



**HAL**  
open science

## **“Hidden” biodiversity: a new amphipod genus dominates epifauna in association with a mesophotic black coral forest**

Sandra Navarro-Mayoral, Benoit Gouillieux, Victoria Fernandez-Gonzalez, Fernando Tuya, Ninon Lecoquierre, Lorenzo Bramanti, Lucas Terrana, Fernando Espino, Jean-François Flot, Ricardo Haroun, et al.

### ► To cite this version:

Sandra Navarro-Mayoral, Benoit Gouillieux, Victoria Fernandez-Gonzalez, Fernando Tuya, Ninon Lecoquierre, et al.. “Hidden” biodiversity: a new amphipod genus dominates epifauna in association with a mesophotic black coral forest. Coral Reefs, In press, 10.1007/s00338-024-02491-y . hal-04551803

**HAL Id: hal-04551803**

**<https://hal.science/hal-04551803>**

Submitted on 18 Apr 2024

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



REPORT

# “Hidden” biodiversity: a new amphipod genus dominates epifauna in association with a mesophotic black coral forest

Sandra Navarro-Mayoral<sup>1</sup> · Benoit Gouillieux<sup>2</sup> · Victoria Fernandez-Gonzalez<sup>3</sup> · Fernando Tuya<sup>1</sup> · Ninon Lecoquierre<sup>4</sup> · Lorenzo Bramanti<sup>5,8</sup> · Lucas Terrana<sup>6,7</sup> · Fernando Espino<sup>1</sup> · Jean-François Flot<sup>4,10</sup> · Ricardo Haroun<sup>1</sup> · Francisco Otero-Ferrer<sup>1,9</sup>

Received: 30 January 2023 / Accepted: 10 March 2024  
© The Author(s) 2024

**Abstract** Black corals are important components of mesophotic and deep-water marine habitats. Their presence at great depths (e.g., 50 to 200 m) makes accessibility difficult, limiting our understanding of the associated biodiversity. Amphipods dominate vagile epifauna in marine habitats around the world, fulfilling important ecosystem functions. However, there are no studies on amphipods exclusively associated with black corals, including relationships between their ecological patterns (e.g., abundances) and the size of coral colonies. We investigated the epifaunal composition

and abundance associated with black coral colonies of *Antipathella wollastoni* in the subtropical eastern Atlantic Ocean. In total, 1,736 epifaunal individuals were identified, of which 1,706 (98.27%) were amphipods, belonging to 6 taxa. We identified and described a new amphipod genus and species within the Stenothoidae family, *Wollastenothoe minuta* gen. nov., sp. nov., which outnumbered the amphipod assemblage (86.15%) and provided a complete taxonomic key of Stenothoidae family including this new finding. For the first time, the association between an amphipod species and a black coral was described, including a strong correlation between coral colony size and amphipod abundances. This study demonstrates that epifauna associated with mesophotic black corals remains largely undescribed.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s00338-024-02491-y>.

✉ Sandra Navarro-Mayoral  
sandra.navarro@ulpgc.es

Benoit Gouillieux  
benoit.gouillieux@u-bordeaux.fr

Victoria Fernandez-Gonzalez  
victoria.fernandez@ua.es

Fernando Tuya  
fernando.tuya@ulpgc.es

Ninon Lecoquierre  
ninon.lecoquierre3@gmail.com

Lorenzo Bramanti  
lorenzo.bramanti@obs-banyuls.fr

Lucas Terrana  
lucas.terrana@tournai.be

Fernando Espino  
fesprod@gobiernodecanarias.org

Jean-François Flot  
jean-francois.flot@ulb.be

Ricardo Haroun  
ricardo.haroun@ulpgc.es

Francisco Otero-Ferrer  
francisco.otero@ulpgc.es

<sup>1</sup> Biodiversity and Conservation Research Group, IU-ECOQUA, Scientific and Technological Marine Park of the University of Las Palmas de Gran Canaria, Crta Taliarte, s/n, 35214 Telde, Canary Islands, Spain

<sup>2</sup> UMR 5805, EPOC, Bordeaux INP, CNRS, Univ. Bordeaux, 33600 Pessac, France

<sup>3</sup> Department of Marine Sciences and Applied Biology, University of Alicante, Alicante, Spain

<sup>4</sup> Evolutionary Biology and Ecology, Université libre de Bruxelles (ULB), Brussels, Belgium

<sup>5</sup> CNRS-Sorbonne\_ Université, Laboratoire d'Ecogéochimie Des Environnements Benthiques, LECOB, Observatoire Océanologique de Banyuls Sur Mer, 66650 Banyuls Sur Mer, France

<sup>6</sup> Natural History Museum and Vivarium of Tournai, Rue Saint-Martin 52, 7500 Tournai, Belgium

<sup>7</sup> Biology of Marine Organisms and Biomimetics, University of Mons, Avenue du Champ de Mars 6, 7000 Mons, Belgium

**Keywords** Stenothoidae · Key to species · *Antipathella wollastoni* · Epifauna · Marine animal forests

## Introduction

Corals are key components of sublittoral ecosystems not only in tropical (Spalding et al. 2001), but also subtropical (Czechowska et al. 2020), temperate, and cold ecosystems (Orejas et al. 2009; Bo et al. 2014; Buhl-Mortensen et al. 2018). While there are an increasing number in the studies on the classes of Scleractinia and Octocorallia, inhabiting various depth zones, Antipatharia (Cnidaria: Anthozoa: Hexacorallia) has received relatively less attention (Bo et al. 2012). Antipatharians, commonly known as black corals, encompasses over 300 accepted species (Molodtsova and Opresko 2023) and, under favorable environmental conditions, can form dense aggregations, creating “coral forests” (a type of animal forests, sensu Rossi et al. 2017) or “coral gardens” (sensu Hall-Spencer and Tasker 2006). These communities have some structural and functional similarities with terrestrial forests, with the main difference that they are dominated by animals instead of plants (Rossi et al. 2017). Their colony morphology varies from branched, bush-like, and feather-like to whip types (Wagner et al. 2012). The dense canopies they form can change local physical conditions and generate a three-dimensional habitat, which provide shelter to associated species and, ultimately, increase biodiversity (Freiwald et al. 2004; Buhl-Mortensen et al. 2010; De Clippele et al. 2019). One of the main components of the visible black coral forests-associated biodiversity is accounted by epifauna (i.e., crustaceans, polychaetes and molluscs, Lavelle 2012; Wagner et al. 2012), which can find habitat (Herler 2007), food (Angel 1990; Bo et al. 2012), and protection against predators (Lavelle 2012).

Amphipods are one of the most abundant and diverse taxa of marine macro-invertebrates (Arfianti et al. 2018), as well as a diverse and important component of deep-sea habitats worldwide (Arfianti and Costello 2020a, b). Amphipods include species with different trophic strategies (e.g., detritivores, omnivores, carnivores, and herbivores), and they are predated by other crustaceans, polychaetes, and fishes (Guerra-García et al. 2014; Jiménez Prada et al. 2015). Moreover, they play an important role in marine food webs, by directly or indirectly recycling nutrients and linking

different trophic levels (Karlson et al. 2007; Havermans and Smetacek 2018).

