentata* (Lamouroux, 1816) (Table 1). In Normandy, France, populations were found on the bryozoans *B. neritina*, *Tricellaria inopinata* d'Hondt & Occhipinti Ambrogi, 1985 and *Watersipora subatra* (Ortmann, 1890), as well as the ascidians *Botrylloides* spp. and *Botryllus schlosseri* (Pallas, 1766). Based on these Normandy collections, *A. longimerus* appears to inhabit pontoons more readily than piles in marinas, and high abundances were measured on PVC plates, particularly sanded ones compared with smooth ones (Fig. 4, Text S1). In Tunisia, *A. longimerus* was found in natural habitats, associated with algae (*Ulva* spp.) on muddy sediments (2-6 m depth) and seagrass (Table 1).

In the Ría de Vigo, NW Iberian Peninsula, *A. longimerus* coexisted with other amphipods such as *Ampithoe ramondi* Audouin, 1826, *Aora gracilis* (Spence Bate, 1857), *Caprella acanthifera* Leach, 1814, *Caprella equilibra* Say, 1818, *Dexamine spinosa* (Montagu, 1813), *Jassa herdmani* (Walker, 1893), *Monocorophium sextonae* (Crawford, 1937), *Stenothoe monoculoides* (Montagu, 1813), *Stenothoe valida* Dana, 1852, *Phtisica marina* Slabber, 1769, and the NIS *Caprella mutica* Schurin, 1935, *Ericthonius pugnax* (Dana, 1852) and *Jassa slatteryi* Conlan, 1990. In Normandy, the dominant amphi-

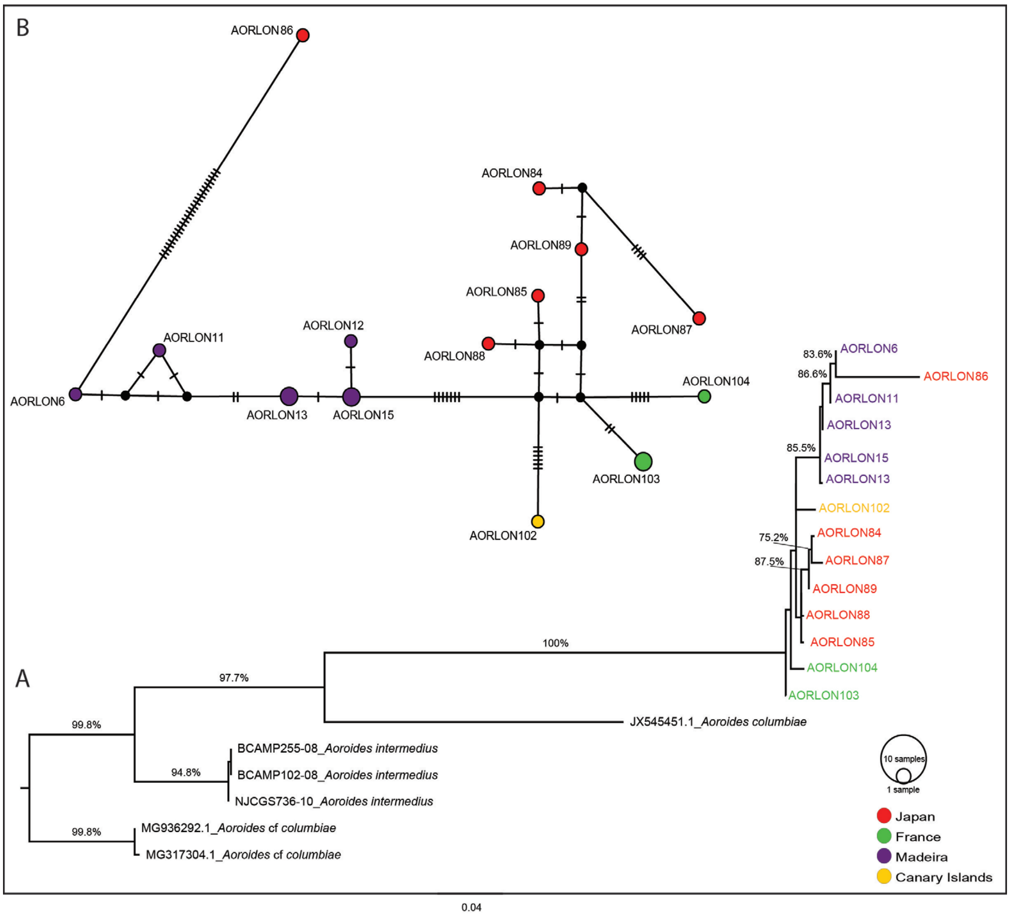

Fig. 2: Maximum likelihood phylogeny of the CO1 haplotypes (A) and relative median joining haplotype network (B). Only bootstrap support values >70% are shown on branches for each subsequent node (1000 bootstrap). The colours refer to the sampling areas and the size of the circles is proportional to the number of specimens with the same haplotype. Black circles refer to missing haplotypes, and small vertical bars on branches represent the mutation steps between two haplotypes.