The amphipod family Stenothoidae includes marine benthic species ranging from the shallow subtidal to depths over 3,000 m (Krapp-Schickel 2015; Krapp-Schickel and Vader 2015). Several species of Stenothoidae have received attention from the scientific community due to their biological association (i.e., commensalism) with marine sessile cnidaria, such as anemones (Vader and Krapp-Schickel 1996; Auster et al. 2011) and hydrozoans (Lewis 1992), on which they find food, nesting grounds, and shelter (Marin and Sinelnikov 2017). However, to date, there are no studies on amphipods and their ecological interactions with black corals.

In the present study, we investigated the epifaunal composition and abundance in mesophotic forests created by the black coral *Antipathella wollastoni* (Gray 1857) from Lanzarote Island over time (Canary Islands, eastern Atlantic Ocean). Identification of sampled specimens has been performed in a robust taxonomic framework and resulted in the description of a new amphipod genus and species within the Stenothoidae family, for which a complete key to genera is provided. Then, we described the first biological association between an amphipod species (i.e., *Wollastenothoe minuta* gen. nov., sp. nov.) and a black coral species. Specifically, the relationship between coral colony size and amphipod abundances was tested for both the entire amphipod assemblage and the new described species, suggesting an exclusive association.

## Material and methods

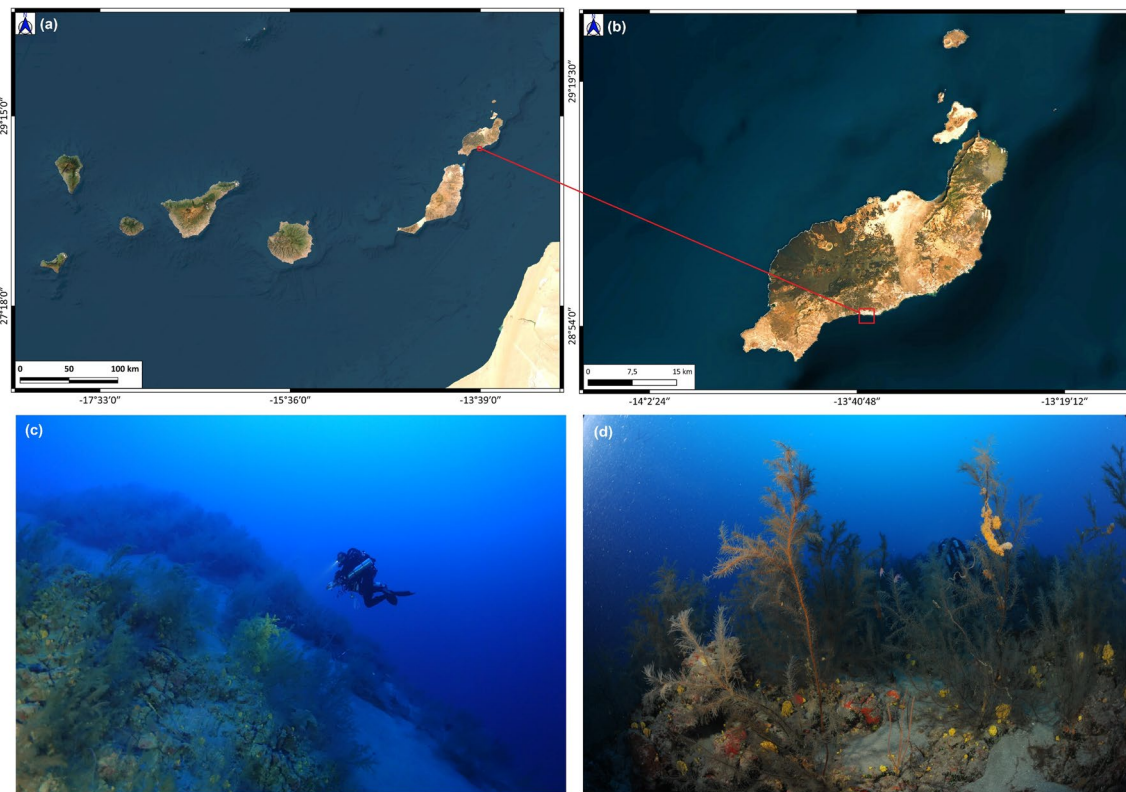
### Study region

The study was conducted in the Southeastern coast of Lanzarote Island (Canary Islands, eastern Atlantic Ocean) at Puerto del Carmen (28°55'26.81" N, 13° 39' 12.61" W) (Fig. 1a, b). The site was selected based on previous records of *A. wollastoni* in the shallower limits of its depth distribution range (ca. 60 m depth, Fig. 1c, d) (Bianchi et al. 2000; Czechowska et al. 2020). In this area, local topography is characterized by narrow rocky shelves and steep slopes, typical of oceanic volcanic islands (Acosta et al. 2005; Tuya et al. 2021). Local hydrography is complex, with NE trade winds affecting shallow subtidal habitats by generating wind waves and near-bottom turbulence (Mann and Lazier 2013). The high nutrient load transported by currents may affect the upper limit of black coral distribution, by either providing food or physically smothering the corals (Wagner et al. 2012; Czechowska et al. 2020).

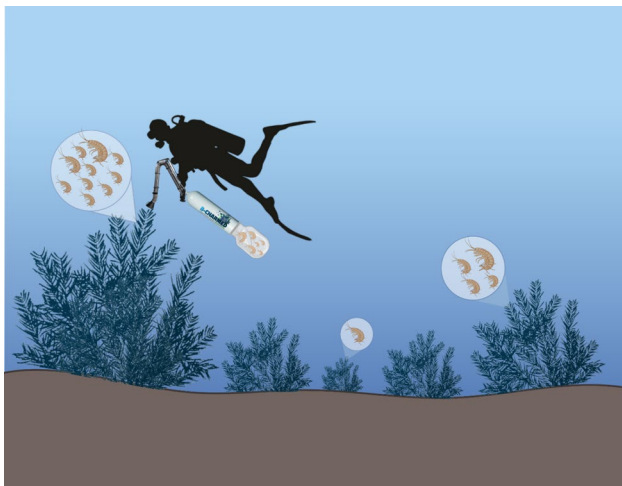
<sup>8</sup> Under The Pole Expeditions, 1 Rue Des Senneurs, 29900 Concarneau, France

<sup>9</sup> Department of Origins and Evolution, Muséum National d'Histoire Naturelle, MNHN, 75 Rue Cuvier, 75005 Paris, France

<sup>10</sup> Interuniversity Institute of Bioinformatics in Brussels – (IB)<sup>2</sup>, Brussels, Belgium



**Fig. 1** Map of the Canary Islands in the eastern Atlantic Ocean (a), including the study site located in the Southeastern coast of Lanzarote Island (b). Mesophotic black coral forest of *Antipathella wollastoni* (c and d)



**Fig. 2** Epifauna was collected in mesophotic forests of *A. wollastoni* by sucking up coral branches through a small vacuum cleaner for 20 s

### Sampling design and collection of samples

Epifauna was collected in mesophotic monospecific forests of *A. wollastoni* at three times during 2021: T1 (February),

T2 (April), and T3 (October). At each time, 10 colonies spanning between 40 and 180 cm (total height from the seafloor to the upper tip of the colony) were selected randomly, for a total of 30 colonies. All sampling was carried out at the same depth (*ca.* 60 m), taking care to not sample twice the same area. Sampling was carried out by two divers using mixed-gas rebreather diving. On each colony, samples of associated epifauna were collected by sucking up on their top branches through a vacuum cleaner for 20 s (Fig. 2). The temperature was monitored between February and October 2021 by a temperature data logger (Hobo data-logger Pedant Temp-Light, Onset Computer Corporation, USA; sampling frequency 15 min) positioned next to the black corals.

### Specimen processing

Collected epifauna was directly brought to the laboratory after surfacing in sealed containers filled with seawater. Then, each sample was carefully inspected, rinsed, and sorted to separate epifauna from marine debris and coral mucus. Each organism was then stored in 96% ethanol and identified to the lowest taxonomical level. Identifications were implemented by using a stereoscopic microscope (Leica, EZ4W, Wetzlar,



Germany). The taxonomic guide provided by Barnard and Karaman (1991), Ruffo (1998), and specific references from the Stenothoidae family (i.e., Krapp-Schickel 2000, 2011, 2015) was used for amphipod identification. Specifically, 68 specimens of the new amphipod genus/species were dissected in alcohol and mounted on microscope slides using dimethylhydantoin–formaldehyde resin for morphological description. Appendages were observed under a Nikon SMZ800N stereomicroscope and a Nikon Eclipse Ci microscope and photographed with a Nikon DS-Fi2 camera. Body length (BL) was measured with NIS-Elements Analysis software from the anterior margin of the head to the posterior end of the telson. Drawings were carried out from pictures using Inkscape software (v.0.48). For scanning electron microscope (SEM) observations, 12 specimens were dehydrated in a graded ethanol series, critical point dried, using carbon dioxide as a medium, mounted on stubs, coated with gold for 60 s sputter coated with gold, and photographed with a Hitachi tabletop microscope TM3030Plus.

### DNA sequencing

DNA extraction was performed on a pool of 23 ethanol-preserved specimens using the MagAttract DNA Extraction Kit (Qiagen) following the manufacturer's protocol. Folmer's 658-bp fragment of the first subunit of cytochrome *c* oxidase mitochondrial gene (COI) was amplified using primers LCO1490 and HCO2198 (Folmer et al. 1994). In addition, a fragment of the 28S rRNA gene (28S) was amplified using primers from Verovnik et al. (2005). All amplifications were performed using DreamTaq Green PCR Master Mix (ThermoScientific). For COI, the PCR protocol involved an initial denaturation period at 94 °C for 3 min, followed by 50 cycles of denaturation at 94 °C for 30 s, annealing at 45 °C for 1 min, and elongation at 72 °C for 1 min. For 28S, the PCR protocol comprised an initial denaturation period at 94 °C for 3 min, then 40 cycles of denaturation at 94 °C for 20 s, annealing at 50 °C for 50 s, and elongation at 72 °C for 1 min. PCR products were checked on 1% agarose gel, and subsequently, 1–2 µL of each PCR product (depending on band intensity) was pooled (together with other PCR products from unrelated research projects). The pool was then cleaned up using the InnuPREP PCRpure Kit (Innuscreen) and used to prepare a SKQ-LSK114 library that was sequenced on a FLO-FLG114 Nanopore Flongle flow cell featuring R10.4.1 pore proteins. The resulting reads (1264 for COI and 1932 for 28S) were assembled using amplicon\_sorter (Vierstraete and Braeckman 2022).

### Phylogenetic analyses

For the COI marker, all Stenothoidae sequences available in GenBank on 19 November 2023 were collected and

complemented with sequences of *Iphimedia obesa* and *Gitana sarsi* as outgroups. Alignment was performed by hand in MEGA11 (Tamura et al. 2021) taking into account the amino acid translation of the sequences, followed by maximum likelihood phylogenetic analysis using IQtree2 (Minh et al. 2020) with automatic model selection (Kalyanamoorthy et al. 2017) and 100,000 ultrafast bootstraps (Hoang et al. 2018). The resulting Newick tree was displayed, re-rooted, and turned into PDF in MEGA11.

### Statistical analyses

All modeling and testing were conducted using R (Rstudio Team 2022). Mixed effects generalized linear models (GLMs) were fitted to univariate responses, including the total abundance of amphipods and the abundance of the new genus and species, *Wollastenothoe minuta* gen. nov., sp. nov. GLMs were fitted by means of the 'lme4' (Bates et al. 2014) and 'lmerTest' packages (Kuznetsova et al. 2017) considering time (three levels) as a random factor and the size of colonies of *A. wollastoni* as a covariate. Models were fitted using a 'negative binomial', as the family distribution of residuals, with a 'log' link function. For all fitted GLMs, diagnosis plots of residuals and Q-Q plots were visually inspected to check the appropriateness of the fitted models (Harrison et al. 2018). We realized simple linear regressions tested whether the total abundance of amphipod and the abundance of *W. minuta* gen. nov., sp. nov., were predicted by the colony size.

## Results

### Taxonomy

Class Malacostraca Latreille 1806

Order Amphipoda Latreille 1816

Suborder Senticaudata Lowry & Myers 2013

Family Stenothoidae Boeck 1871

Genus *Wollastenothoe* Gouillieux & Navarro-Mayoral gen. nov.

urn:lsid:zoobank.org:act:5FFE2706-D2F1-4EB9-B6A8-B341FF6D10D5.

Type species. *Wollastenothoe minuta* Gouillieux & Navarro-Mayoral gen. nov., sp. nov., here designated.

### Diagnosis of the new genus

Body dorsally smooth. Head without rostrum. Antenna 1 article 1 not nasiform; accessory flagellum with 1 article. Mandible palp with 1 article, molar process conical. Maxilla 1 palp with 2 articles. Gnathopod 1 and 2 subchelate,

subequal. P5 basis rectilinear without posterodistal lobe. P6-7 basis widened.

### Etymology

The genus name, *Wollastenothoe*, refers the combination of host name corresponding to the species of black coral (i.e., *Antipathella wollastoni*) with the genus name *Stenothoe* belonging to the Stenothoidae family.

### Remarks on genus assignation and Stenothoidae diagnosis

Characters of the present new genus agree with the diagnosis of the Stenothoidae family except for the molar process of the mandible. In the present new genus, molar process is slightly developed, conical, whereas the diagnosis for the family Stenothoidae includes a molar process evanescent. This conical shape of the molar process is already present in other genera of Stenothoidae, such as *Antatelson*, *Pseudothamatelson*, *Ptychotelson*, *Raukumara* or *Thamatelsonella*. According to Horton et al. (2022), 46 genera belong to the family Stenothoidae, and only 12 present a mandibular palp uniaarticulate: *Ausatelson* J.L. Barnard 1972; *Metopelloides* Gurjanova 1938; *Paraprobolisca* Ren in Ren & Huang 1991; *Prostenothoe* Gurjanova 1938; *Prothamatelson* Schellenberg 1931; *Pseudothamatelson* Schellenberg 1931; *Ptychotelson* Krapp-Schickel 2000; *Stenothoides* Chevreux 1900; *Stenula* J.L. Barnard 1962; *Victometopa* Krapp-Schickel 2011; *Vonimetopa* Barnard & Karaman 1987 and *Zaikometopa* Barnard & Karaman 1987. *Wollastenothoe* gen. nov. can be distinguished from *Ausatelson*, *Metopelloides*, *Prostenothoe*, *Prothamatelson*, *Ptychotelson*, *Stenula*, *Vonimetopa* and *Zaikometopa* by the presence of an uniaarticulate accessory flagellum (vs absence), with *Paraprobolisca* and *Pseudothamatelson* by pereopod 7 basis expanded (vs rectilinear), with *Victometopa* by pereopod 5 without posterodistal lobe (vs with) and with *Stenothoides* by 2-articulate maxilla 1 palp (vs 1-articulate). In the case of *Paraprobolisca*, the only species of this genus, *Paraprobolisca leptopoda* Ren in Ren & Huang 1991 was synonymized with *Probolisca ovata* (Stebbing 1888) by Krapp-Schickel and Koenemann (2006). They based their diagnosis on the morphological similarities of the gnathopods and the mouthparts and considered that the uropod 3 described as being one-articulated in *Paraprobolisca leptopoda*, a character of the genus, has simply been overlooked and should be two-articulated as for *Probolisca ovata*. Even if most of species have uropod 3 ramus two-articulated, some have an one-articulated uropod 3 ramus as some *Raukumara* J.L. Barnard 1972 species. Furthermore, *Probolisca*