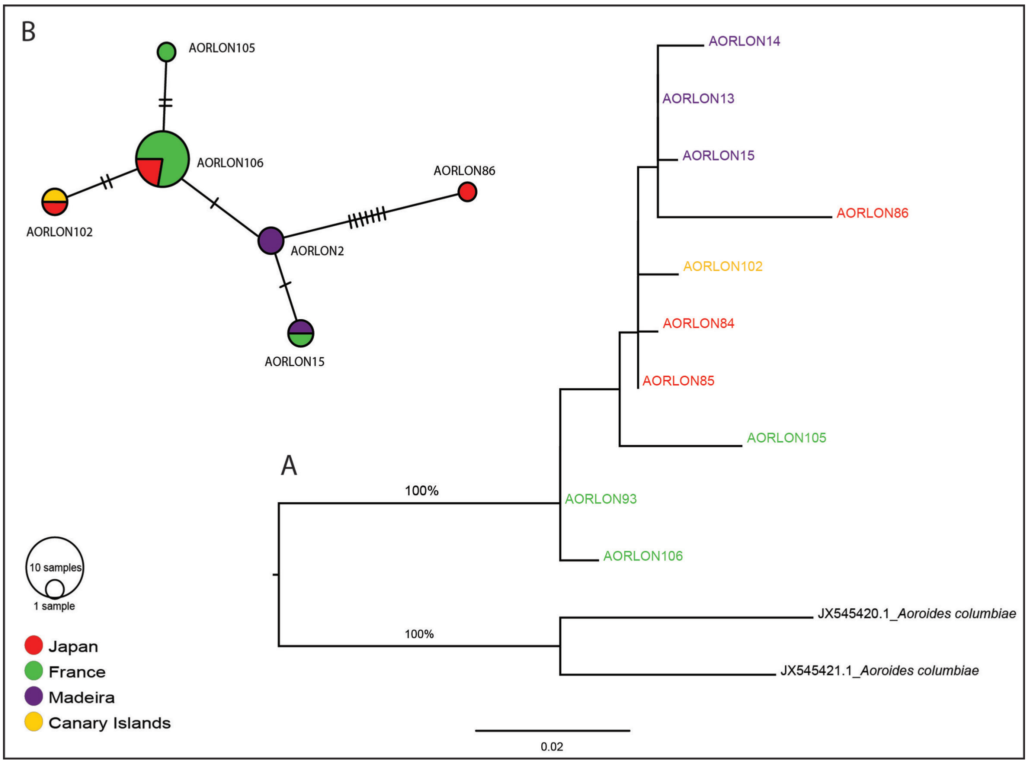

Fig. 3: Maximum likelihood phylogeny of the 16S haplotypes (A) and relative median joining haplotype network (B). For the phylogeny, only bootstrap support values >70% are shown on branches for each subsequent node (1000 bootstrap). The colours refer to the sampling areas and the size of the circles is proportional to the number of specimens with the same haplotype. Black circles refer to missing haplotypes, and small vertical bars on branches represent the mutation steps between two haplotypes.

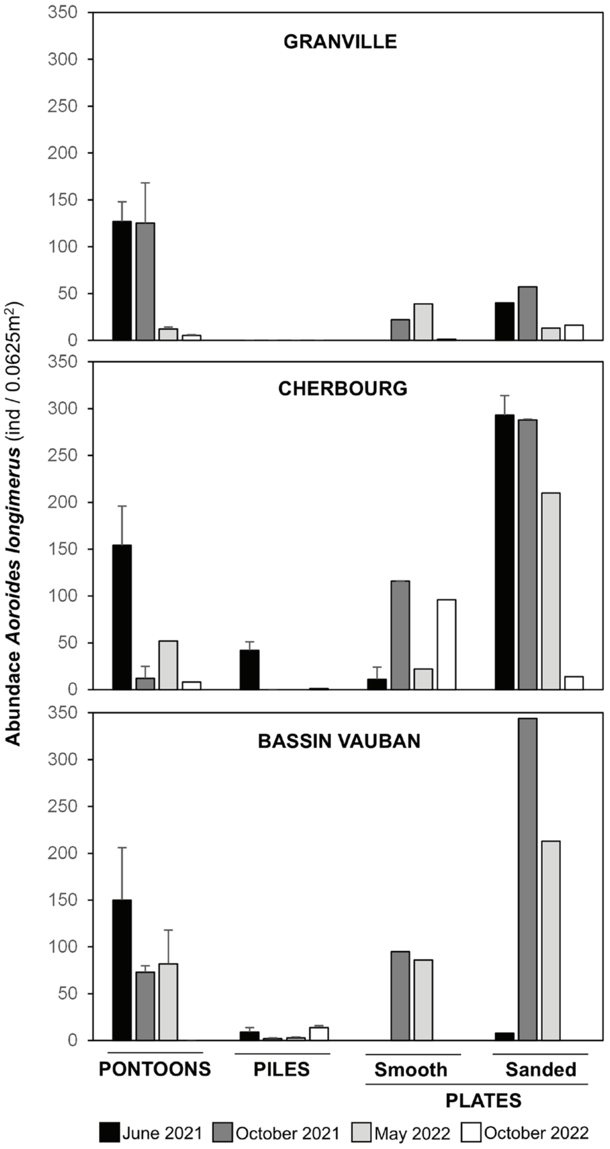

Fig. 4: Abundance of *Aoroides longimerus* Ren & Zheng, 1996 (ind/0.0625m^2) on pontoons, piles and PVC plates (smooth and sanded) of three marinas from Normandy, France (see Text S1 for detailed protocol). Data for pontoons and piles represent mean values with standard error from three replicates; data for plates correspond to a single plate per marina deployed for ca. 6 months prior sampling times (June 2021, October 2021, May 2022 and October 2022). Although the species was also present in Dieppe marina, it was only found in very low abundances in October 2022 and data was not represented in the figure.

pods cohabiting with *A. longimerus* were *Ericthonius punctatus* (Spence Bate, 1857), *Ischyrocerus anguipes* Krøyer, 1838, *Leptocheirus pilosus* Zaddach, 1844, *Leucothoe spinicarpa* (Abildgaard, 1789), *Monocorophium acherusicum* (A. Costa, 1853), *M. sextonae* and the NIS *Caprella mutica*. In the Gulf of La Spezia, Italy, *A. longimerus* was sharing habitat with *Apocorophium acutum* (Chevreux, 1908), *Elasmopus rapax* Costa, 1853, *Ericthonius punctatus* and the NIS *Jassa slatteryi* and *Laticorophium baconi* (Shoemaker, 1834).

Aoroides longimerus clearly showed a detritivorous diet. Digestive contents were found in 102 of the 125 specimens analysed and consisted almost exclusively of detritus in all specimens, regardless of sex, location and sampling time. The total area of the whole digestive tract occupied by detritus ranged from 30% to 100%. Although copepods were also found in the gut contents of six specimens, they were probably ingested accidentally alongside the detritus.

Discussion

Taxonomic remarks on Aoroides

The presence of merochelate gnathopod 1 in *Aoroides* males has also been observed in males of *Aora* Krøyer, 1845, a genus typically found in European waters. However, these two genera can be readily distinguished by the following characteristics, which are even present in females and juveniles: (i) the accessory flagellum in antenna 1 is present in *Aora*, but absent in *Aoroides*; and (ii) the article 3 of the mandibular palp is semifalciform and highly setose (bearing short and pectinate setae) in *Aora*, whereas in *Aoroides* it is rectilinear and poorly setose, with few terminal long setae, except in the two species that lack mandibular palp (Gouillieux *et al*., 2015; Dauvin *et al*., 2020).

Aoroides longimerus was originally described by Ren & Zheng in 1996 based mainly on the setose gnathopod 1 of the male and round-triangle eyes. The genus *Aoroides* currently contains 21 valid species (WoRMS Editorial Board, 2025).

Aoroides columbiae, the type species of the genus, was originally described based on females found in Puget Sound, so information about the male gnathopod 1 was lacking. Although the description and figures were incomplete, the mandibular palp differs from that of *A. longimerus* (three setae on distal article and one seta on second article in *A. columbiae* compared to only two apical setae in *A. longimerus*). Conlan & Bousfield (1982) redescribed the species including male figures and a description. Although the male gnathopod 1 in *A. columbiae* is very setose, as in *A. longimerus*, the dorsal (= anterior) margin of the carpus is bare, except for a distal group of short setae. In contrast, this dorsal margin is densely covered by setae in *A. longimerus*. Furthermore, Conlan & Bousfield (1982) indicated simple setae on the distal end of coxa of gnathopod 1, while they are plumose in *A. longimerus* (Fig. 1).

Aoroides secundus Gurjanova, 1938, was described in the Japan Sea based on a single male specimen. Its eyes are narrow and reniform, differing from those of *A. longimerus*. The species was redescribed by Ariyama (2004), who pointed out that *A. secundus* can be distinguished from *A. longimerus* by the coxae of gnathopod 1 (with plumose setae *in A. longimerus* and lacking plumose setae in *A. secundus*). Indeed, Kim *et al*. (2024) pointed out the presence of only two simple setae in the coxa of *A. secundus*.

Aoroides nahili Barnard, 1970 was described from Oahu, Hawaiian Islands. Despite the incompleteness of its description and illustrations, it can be distinguished from *A. longimerus* by the presence of three setae on the mandibular palp and a non-densely setose male gnathopod 1 (see Barnard, 1970).

Conlan & Bousfield (1982) described four species of *Aoroides* (*Aoroides exilis* Conlan & Bousfield, 1982, *Aoroides inermis* Conlan & Bousfield, 1982, *Aoroides intermedius* Conlan & Bousfield, 1982 and *Aoroides spinosus* Conlan & Bousfield, 1982). They also elaborated a key to distinguish the seven species described so far. While *A. inermis* and *A. intermedius* have a seta on the article 2 of the mandibular palp, this seta is absent in *A. exilis* and *A. spinosus*, as well as in *A. longimerus*. These three species can be further differentiated because the dorsal (= anterior) margin of the carpus is bare or scarcely setose in *A. exilis* and *A. spinosus*, but densely setose in *A. longimerus*.

Myers (1995) described *Aoroides vitiosus* Myers, 1995 from the north coast of Papua New Guinea. The species resembles *A. nahili* from Hawaii in having a scarcely setose gnathopod 1, but it differs by the absence of a mandibular palp. Indeed, the absence of a mandibular palp could be considered sufficient for the establishment of a new genus. However, based on the similarity of this species to *A. nahili*, which has a typical *Aoroides* form mandibular palp, Myers (1995) maintained this species within the genus and suggested that the diagnosis of the genus should be modified to include species lacking a mandibular palp.

Ariyama (2004) described seven species from Osaka Bay, central Japan (*Aoroides columnaris* Ariyama, 2004, *Aoroides curvipes* Ariyama, 2004, *Aoroides ellipticus* Ariyama, 2004, *Aoroides myojinensis* Ariyama, 2004, *Aoroides punctatus* Ariyama, 2004, *Aoroides rubellus* Ariyama, 2004 and *Aoroides semicurvatus* Ariyama, 2004) and redescribed *A. longimerus* and *A. secundus*, providing a key to *Aoroides* species. Males of *A. columnaris*, *A. curvipes* and *A. semicurvatus* have poorly setose gnathopod 1, while the remaining species have densely setose gnathopod 1. However, *A. ellipticus*, *A. punctatus* and *A. rubellus* have a few or no setae on the dorsal (= anterior) margin of the carpus. Ariyama (2004) pointed out that *A. longimerus* can be distinguished from the *A. myojinensis* by the presence of several plumose setae on the anterior margin of coxa 1.

Myers (2009) described two additional species, *Aoroides palfreyensis* Myers, 2009 and *Aoroides parvus* Myers, 2009, from the Great Barrier Reef, Australia. Both species are characterised by a poorly setose male gnathopod 1. Additionally, *A. palfreyensis* lacks a mandibular palp, like *A. vitiosus*.

Another *Aoroides* species, *Aoroides sagamiensis* Ariyama & Kohtsuka, 2022 was described from Japan. Ariyama & Kohtsuka (2022) pointed out the distinctive male gnathopod 1 of this species, which has a poorly setose basis and heavily setose merus, close to *A. rubellus*.

Ariyama & Kawabe (2022) described *Aoroides macrops* Ariyama & Kawabe, 2022, also from Japan. *A. macrops* is probably one of the most morphologically similar species to *A. longimerus*, as it has a heavily setose male gnathopod 1, with the coxa bearing several plumose setae anteriorly, and the uropod 2 with a short inter-ramal process (Ariyama & Kawabe, 2022). However, *A. macrops* can be distinguished from the Japanese specimens of *A. longimerus* by having (i) larger eyes, (ii) shorter peduncular article 4 of the antenna 2 (with a length/body length ratio of 0.11-0.12, compared to ca. 0.14 in *A. longimerus*), (iii) shorter carpus of the male gnathopod 1 (with a length/body length ratio of 0.13-0.16, compared to 0.19-0.21 in A. *longimerus*), (iv) shorter carpus of the pereopods 3 and 4 (with a length/width ratio of ca. 1.7 compared to 1.9-2.3 in *A. longimerus*), and (v) single marginal robust seta each on the uropod 3 rami (usually two or three in *A. longimerus*) (see Ariyama & Kawabe, 2022 for details).

Kim *et al*. (2024) described the species *Aoroides gracilicrus* Kim, Choi, Kim, Im & Kim, 2024 from South Korea. It is also morphologically similar to *A. longimerus* but it can be distinguished by the presence of a single anterior robust and plumose setae in gnathopod 1 coxa (in contrast to the multiple plumose setae in *A. longimerus*), and the absence of setae on both rami of uropod 3 (in contrast to the robust setae present in *A. longimerus*).

Morphological and molecular characteristics ascertaining **Aoroides longimerus** *presence in Europe*

Among the described *Aoroides* species, three have recently been reported in European waters: *A. longimerus*, *A. semicurvatus* and *A. curvipes* (Gouillieux *et al*., 2015). *Aoroides longimerus* can be easily distinguished from the other two NIS, mainly by the male gnathopod 1 densely setose (Ariyama, 2004; Gouillieux *et al*., 2015).