*ovata* presents uropods 1 and 2 peduncles marginally bares, whereas *Paraprobolisca leptopoda* has uropods 1 and 2 peduncles with many robust setae along outer margin. Thus, based on the original descriptions, we consider *Paraprobolisca leptopoda* as a valid species that should not be synonymized with *Probolisca ovata*.

***Wollastenothoe minuta*** Gouillieux & Navarro-Mayoral sp. nov.

urn:lsid:zoobank.org:act:7A70A805-5499-4FC6-93AD-1A8CE17C53DE **Description of *Wollastenothoe minuta*.**

Type material.

Holotype: brooding female, BL = 1.38 mm, 1 egg (MNHN-IU-2016-3389). Paratypes: brooding female, BL = 1.21 mm, 1 egg, dissected specimen, 11 slides (MNHN-IU-2016-3388); brooding female, BL = 1.45 mm, 2 eggs, dissected specimen, 11 slides (MNHN-IU-2016-3387); female with oostegites, BL = 1.37 mm, dissected specimen, 12 slides (MNHN-IU-2021-8807). Atlantic Ocean, European waters, Canary Islands, Puerto del Carmen in Lanzarote Island. 28°55'26"81" N, 13°39'12"61" W, October 2021, 60 m depth, collected by technical diving and rebreathers with the air-vacuum method on black coral branches. Collectors: Francisco Otero-Ferrer, Lorenzo Bramanti and Lucas Terrana.

Additional material: 5 juveniles, 53 females and 10 specimens sex not determined (MNHN-IU-2016-3359), 12 specimens used for SEM pictures (MNHN-IU-2021-8808). Same data as holotype and paratypes.

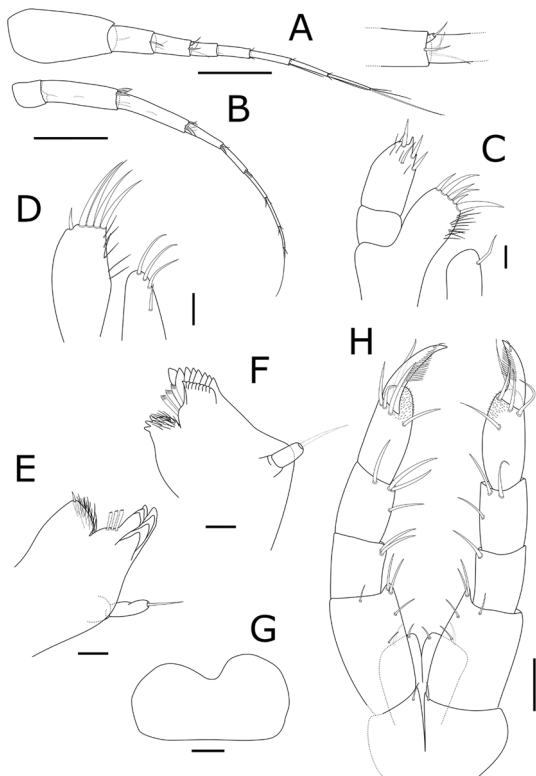
### Diagnosis

Body length less than 1.5 mm. Antenna subequal, shorter than half length of body. Antenna 1 accessory flagellum with 1 small article. Gnathopod 1 and 2 subchelate, subequal. Pereonite 4 slightly longer than pereonite 3. Coxa 4 ventral margin concave. Coxae 5–7 posterior margin with a notch. P5 basis rectilinear without posterodistal lobe. P6-7 basis widened with posterodistal lobe reaching along half of ischium, merus posterodistal lobe reaching more than half length of carpus. Telson with dorsal spines.

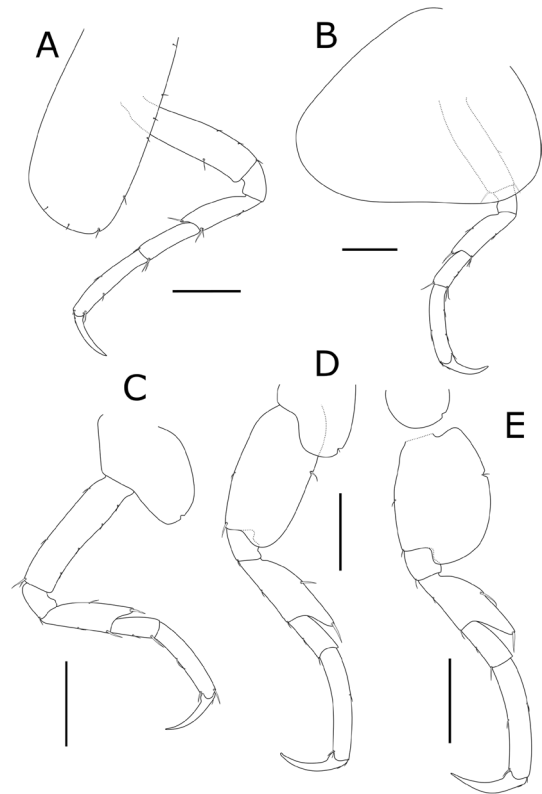
Description based on holotype and paratypes (Figs. 3, 4, 5, 6, 7).

**Body** (Fig. 6a) dorsally smooth, very compressed laterally. Pereonite 4 slightly longer than pereonite 3. Urosomites free.