When the specimens from the present study were compared with the 21 known *Aoroides* species, they were found to fully agree with the detailed description of *A. longimerus* from Japan (see Ariyama, 2004). The main diagnostic characteristics are: (i) fully setose gnathopod 1, with coxa provided with a bunch of plumose setae, (ii) article 2 of the mandible palp without setae and article 3 (distal one) bearing two apical setae, and (iii) both rami of uropod 3 armed with robust setae (see Fig. 1). The description of Japanese specimens (Ariyama, 2004) and those from the introduced range also align with the type specimens from China (Ren & Zheng, 1996), except for larger eyes and a single marginal robust seta on the uropod 3 rami in the Chinese specimens (see Fig. 2-1 and 2-9 respectively) (Ariyama & Kawabe, 2022). Although Figure 2 in Ren & Zheng (1996) shows a cluster of setae on the coxa of gnathopod 1, the description does not indicate whether they are simple or plumose. The type material of *A. longimerus* (four male paratypes 92CA-002, as detailed in Ren & Zheng, 1996) was examined by one of the coauthors (YW). Despite some specimens being poorly preserved and some characters being uncheckable, the examination confirmed the presence of a bunch of plumose setae in the coxa of gnathopod 1. The number of marginal spines in the uropod 3 rami was variable (1 or 2) depending on the paratype. Indeed, Ariyama (2004) pointed out that the number of spines on the outer and inner ramus of uropod 3 ranged from one to three, thus supporting the variability of this character. Consequently, although the uropods of Japanese and European specimens are more armed (Ariyama, 2004; Fig. 1, present study), this character appears to be variable.

Molecular data corroborate morphological evidence. DNA results from the present study indicate that the specimens from Japan and those from the introduced range belong to the same species. However, one female specimen collected in Japan, AORLON86, clearly diverged from all the others, regardless of the method used (Figs. 2 and 3). As identifying females is very difficult, this specimen probably belongs to a different species of *Aoroides*. In fact, *A. secundus* dwells in a similar environment to that of *A. longimerus* in Hannan City (HA, pers. obs.). Alternatively, this finding could also suggest the presence of a species complex. The possible cryptic taxonomic diversity of *A. longimerus* in its native range should be further investigated through morphological studies and deeper molecular analyses (e.g., use of other genes such as 28S) of newly collected specimens. Unfortunately, fresh material of *A. longimerus* from China could not be collected during the present study, and, as a result, Chinese populations could not be incorporated into molecular analyses to confirm that Japanese and Chinese specimens belong to the same species. New collections from the type locality in China are essential to resolve this taxonomic uncertainty. This information is critical to assess the likelihood of multiple taxa being introduced or spreading (secondary introductions) in the future.

Ecological remarks

In its native range, *A. longimerus* lives in association with sessile invertebrates (such as ascidians, bryozoans, hydrozoans and sponges), as well as among algae in shallow subtidal waters, in sediments, on pebble or shell bottoms, under stones in the intertidal, and within artificial substrates (Ren & Zhen, 1996; Ariyama, 2004, 2022; present study) (Table 1). It is interesting to note that the species was first described by Ren & Zheng (1996) based on specimens found in fouling communities. These authors reported 22 species of fouling amphipods from test plates, buoys, mariculture net cages and intertidal zones in Dayawan (Guangdong province, South China Sea), but did not specify whether *A. longimerus* occurred across all these habitats. Most of the current data on its habitat use in the native range come from Japanese populations.

Within its introduced range, *A. longimerus* is primarily associated with fouling communities in aquaculture facilities, marinas and ports (e.g., pontoons, ropes, piles and PVC plates), typically among mussels, ascidians and bryozoans (Gouillieux *et al*., 2015; Dauvin *et al*., 2020; present study). The species has also been recorded on ship hulls (Ulman *et al*., 2017). In addition to artificial habitats, *A. longimerus* has been found in natural environments such as macroalgal beds, slipper limpet aggregations, oyster reefs, and seagrass meadows (Gouilleux *et al*., 2015; present study) (Table 1).

Establishment and introduction pathways

Aoroides longimerus is now recorded across both Mediterranean and Atlantic waters (Table 1). The species was first detected in mainland Portugal in the marinas of Cascais and Sines in 2011. It was subsequently recorded again in Sines (both at the marina and the commercial terminals of the Port of Sines) in 2019, 2022, and 2023, suggesting well-established population in this area. Similarly, *A. longimerus* was found in Madeira in 2019 and again in 2024. It is also well established in France, at least in Normandy (collected in 2019, 2021 and 2022) and in the Bay of Brest (collected in 2014 and 2024), as well as in Italy (collected in the Gulf of La Spezia between 2018 and 2022). In the Netherlands, the species was collected from Kortgene, Delta marina, in 2020 and 2024. In Spain, populations of the Ría de Vigo, Galicia, seem well-established, with collections from April to August 2019, and again during 2021-2022. In Tunisia, the species was collected in several sampling events at Shira fishing port between March and November 2023. Overall, these records indicate the presence of stable populations of *A.*

longimerus in the Netherlands, France, Portugal, Spain, Tunisia, and Italy.

The haplotype network for the 16S marker showed shared haplotypes among Japan, Canary Islands and France (Fig. 3) that may suggest a common origin for the individuals introduced in Europe. However, the notable molecular divergence observed with the CO1 marker between the samples collected in Madeira and those collected in France and the Canary Islands suggests that multiple introductions may have occurred from different source populations within the native range, as often documented in marine species (Rius *et al*., 2015). This hypothesis should be investigated in future genetic studies with a larger sampling across both native and introduced regions.

The original description of the species from China based on specimens collected from fouling communities, supports the idea that this species has been spread to other areas via anthropogenic vectors.

Unlike other small non-indigenous amphipods, such as *Caprella scaura* Templeton, 1836, *Laticorophium baconi* or *Stenothoe georgiana* Bynum & Fox, 1977, which were documented in Australian waters in 1890, 1990 and 2017, respectively (Ros *et al*., 2014; Martínez-Laiz *et al*., 2020; Guerra-García *et al*., 2023), *A. longimerus* has not yet been reported from Australia. Nevertheless, the information provided in this study (Table S1) is mainly based on revised samples collected between 1964 and 2002. Further research is required to ascertain whether the species could have arrived in Australia within the last 20 years. In contrast to other amphipod species such as *L. baconi* or *C. scaura*, which are widely distributed across their introduced ranges (Ros *et al*., 2014; Guerra-García *et al*., 2023), *A. longimerus* is absent from many marinas, ports and aquaculture facilities in the Iberian Peninsula, Italy, Tunisia, the Netherlands, Croatia, Greece and Saudi Arabia (Table S1). This pattern could indicate that, while marinas and port facilities are key for the secondary spread of *A. longimerus*, this species may have a more limited ability to spread within these environments than other non-indigenous amphipods. Alternatively, *A. longimerus* could still be in the early stage of its introduction since this study confirms the capacity to survive during seasonal fluctuations throughout the year and its remarkable colonisation capacity based on its settlement on PVC plates (see Table 1 and Fig. 3). Therefore, special attention must be paid to the potential threat of further spread in the coming years.

Gouillieux *et al.* (2015) suggested that *A. longimerus* could been accidentally introduced in Arcachon Bay and Hossegor Lake through oyster transfers and in the Bay of Brest possibly through both oyster transfers and shipping. Similarly, Dauvin *et al.* (2020) suggested that *A. longimerus* was unintentionally introduced in Normandy through oyster transfers from French production centres of the oyster *Magallana gigas* (Thunberg, 1793). Indeed, Saint-Vaast-la-Hougue (Table 1) is a key location in Normandy for oyster production, with continuous transfers between production centres of the Bay of Biscay and the English Channel (Dauvin *et al*., 2020). Along the Iberian Peninsula, an important population was found in marinas within the Ría de Vigo, Galicia, while the species remains absent from most other sampled marinas across Spain and Portugal (Table S1). The high intensity of aquaculture activities along the Galician coasts (Almón *et al*., 2014), primarily mussel and oyster farms (Ruiz *et al*., 1992), supports the hypothesis that aquaculture may be the main vector for NIS introductions in this region, which is considered a hotspot for invasions (Pascual *et al*., 2010). Indeed, this study confirms the presence of *A. longimerus* in a mussel farm in the Ría de Vigo. In the Gulf of La Spezia, Italy, the species was first observed in 2018 at only one locality (Santa Teresa), which is the only site located in front of a mussel farm. The species was not recorded in other locations until 2021, suggesting initial introduction via aquaculture, followed by secondary spread to adjacent marinas. Additionally, the growing number of oyster hatcheries in France (Iitembu *et al*., 2023) may have played an important role in the secondary spread of *A. longimerus* through the movement of oyster seed stock exported to other European countries. In any case, the current distribution of *A. longimerus* may be explained by multiple vectors and pathways, as often shown for marine NIS (Ojaveer *et al*., 2018; Bailey *et al*., 2020). These authors also underlined the large uncertainties in pathways' assessment for marine NIS, emphasizing the need for caution and continued investigation regarding this topic.

Most records of *A. longimerus* in natural environments are in its native range, while in the introduced range, the species mainly inhabits artificial substrates (Table 1). For example, in the Iberian Peninsula, *A. longimerus* has not yet been found in natural environments despite recent efforts to characterise epifaunal communities inhabiting subtidal algae and other substrates (e.g., Navarro-Barranco *et al*., 2015, 2018, 2019, 2021, 2023). This pattern is common among non-indigenous amphipods in European waters, such as *Caprella scaura* (Ros *et al*., 2014), *Paracaprella pusilla* Mayer, 1890 (Ros & Guerra-García, 2012), *Stenothoe georgiana* (Martínez-Laiz *et al*., 2020) and *Laticorophium baconi* (Guerra-García *et al*., 2023). However, unlike other NIS of the genus *Aoroides* (i.e., *A. curvipes* and *A. semicurvatus*), which are restricted to aquaculture oyster facilities, *A. longimerus* has been observed in diverse subtidal habitats in Arcachon Bay (Gouillieux *et al*., 2015). These authors hypothesised that *A. longimerus* may have dispersed from oyster beds in Arcachon Bay, through natural migration or hull fouling of recreational boats, subsequently establishing successful populations in natural habitats such as seagrass meadows or littoral limpet beds. In fact, the present study also confirms the presence of *A. longimerus* in natural habitats within its introduced range, such as Kneiss Islands in Tunisia. These islands are notable for their mud and sand flats, which are of international importance for their bird diversity. The area was declared a national nature reserve in 1993 and subsequently designated a "Specially Protected Area of Mediterranean Importance" (SPAMI) in 2001, an "Important Bird Area" (IBA) in 2003 and a "RAMSAR site" in 2007 (Moshabi *et al*., 2020). The detection of *A. longimerus* in such ecologically sensitive and protected habitats highlights the urgent need to implement robust monitoring and surveillance programmes aimed at the early detection of further potential introduction and spread of *A. longimerus* into other natural habitats, where it could eventually alter the composition and ecological dynamics of the native communities.

Importance of scientific collaboration

Gouillieux *et al.* (2015) suggested that species of *Aoroides* may have been present in European waters for decades, yet remained unobserved due to the following factors: (i) the genus is not listed in the taxonomic keys generally used to identify amphipods in European waters (e.g., Chevreux & Fage, 1925; Lincoln, 1979; Ruffo, 1982); (ii) specimens are fragile, often loosing gnathopods and antennae during the sieving process, which makes identification difficult and increases the likelihood of confusion with *Aora* genus; (iii) *Aoroides* species occur in particular habitats, such as fouling communities in artificial environments, that are not usually sampled in routine benthic surveys using corers or grabs. In this sense, increased taxonomic and sampling efforts are therefore essential for accurately assessing the status of *Aoroides* in the Mediterranean and adjacent Atlantic waters.

Scientific collaboration, taxonomic expertise, and knowledge dissemination have been crucial to update the distribution of various non-indigenous amphipods in recent years (e.g., Martínez-Laiz *et al.*, 2020; Guerra-García *et al.*, 2023). Indeed, several strategies have been proposed to ensure that NIS information is properly disseminated at all levels (Martínez-Laiz *et al.*, 2020; Carvalho *et al.*, 2023). The following actions are to be taken: (i) facilitation of enhanced opportunities for knowledge exchange between senior and early-career taxonomists; (ii) development of training programmes and online courses to build taxonomic capacity, especially in under-represented regions and institutions; (iii) establishment of expert networks that bring together taxonomists, molecular scientists and invasion ecologists; (iv) support for participation of researchers in international events such as workshops and conferences focused on taxonomy and bioinvasions; (v) creation of open-access identification keys and field guides for NIS, including both morphological and molecular tools; (vi) development of internationally coordinated long-term monitoring programmes; (vii) increase of opportunities for information exchange between research scientists, environmental management agencies and other stakeholders, including funding agencies; (viii) regular update of open-access NIS databases, ensuring the accuracy and relevance of available information; and (ix) implementation of citizen science initiatives to support early detection and data collection on NIS, encouraging public engagement.

Scientific collaboration has resulted not only in providing an accurate distribution of the species but also backdating previous records (see Galanidi *et al.*, 2025). The present study exemplifies how collaboration and information exchange among researchers can lead to the re-examination of historical material, the collection of new samples, the integration of molecular tools, and the revision of morphological characters. These joint efforts provide a crucial baseline for further monitoring programmes and the development of effective management strategies.