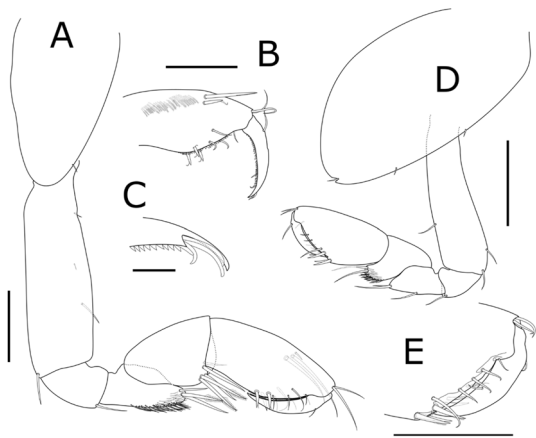
**Head. Antennae** subequal in length, setose. **Antenna 1** (Fig. 3aA) peduncle article 1 slightly tapering distally, about 2 times longer than wide; article 2 cylindrical, about half length of article 1; article 3 cylindrical, subequal to article 2; flagellum consists of 4 articles increasing in length, accessory flagellum 1 articulate, very small, with 1 to 3 distal setae. **Antenna 2** (Fig. 3bB) peduncular article 3 cylindrical, as long as wide;



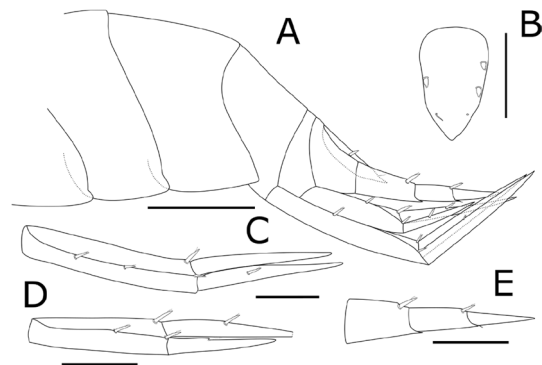
**Fig. 3** *Wollastenotheoe minuta* gen. nov., sp. nov. **a, b, e, f, h**: Paratype MNHN-IU-2016-3387, BL: 1.37 mm. **c, d**: Paratype MNHN-IU-2016-3388, BL: 1.21 mm. **g**: Based on SEM picture, MNHN-IU-2021-8808. **a** Right antenna 1 with a focus on accessory flagellum; **b** Right antenna 2; **c** Left maxilla 1; **d** Left maxilla 2, **e** Mandible left; **f** Mandible right; **g** Upper lip; **h** Maxilliped. Scale bars: **a, b**: 0.1 mm; **c-g**: 0.01 mm; **h**: 0.025 mm



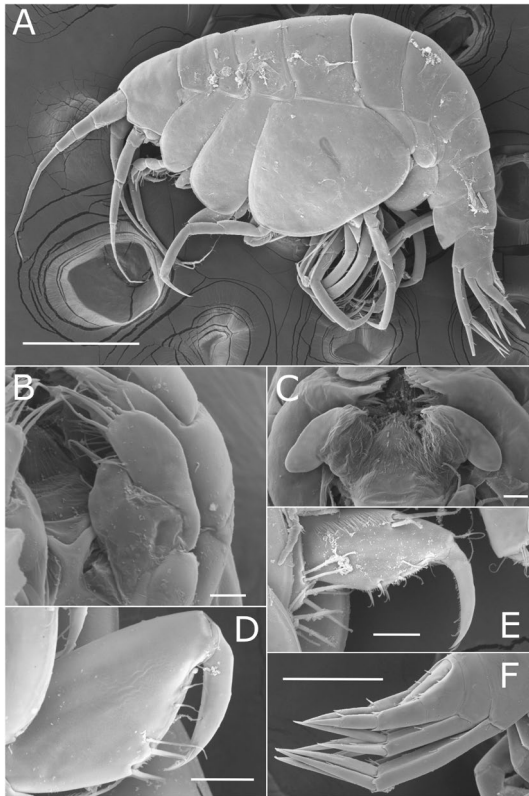
**Fig. 5** *Wollastenotheoe minuta* gen. nov., sp. nov. **a, b**: Paratype MNHN-IU-2016-3387, BL: 1.37 mm. **c, e**: Paratype MNHN-IU-2016-3388, BL=1.21 mm. **a-e**: Left pereopods 3-7. Scale bars: **a-e**: 0.1 mm



**Fig. 4** *Wollastenotheoe minuta* gen. nov., sp. nov. **a, d**: Paratype MNHN-IU-2016-3387, BL: 1.37. **b, c, e**: Based on SEM picture. **a** Gnathopod 1 right, outer view; **b** Gnathopod 1 left, propodus and dactylus, inner view; **c** Gnathopod 2, distal part of dactylus, outer view; **d** Gnathopod 1 left outer view; **e** Gnathopod 2 right, propodus and dactylus, outer view. Scale bars: **a, b, e**: 0.05 mm; **c**: 0.01 mm; **d**: 0.1 mm



**Fig. 6** *Wollastenotheoe minuta* gen. nov., sp. nov. **a**: Paratype MNHN-IU-2016-3388. **b**: Based on SEM picture, MNHN-IU-2021-8808. **c, d, e**: Paratype MNHN-IU-2016-3388, BL: 1.21 mm. **a** Posterior part, lateral view; **b** Telson, dorsal view; **c** Right uropod 1; **d** Left uropod 2, distal part of outer ramus broken; **e** right uropod 3. Scale bars: **a**: 0.1 mm; **b-e**: 0.05 mm



**Fig. 7** *Wollastenothoe minuta* gen. nov., sp. nov. SEM pictures, MNHN-IU-2021-8808. **a** Lateral view; **b** Maxilla 2, left; **c** Lower lip; **d** Gnathopod 2, outer face, dactylus and propodus; **e** Gnathopod 1, inner face, dactylus and propodus; **f** Urosome, lateral view. Scale bars: **a**: 0.25 mm; **b**: 0.01 mm; **c**: 0.01 mm, **d**, **e**: 0.02; **f**: 0.1 mm

article 4 and 5 subequal, about 2.8 times longer than article 3; flagellum consists of 5 articles of decreasing length.

**Mouthparts.** **Upper lip** (Fig. 3g) cleft at the apex, asymmetric lobes. **Mandible** (Fig. 3e–f) Palp uni-articulate with 1 or 2 distal setae, about 1.4 to 2.6 longer than wide, partial suture line sometimes visible at the base of the palp; incisor and lacinia mobilis multi-dentate; accessory setarow consists of 3 blades with comb-shaped distal part; molar process slightly developed, conical, finely setose. **Lower Lip** (Fig. 7c) Lower lip with many setae, inner lobes coalesced, mandibular lobes well developed. **Maxilla 1** (Fig. 3c) inner plate inner margin with a single simple setae, outer plate distal part with 6 large stiff robust setae; palp two-articulate, article 1 smooth, about 2 times shorter than article 2; article 2, with three distolateral robust setae, a subdistal simple seta and some little simple setae on distal part and inner plate. **Maxilla 2** (Fig. 3d, 7b) inner plate with 4 long robust setae; apical margin rounded and armed with 3 setae;

outer plate inner margin with row of 6 simple setae, distal part with 4 long and 1 short robust setae. **Maxilliped** (Fig. 3h) with reduced outer plate, inner plate with 2 distal simple setae; palp 4-articulate: article 3 the longest, with many very small setae distally; article 4 with lateral row of setae.

**Gnathopods.** **Gnathopod 1** (Figs. 4a, b, 7e) subchelate, slightly smaller to gnathopod 2; coxa tapering distally, about 1.5 times longer than wide; basis and ischium with few setae; merus posterior and distal margins with dense small simple setae, posterodistal margin with long simple and plumose setae; carpus widening distally, posterodistal corner with long simple and plumose setae; propodus about twice as long as wide, dorsal margin bare except 2 dorsodistal setae, inner face with row of fine and small plumose setae and 2 or 3 long subdorsal setae; propodus palmar edge serrate, 3 stout robust setae at the base of propodus; dactylus with serrate cutting margin and 2 or 3 simple setae, subdistal notch with 4 setae. **Gnathopod 2** (Figs. 4c–e, 7d) subchelate; coxa anteroventral margin regularly rounded, 1.8 times longer than wide, posteroventral corner notched; basis to carpus similar to gnathopod 1; propodus about twice as long as wide, dorsal margin bare except 2 dorsodistal setae; propodus palmar edge not serrated except a small part between 4 stout robust setae at the base of propodus; dactylus with 1 or 2 simple setae along cutting margin, not serrate, subdistal setae present without subdistal notch.