Acknowledgements

The study was conducted within the collaborative initiatives MEDAMP (Mediterranean and Adjacent Seas Amphipod Reference Library) and PoLBOL (Polish Barcode of Life) and was also supported by the Horizon Europe “Biodiversity Genomics Europe” project (Project: 101059492 –BGE– HORIZON-CL6-2021-BIODIV-01). Financial support for this study was provided by the Ministerio de Economía y Competitividad (Project CGL2017-82739-P) co-financed by the ERDF, European Union, and predoctoral grants from the Spanish Government to PS-A (Reference FPU20/04016) and SR-V (Reference FPU21/02406). J-P P was supported by the project CHABIMANOR (Caractérisation des Habitats Biogéniques de substrats durs dans les MArinas NORmandes) financed by “Agence de l’Eau Seine-Normandie”. J-C L received funding from the European Union’s Horizon 2020 research programme under the Marie Skłodowska-Curie grant agreement no. 899546. IG was supported by EMERGIA contract funded by Junta de Andalucía (DGP_EMEC_2023_00528). PR was financed by Fundação para a Ciência e Tecnologia (FCT) through the strategic project [UIDB/ 04292] granted to MARE UI&I. J C-C was funded by national funds through FCT—Fundação para a Ciência e Tecnologia, IP, under the Scientific Employment Stimulus Institutional Call (CEEC-INST/00098/2018). SC received baseline funding from KAUST. EM and AB thank their colleagues Marco Lezzi, Rocco Auriemma, Giuseppe Catalano and Yann Toso who helped with the sorting of Italian samples. PS-A thanks his colleague Sergio C. García-Gómez for his support and advice during the identification process. We acknowledge the staff of all the marinas, ports, and aquaculture facilities who granted permission for conducting the sampling and observational field studies.

References

Almón, B., Pérez, J., Bañón, R., Trigo, J., 2014. First record of *Caprella mutica* from the Iberian Peninsula: expansion southwards in European waters. *Marine Biodiversity Records*, 7, e30.

Arfianti, T., Costello, M.J., 2020. Global biogeography of marine amphipod crustaceans: latitude, regionalization, and beta diversity. *Marine Ecology Progress Series*, 638, 83-94.

Ariyama, H., 2004. Nine species of the genus *Aoroides* (Crustacea: Amphipoda: Aoridae) from Osaka Bay, Central Japan. *Publications of the Seto Marine Biological Laboratory*, 40 (1-2), 1-66.

Ariyama, H., 2022. Guidebook of Gammaridean Amphipoda. Kaibundo, Tokyo, 160 pp. (in Japanese).

Ariyama, H., Kawabe, K., 2022. Two new species of Aoridae from Chichijima Island, the Ogasawara Islands in Japan (Crustacea: Amphipoda). *Species Diversity*, 27 (1), 113-128.

Ariyama, H., Kohtsuka, H., 2022. Three new species of the family Aoridae collected from Sagami Bay, central Japan (Crustacea: Amphipoda). *Zootaxa*, 5159 (3), 393-413.

Bailey, S.A., Brown, L., Campbell, M.L., Canning-Clode, J., Carlton, J.T. *et al*., 2020. Trends in the detection of aquatic non-indigenous species across global marine, estuarine and freshwater ecosystems: A 50-year perspective. *Diversity and Distributions*, 26 (12), 1780-1797.

Barnard, J.L., 1970. Sublittoral Gammaridea (Amphipoda) of the Hawaiian Islands. *Smithsonian Contributions to Zoology*, 34, 1-286.

Barnard, J.L., Karaman, G.S., 1991. The families and genera of marine gammaridean Amphipoda (except marine gammaroids). *Records of the Australian Museum*, (Suppl. 13) Part 1, 1-417.

Bell, S.S., 1991. Amphipods as insect equivalents? An alternative view. *Ecology*, 72 (1), 350-354.

Bello, C.L., Cabrera, M.I., 1999. Uso de la técnica microhistológica de Cavender y Hansen en la identificación de insectos acuáticos. *Boletín Entomológico de Venezuela*, 14, 77-79.

Beermann, J., Hall-Mullen, A.K., Havermans, C., Coolen, J.W.P., Crooijmans, R.P.M.A. *et al*., 2020. Ancient globetrotters connectivity and putative native ranges of two cosmopolitan biofouling amphipods. *PeerJ*, 8, e9613.

Carvalho, S., Shchepanik, H., Aylagas, E., Berumen, M.L., Costa, F.O. *et al*., 2023. Hurdles and opportunities in implementing marine biosecurity systems in data-poor regions. *BioScience*, 73 (7), 494-512.

Casquet, J., Thebaud, C., Gillespie, R.G., 2012. Chelex without boiling, a rapid and easy technique to obtain stable amplifiable DNA from small amounts of ethanol-stored spiders. *Molecular Ecology Resources*, 12, 136-141.

Castro, N., Carlton, J.T., Costa, A.C., Marques, C.S., Hewitt, C. *et al*., 2022. Diversity and patterns of marine non-native species in the archipelagos of Macaronesia. *Diversity and Distributions*, 28 (4), 667-684.

Chevreux, E., Fage, L., 1925. Amphipodes. Volume 9. Paris: Office Central de Faunistique, Librairie de la Faculté des Sciences.

Clark, K., Karsch-Mizrachi, I., Lipman, D.J., Ostell, J., Sayers, E.W., 2016. GenBank. Nucleic Acids Research, 44 (D1), D67-72.

CIEMAR, 2021. Substrato duro subtidal. Monitorização de Ambientes Marinhos do Porto de Sines - MAPSi 2018/2020. Relatório final. Laboratório de Ciências do Mar da Universidade de Évora. 191 pp. (report for the Port of Sines Administration).

CIEMAR, 2025. Substrato duro subtidal. Monitorização de Ambientes Marinhos do Porto de Sines - MAPSi 2021/2023. Relatório final. Laboratório de Ciências do Mar da Universidade de Évora. 275 pp. (report for the Port of Sines Administration).

Cuthbert, R.N., Pattison, Z., Taylor, N.G., Verbrugge, L., Diagne, C. *et al*., 2021. Global economic costs of aquatic invasive alien species. *Science of the Total Environment*, 775, 145238.

Conlan, K.E., Bousfield, E.L., 1982. The superfamily Corophioidea in the North Pacific region. Family Aoridae: systematics and distributional ecology. *National Museum of Natural Sciences (Ottawa), Publications in Biological Oceanography*, 10, 77-101.

Dauvin, J.-C., Pezy, J.-P., Raoux, A., 2020. First records of *Aoroides longimerus* Ren and Zheng, 1996, and *A. semicurvatus* Ariyama, 2004 (Crustacea, Amphipoda), in the English Channel, France. *BioInvasions Records*, 4, 753-762.

DQEM, 2020. Estratégia Marinha. Relatório do 2º ciclo, Parte D - Reavaliação do Estado Ambiental e Definição de Metas, subdivisão dos Açores. Governo dos Açores, Diretiva Quadro Estratégia Marinha, março 2020.

Faasse, M., Gittenberger, A., 2021. De exotische vlokreeften *Aoroides longimerus* en *Erichthonius didymus* bereiken Nederland (Crustacea: Amphipoda). *Nederlandse Faunistische Mededelingen*, 57, 81-88.

Galanidi, M., Gratsia, E., Zenetos, A., 2025. Backdating first records of non-indigenous species in the Mediterranean: are initial findings underestimated? *Mediterranean Marine Science*, 26 (3), 642-656.

Gouillieux, B., Lavesque, N., Leclerc, J.-C., Le Garrec, V., Viard, F. *et al*., 2015. Three non-indigenous species of *Aoroides* (Crustacea: Amphipoda: Aoridae) from the French Atlantic Coast. *Journal of the Marine Biological Association of the United Kingdom*, 96 (8), 1651-1659.

Guerra-García, J.M., Tierno de Figueroa, J.T., Navarro-Barranco, C., Ros, M., Sánchez-Moyano, J.E. *et al*., 2014. Dietary analysis of the marine Amphipoda (Crustacea: Peracarida) from the Iberian Peninsula. *Journal of Sea Research*, 85, 508-517.

Guerra-García, J.M., Revanales, T., Saenz-Arias, P., Navarro-Barranco, C., Ruiz-Velasco, S. *et al*., 2023. Quick spreading of the exotic amphipod *Laticorophium baconi* (Shoemaker, 1934): another small stowaway overlooked? *Mediterranean Marine Science*, 24 (3), 644-665.

Guindon, S., Dufayard, J., Lefort, V., Anisimova, M., Hordijk, W.O.G. *et al*., 2010. New algorithms and methods to estimate maximum-likelihood phylogenies: Assessing the performance of PhyML 3 .0. *Systematic Biology*, 59 (3), 307-321.

Gurjanova, E., 1938. Amphipoda, Gammaroidea zalikov Siaukhu i Sudzukhe (Yaponskoe More). [Amphipoda, Gammaroidea of Siaukhu Bay and Sudzukhe Bay (Japan Sea)]. Reports of the Japan Sea Hydrobiological Expedition of the Zoological Institute of the Academy of Sciences USSR in 1934. 1, 241-404.

Hou, Z., Fu, J., Li, S.A., 2007. Molecular phylogeny of the genus *Gammarus* (Crustacea: Amphipoda) based on mitochondrial and nuclear gene sequences. *Molecular Phylogenetics and Evolution*, 45 (2), 596-611.

ICES, 2018. Interim Report of the Working Group on Introductions and Transfers of Marine Organisms (WGITMO). 7-9 March 2018, Madeira, Portugal. ICES CM 2018/HAPISG:11. 179 pp.

Iitembu, J.A., Fitzgerald, D., Altintzoglou, T., Boudry, P., Britz, P. *et al*., 2023. Comparative description and analysis of oyster aquaculture in selected Atlantic regions: production, market dynamics, and consumption patterns. *Fishes*, 8 (12), 584.

Kim, J., Choi, J. H., Kim, Y. J., Im, H.W., Kim, Y. H., 2024. Two new species of the family Aoridae (Crustacea, Malacostraca, Amphipoda) from Korean waters. *ZooKeys*, 1210, 117-132.

Larkin, M.A., Blackshields, G., Brown, N.P., Chenna, R., McGettigan, P.A. *et al*., 2007. Clustal W and Clustal X version 2.0. *Bioinformatics*, 23, 2947-2948.

Lefort, V., Longueville, J.-E., Gascuel, O., 2017. SMS: Smart model selection in PhyML. *Molecular Biology and Evolution*, 34 (9): 2422-2424.

Lincoln, R.J., 1979. British marine Amphipoda: Gammaridea. London: British Museum (Natural History).

Lobo, J., Costa, P.M., Teixeira, M.A., Ferreira, M.S.G., Costa, M.H. *et al.*, 2013. Enhanced primers for amplification of DNA barcodes from a broad range of marine metazoans. *BMC Ecology*, 13, 34.

Macdonald III, K.S., Yampolsky, L., Duffy, J.E., 2005. Molecular and morphological evolution of the amphipod radiation of Lake Baikal. *Molecular Phylogenetics and Evolution*, 35, 323-343.

Marchini, A., Cardeccia, A., 2017. Alien amphipods in a sea of troubles: cryptogenic species, unresolved taxonomy and overlooked introductions. *Marine Biology*, 164 (4), 69.

Martínez-Laiz, G., Ros, M., Guerra-García, J.M., Marchini, A., Fernandez-Gonzalez, V., *et al*., 2020. Scientific collaboration for early detection of invaders results in a significant update on estimated range: Lessons from *Stenothoe georgiana* Bynum & Fox 1977. *Mediterranean Marine Science*, 21 (2), 464-481.

Martínez-Laiz, G., MacLeod, C.D., Hesketh, A.V., Konecny, C.A., Ros, M. *et al*., 2022. The journey of hull-fouling mobile invaders: basibionts and boldness mediate dislodgement risk during transit. *Biofouling*, 38 (8), 837-851.

Mosbahi, N., Boudaya, L., Neifar, L., Dauvin, J.C., 2020. Do intertidal *Zostera noltei* meadows represent a favourable habitat for amphipods? The case of the Kneiss Islands (Gulf of Gabès: Central Mediterranean Sea). *Marine Ecology*, 41 (3), 1-16.

Myers, A.A., 1995. The Amphipoda (Crustacea) of Madang Lagoon: Aoridae, Isaeidae, Ischyroceridae and Neomegamphopidae. In Lowry, J.K. (Ed.). The Amphipoda (Crustacea) of Madang Lagoon, Papua New Guinea, Part 1. *Records of the Australian Museum, Supplement*, 22, 25-95.

Myers, A.A., 2009. Aoridae. In: Lowry, J.K., Myers, A.A. (Eds.) Benthic Amphipoda (Crustacea: Peracarida) of the Great Barrier Reef, Australia. *Zootaxa*, 2260, 220-278.

Navarro-Barranco, C., Guerra-García, J.M., Sánchez-Tocino, L., Ros, M., Florido, M. *et al*., 2015. Colonization and successional patterns of the mobile epifaunal community along an environmental gradient in a marine cave. *Marine Ecology Progress Series*, 521, 105-115.