**Pereopods.** **Pereopods 3–7** subequal in length, with few setae; ischium posterodistal seta absent for pereopods 3–4, present for pereopods 5–7; merus with distal lobe increasing in length, dactylus with dorsal seta. **Pereopod 3** (Fig. 5a) coxa elongate, somewhat rectangular, posteroventral corner notched; length ratio of articles from basis to dactylus about 3.3:1:1.9:1.8:2.7:1.5; basis rectilinear, about 3.8 times longer than wide; merus about twice as long as wide, with small distodorsal lobe reaching 0.2 length of carpus; carpus 3.5 as long as wide; propodus elongated, about 5.5 times longer than wide. **Pereopod 4** (Fig. 5b) similar in shape to pereopod 3 except for coxa very large, subtriangular, about the same length as the first four segments of the thorax, reaching half-length of ischium, smooth, unarmed, ventral margin slightly concave; length ratio of articles from basis to dactylus about 4.5:1:2.7:1.8:3.3:1.7. **Pereopods 5–7** ischium to dactylus similar in shape, merus increasingly expanded. **Pereopod 5** (Fig. 5c) coxa mostly developed posteriorly, posterior margin notched with a simple seta inside; length ratio of articles from basis to dactylus about 4.3:1:2.1:1.4:2.8:1.8; basis rectilinear, without posterodistal lobe. **Pereopod 6** (Fig. 5d) coxa posterior margin notched with a simple seta inside; length ratio of articles from basis



to dactylus about 5:1:2.6:1.6:4:2; basis slightly expanded, about 2 times longer than wide, posterior margin notched with a simple seta inside, posterodistal lobe reaching half-length of ischium. **Pereopod 7** (Fig. 5e) coxa rounded, posterior margin notched with a simple seta inside; length ratio of articles from basis to dactylus about 6.3:1:2:1.6:3.8:2.1; basis expanded, slightly longer than wide, posterior margin notched with a simple seta inside, posterodistal lobe reaching two-thirds of ischium length; merus about 1.4 longer than wide, posterodistal lobe reaching 0.7 length of carpus.

**Epimeral plates** (Fig. 6a) 1–3 smooth, posteroventral corner weakly produced in a blunt lobe, more or less pronounced; posterior margin weakly convex.

**Uropods** (Figs. 6a, 7f). **Uropod 1** (Fig. 6c) biramous; peduncle about 1.2 times longer than rami, with 2 robust setae on outer margin and a distal one, and 1 distal robust seta on inner margin; rami subequal, outer ramus with 1 dorsal robust seta, inner ramus with or without 1 dorsal robust seta. **Uropod 2** (Fig. 6d) biramous; peduncle with 2 robust setae on outer margin and 1 distal robust seta on inner margin; rami unequal, inner ramus slightly longer than peduncle, 1.3 times longer than outer ramus, with 1 dorsal robust seta, inner ramus slightly smaller

than peduncle, with or without 1 dorsal robust seta. **Uropod 3** (Fig. 6e) uniramous, ramus 2-articulate, length ratio of peduncle and articles variable between 1:1:1.1 and 1.4:1:1.2; peduncle with 1 dorsodistal robust seta, ventrodistal corner produced into a small tooth; article 1 with 1 dorsodistal robust seta, ventrodistal corner produced into a small tooth with 1 simple seta, article 2 unarmed, smooth.

**Telson** (Fig. 6b) entire, tapering distally, with 1 or 2 lateral robust setae and a small subdistal seta on each side.

**Male**: unknown.

**Color in vivo**: Whitish brown.

**Type locality**. Puerto del Carmen (28°55'26.81" N, 13° 39' 12.61" W), Lanzarote, Canary Islands, Spain.

**Etymology**. The epithet specific of the species, *minuta*, refers to its small size.

**Key to Genera of Stenothoidae (based on Barnard & Karaman 1991 key with inclusion of recent subsequent new genera descriptions)**