Navarro-Barranco, C., Florido, M., Ros, M., González-Romero, P., Guerra-García, J.M., 2018. Impoverished mobile epifaunal assemblages associated with the invasive macroalga *Asparagopsis taxiformis* in the Mediterranean Sea. *Marine Environmental Research*, 141, 44-52.

Navarro-Barranco, C., Muñoz-Gómez, B., Saiz, D., Ros, M., Guerra-García, J.M. *et al*., 2019. Can invasive habitat-forming species play the same role as native ones? The case of the exotic marine macroalga *Rugulopteryx okamurae* in the Strait of Gibraltar. *Biological Invasions*, 21, 3319-3334.

Navarro-Barranco, C., Moreira, J., Espinosa, F., Ros, M., Rallis, I. *et al*., 2021. Evaluating the vulnerability of coralligenous epifauna to macroalgal invasions. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 31 (9), 2305-2319.

Navarro-Barranco, C., Lanza-Arroyo, P., Gutiérrez-Serrano, J., Moreira, J., 2023. Amphipod assemblages associated with native habitat-forming seaweeds of the Alboran Sea: influence by environmental protection and biogeographical patterns. *Marine and Freshwater Research*, 74, 50-64.

Ojaveer, H., Galil, B.S., Carlton, J.T., Alleway, H., Goulletquer, P. *et al*., 2018. Historical baselines in marine bioinvasions: Implications for policy and management. *PloS ONE*, 13 (8), e0202383.

Palumbi, S.R., 1996. What can molecular genetics contribute to marine biogeography? An urchin's tale. *Journal of Experimental Marine Biology and Ecology*, 203 (1), 75-92.

Pascual, S., Villalba, A., Abollo, E., Garci, M., González, A.F. *et al*., 2010. The mussel *Xenostrobus securis*: a well-established alien invader in the Ria de Vigo (Spain, NE Atlantic). *Biological Invasions*, 12, 2091-2103.

Ratnasingham, S., Wei, C., Chan, D., Agda, J., Agda, J., *et al*. 2024. BOLD v4: A centralized bioinformatics platform for DNA-based biodiversity data. *Methods in Molecular Biology*, 2744, 403-441.

Ren, X., Zheng, C., 1996. Fouling Amphipoda (Crustacea) from Dayawan, Guangdong Province China (South China Sea). *Annual Research Reports*, *Marine Biology Research Station at Dayawan*, *South China Sea Institute of Oceanology*, *the Chinese Academy of Sciences*, 1, 58-78 [in Chinese with English abstract and descriptions of new species].

Rius, M., Turon, X., Bernard, G., Volckaert, F., Viard, F., 2015. Marine invasion genetics: from spatial and temporal patterns to evolutionary outcomes. *Biological Invasions*, 17 (3), 869-885.

Ros, M., Guerra-García, J.M., 2012. On the occurrence of the tropical caprellid *Paracaprella pusilla* Mayer, 1890 (Crustacea: Amphipoda) in Europe. *Mediterranean Marine Science*, 13 (1), 134-139.

Ros, M., Guerra-García, J.M., Navarro-Barranco, C., Cabezas, M.P., Vázquez-Luis, M., 2014. The spreading of the non-native caprellid (Crustacea: Amphipoda) *Caprella scaura* Templeton, 1836 into southern Europe and northern Africa: a complicated taxonomic history. *Mediterranean Marine Science*, 15 (1), 145-155.

Ruffo, S. (Ed.), 1982. The Amphipoda of the Mediterranean. Part 1. Gammaridea (Acanthonotozomatidae to Gammaridae). *Mémoires de l'Institut Océanographique de Monaco*, 13, 1-364.

Ruiz, C., Abad, M., Sedano, F., Garcia-Martin, L.O., Sánchez-López, J.L., 1992. Influence of seasonal environmental changes on the gamete production and biochemical composition of *Crassostrea gigas* (Thunberg) in suspended culture in El Grove, Galicia, Spain. *Journal of Experimental Marine Biology and Ecology*, 155 (2), 249-262.

Saenz-Arias, P., Navarro-Barranco, C., Ros, M., Moreira, J., Guerra-García, J.M., 2022a. Exploring biocontamination in associated macrofaunal assemblages in marinas: Soft bottoms vs artificial hard substrate. Where and what to look for? *Marine Pollution Bulletin*, 185, 114346.

Saenz-Arias, P., Navarro-Barranco, C., Guerra-García, J.M., 2022b. Influence of environmental factors and sessile biota on vagile epibionts: The case of amphipods in marinas across a regional scale. *Mediterranean Marine Science*, 23 (1), 1-13.

Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A. *et al*., 2007. Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *BioScience*, 57 (7), 573-583.

Sun, Y., Wong, E., Keppel, E., Williamson, J.E., Kupriyanova, E.K., 2017. A global invader or a complex of regionally distributed species? Clarifying the status of an invasive calcareous tubeworm *Hydroides dianthus* (Verrill, 1873) (Polychaeta: Serpulidae) using DNA barcoding. *Marine Biology*, 164, 1-12.

Tamura, K., Stecher, G., Kumar, S., 2021. MEGA11: Molecular Evolutionary Genetics Analysis version 11. *Molecular Biology and Evolution*, 38 (7), 3022-3027.

Ulman, A., Ferrario, J., Occhpinti-Ambrogi, A., Arvanitidis, C., Bandi, A. *et al*., 2017. A massive update of non-indigenous species records in Mediterranean marinas. *PeerJ*, 5, e3954.

Walker, A.O., 1898. Crustacea collected by W.A. Herdmann, F.R.S., in Puget Sound, Pacific coast of North America, September 1897. *Transactions of the Liverpool Biological Society*, 12, 268-287.

WoRMS Editorial Board, 2025. World register of marine species. https://www. marinespecies.org. at VLIZ.

Zenetos, A., Gratsia, E., Cardoso, A.C., Tsiamis, K., 2019. Time lags in reporting of biological invasions: the case of Mediterranean Sea. *Mediterranean Marine Science*, 20 (2), 469-475.

Supplementary Data

The following supplementary information is available online for the article:

Text S1. Detailed information on sampling surveys.

Table S1. List of localities sampled by the authors where presence of *Aoroides longimerus* Ren & Zheng, 1996 has not been detected.

Table S2. Detailed information on voucher material of *Aoroides longimerus* Ren & Zheng, 1996 deposited in Museo Nacional de Ciencias Naturales de Madrid (MNCN), Spain, and Muséum national d'Histoire Naturelle Paris (MNHN) France, including Museum Catalogue numbers, sampling locations, coordinates, collection date, substrates and number of specimens.