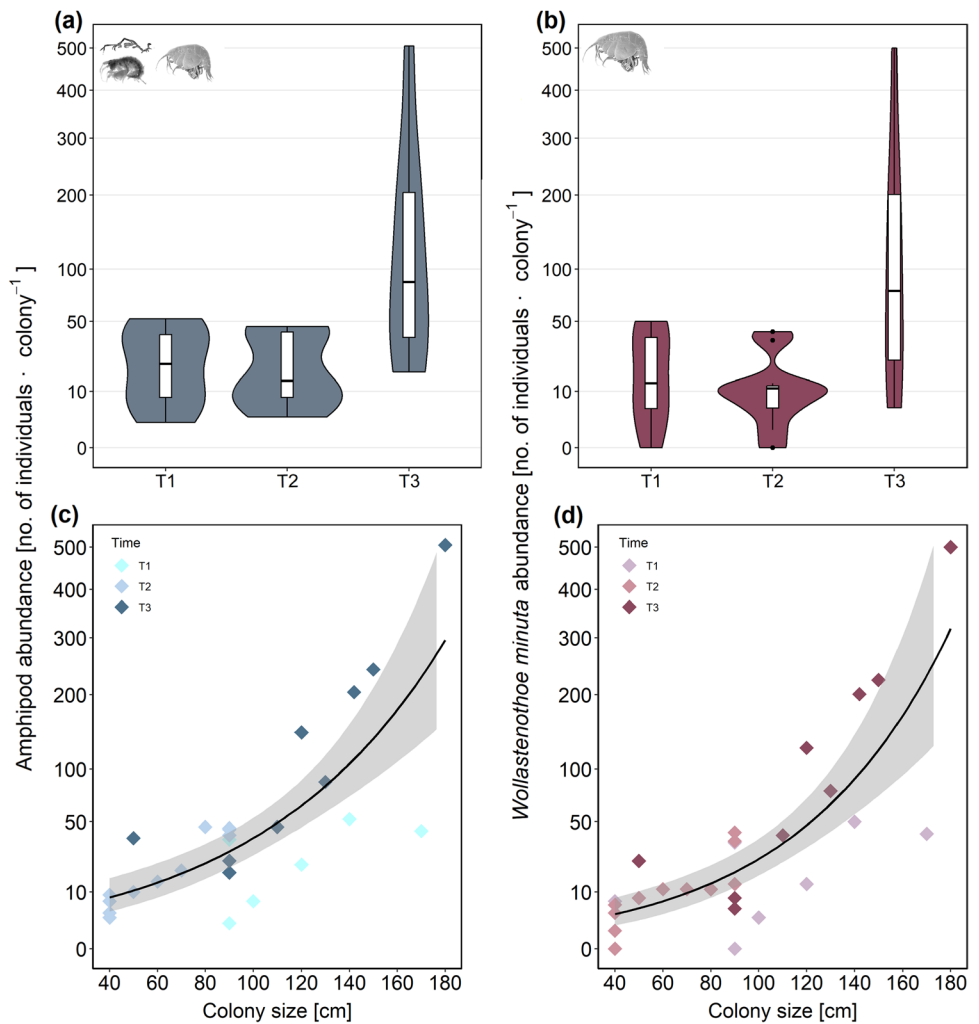
1. Article 2 of pereopod 7 rectilinear.....	2
Article 2 of pereopod 7 expanded .....	26
2. Telson thickened and fleshy .....	3
Telson flat and laminar.....	13
3. Gnathopod 2 chelate.....	4
Gnathopod 2 subchelate or simple.....	6
4. Gnathopod 1 chelate.....	<i>Raumahara</i> J.L. Barnard 1972
Gnathopod 1 subchelate or simple.....	5
5. Article 1 of antenna 1 nasiform .....	<i>Prothaumatelson</i> Schellenberg 1931
Antenna 1 not nasiform .....	<i>Ptychotelson</i> Krapp-Schickel 2000
6. Mandibular palp 2 to 3-articulate .....	7
Mandibular palp 0 to 1-articulate .....	9
7. Article 1 of antenna 1 nasiform .....	8
Article 1 of antenna 1 not nasiform.....	<i>Thaumatelson</i> Walker 1906
8. Pleonite 3 with erect dorsal process .....	<i>Antatelson</i> J.L. Barnard 1972
Pleonite 3 without erect dorsal process .....	<i>Thaumatelsonella</i> Rauschert & Andres 1991
9. Uropod 3 reduced, inner ramus of uropods 1-2 shortened, article 1 of antenna 1 nasiform or not.....	<i>Chuculba</i> J.L. Barnard 1974
Uropods 1-3 ordinary, article 1 of antenna 1 nasiform.....	10
10. Gnathopods 1-2 alike.....	<i>Parathaumatelson</i> Gurjanova 1938
Gnathopods 1-2 dissimilar.....	11
11. Gnathopod 2 dactylus minute.....	<i>Verticotelson</i> Krapp-Schickel 2006
Gnathopod 2 dactylus normal.....	12
12. Urosomite 1 weakly extended posterodorsally, urosomites 2-3 fused .....	<i>Ausatelson</i> J.L. Barnard 1972
Urosomite 1 strongly extended posterodorsally, urosomites 1-3 free.....	<i>Pseudothaumatelson</i> Schellenberg 1931
13. Pleonite 4 with dorsal process .....	14
Pleonite 4 lacking dorsal process .....	19
14. Gnathopods chelate .....	<i>Raumahara</i> J.L. Barnard 1972
Gnathopods subchelate or simple.....	15
15. Palp of mandible 2 to 3-articulate .....	<i>Hardametopa</i> Barnard & Karaman 1991
Palp of mandible 0 – 1-articulate .....	16
16. Palp of mandible absent .....	<i>Yarra</i> Krapp-Schickel 2000
Palp of mandible 1 articulate.....	17
17. Article 1 of antenna 1 not nasiform.....	<i>Paraprobolisca</i> Ren in Ren & Huang 1991
Article 1 of palp 1 nasiform .....	18
18. Inner plates of maxillipeds mostly fused together, pereonite 4 highly elongate, palp of maxilla 1 1-articulate.....	<i>Zaikometopa</i> Barnard & Karaman, 1987
Inner plates of maxillipeds well separated, pereonite 4 slightly elongate and tumid, palp of maxilla 1 2-articulate.....	<i>Pseudothaumatelson</i> Schellenberg 1931
19. Palp of maxilla 1 2-articulate .....	20
Palp of maxilla 1 1-articulate .....	22
20. Palp of mandible 2-3 articulate .....	<i>Probolisca</i> Gurjanova 1938
Palp of mandible 0-1 articulate .....	21
21. Gnathopod 2 subchelate .....	<i>Sandrothoe</i> Krapp-Schickel 2006
Gnathopod 2 chelate.....	<i>Raukumara</i> Krapp-Schickel 2000
22. Mandibular palp absent .....	23
Mandibular palp present.....	24
23. Gnathopod 2 subchelate .....	<i>Parametopella</i> Guryanova 1938
Gnathopod 2 chelate.....	<i>Pycnopyge</i> Krapp-Schickel 2000
24. Mandibular palp 2 to 3-articulate, antenna 1 accessory flagellum present .....	<i>Metopella</i> Sars 1892
Mandibular palp 1-articulate, antenna 1 accessory flagellum absent.....	25
25. Inner plates of maxillipeds partly fused, gnathopod 1 subchelate.....	<i>Metopelloides</i> Gurjanova 1938
Inner plates of maxillipeds fully separated, gnathopod 1 simple, propodus elongate .....	<i>Vonimetopa</i> Barnard & Karaman 1987

26. Article 2 of pereopod 5-7 evenly but weakly expanded.....	<i>Goratelson</i> J.L. Barnard 1972	
Article 2 of pereopods 5-7 diversely expanded.....		27
27. Article 2 of pereopod 6 linear.....		28
Article 2 of pereopod 6 expanded.....		31
28. Pleonite 3 smooth.....		29
Pleonite 3 with dorsal process.....	<i>Mesoproboloides</i> Gurjanova 1938	
29. Mandibular palp 0 to 1-articulate.....	<i>Stenothoides</i> Chevreux 1900	
Mandibular palp 2 to 3-articulate.....		30
30. Article 2 of pereopod 7 tapering, basally expanded, antenna 1 accessory flagellum present.....	<i>Mesometopa</i> Guryanova 1938	
Article 2 of pereopod 7 evenly expanded, antenna 1 accessory flagellum absent.....		
	<i>Metopella</i> Sars 1892	
31. Mandibular palp 0-1 articulate.....		32
Mandibular palp 2-3 articulate.....		41
32. Pereopod 5 basis with posterodistal lobe.....		33
Pereopod 5 basis without posterodistal lobe.....		34
33. Article 1 of antenna 1 not nasiform.....	<i>Victometopa</i> Krapp-Schickel 2011	
Article 1 of antenna 1 nasiform.....	<i>Parametopa</i> Chevreux 1901	
34. Gnathopod 1 > gnathopod 2.....	<i>Sudanea</i> Krapp-Schickel 2015	
Gnathopod 1 = or < gnathopod 2.....		35
35. Palp of maxilla 1 1-articulate.....		36
Palp of maxilla 1 2-articulate.....		37
36. Antenna 1 accessory flagellum, present, minute.....	<i>Wallametopa</i> J.L. Barnard 1974	
Antenna 1 accessory flagellum absent.....	<i>Stenula</i> J.L. Barnard 1962	
37. Head with conspicuous rostrum.....	<i>Synkope</i> Krapp-Schickel 1999	
Head without rostrum.....		38
38. Mandibular palp present.....		39
Mandibular palp absent.....		40
39. Antenna 1 accessory flagellum absent.....	<i>Prostenothoe</i> Gurjanova 1938	
Antenna 1 accessory flagellum, present, minute.....	<b><i>Wollastenotheo</i> gen. nov</b>	
40. Antenna 2 as long as antenna 1, coxa 2 bevelled anteroventrally.....	<i>Stenothoe</i> Dana 1852	
Antenna 2 half as long as antenna 1, coxa 2 subquadrate and protrusive anteroventrally.....		
	<i>Knysmetopa</i> Barnard & Karaman 1987	
41. Pereopod 5 basis without posterodistal lobe.....		42
Pereopod 5 basis with posterodistal lobe.....		46
42. Palp of maxilla 1 1-articulate.....		43
Palp of maxilla 1 2-articulate.....		44
43. Article 1 of antenna 1 not nasiform.....	<i>Metopa</i> Boeck 1871	
Article 1 of antenna 1 nasiform.....	<i>Prometopa</i> Schellenberg 1926	
44. Gnathopod 1 simple, barely subchelate.....	<i>Probolooides</i> Della Valle 1893	
Gnathopod 1 distinctly subchelate.....		45
45. Antenna 1 accessory flagellum absent or 1 articulate.....	<i>Metopoides</i> Della Valle 1893	
Antenna 1 accessory flagellum 2 articulate.....	<i>Aurometopa</i> Barnard & Karaman 1987	
46. Gnathopod 1 simple, barely subchelate.....	<i>Torometopa</i> Barnard & Karaman 1987	
Gnathopod 1 distinctly subchelate.....		47
47. Antenna 1 accessory flagellum absent or 1 articulate.....		48
Antenna 1 accessory flagellum 2 articulate.....		49
48. P6, 7 basis posteriorly narrowing.....	<i>Malvinometopa</i> Krapp-Schickel 2011	
P6, 7 basis regularly rounded.....	<i>Kyphometopa</i> Krapp-Schickel 2013	
49. Gnathopods different in size and shape, gnathopod 1 very weak and elongate, carpus propodus, both long and thin, palm oblique.....	<i>Scaphodactylus</i> Rauschert & Andres 1993	
Gnathopods with relatively small difference in size and shape, gnathopod 1 carpus longer than or equal to propodus, palm rounded.....	<i>Ligulodactylus</i> Krapp-Schickel 2013	

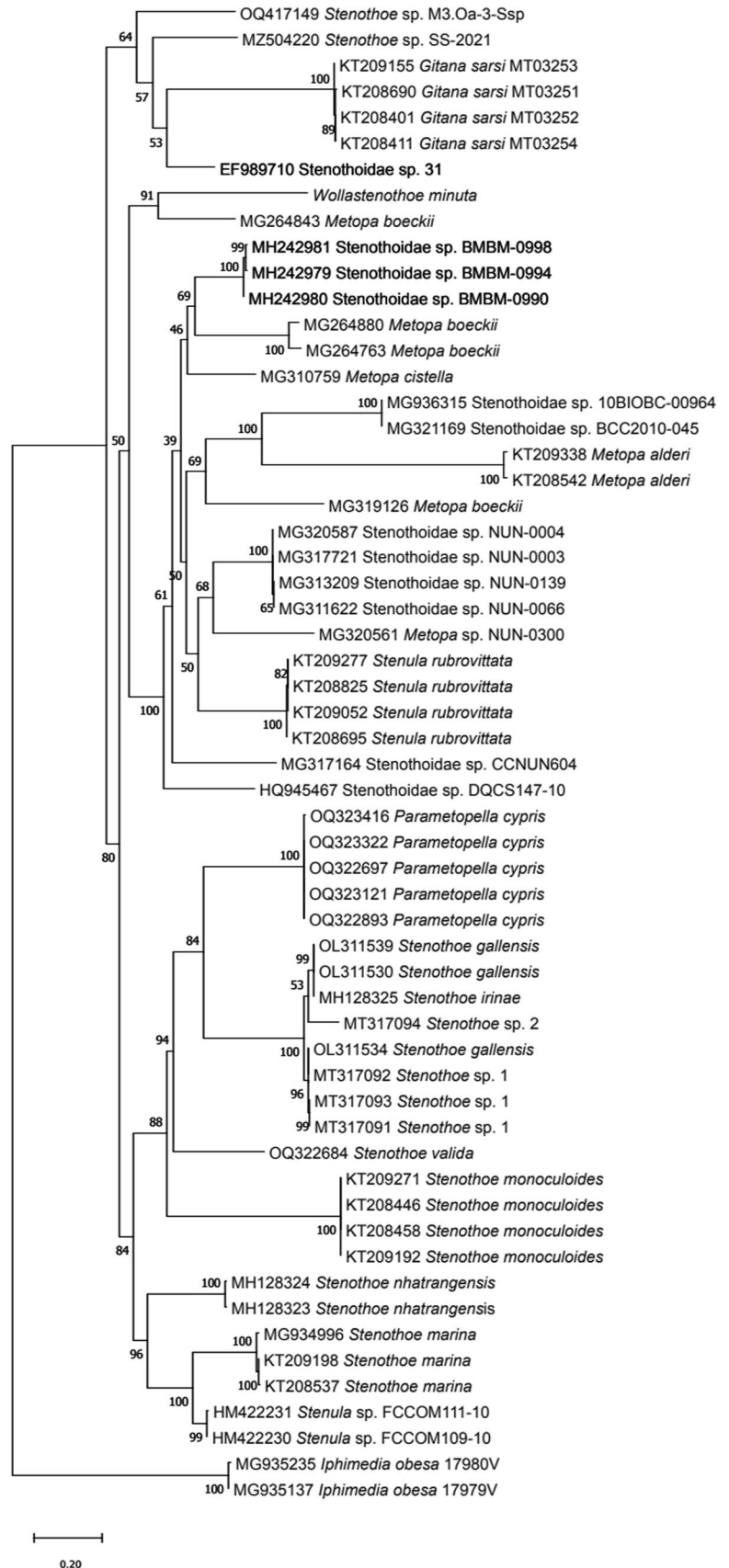
**Table 1** Epifauna living on colonies of the black coral *Antipathella wollastoni*. For each taxon, the total abundances recorded during the study, and their proportion with respect to the total epifaunal abundance, are shown

Phylum	Class	Order	Family/genus/species	Abundance	Relative abundance (%)
Arthropoda	Malacostraca	Amphipoda	<i>Wollastenothoe minuta</i> gen. nov., sp. nov	1496	86.17
Arthropoda	Malacostraca	Amphipoda	<i>Phtisica marina</i>	145	8.35
Arthropoda	Malacostraca	Amphipoda	Pleustidae sp.	62	3.57
Arthropoda	Malacostraca	Amphipoda	<i>Jassa</i> sp.	1	0.06
Arthropoda	Malacostraca	Amphipoda	Oedicerotidae sp.	1	0.06
Arthropoda	Malacostraca	Amphipoda	Lyssianasidae sp.	1	0.06
Arthropoda	Malacostraca	Decapoda	<i>Dardanus arrosor</i>	1	0.06
Arthropoda	Malacostraca	Decapoda	Hippolytidae sp.	17	0.98
Arthropoda	Polychaeta	–	–	4	0.23
Mollusca	Gastropoda	–	–	8	0.46

**Fig. 8** Temporal variation in the total abundance of amphipods (a) and *Wollastenothoe minuta* gen. nov., sp. nov. (b), at T1 (February), T2 (April) and T3 (October). Relationship between colony size of *Antipathella wollastoni* and the total abundance of amphipods (c) and *W. minuta* gen. nov., sp. nov., at different times (d)



**Fig. 9** Maximum-likelihood tree obtained using IQtree2 with 100,000 ultrafast bootstraps showing the relationships between *Wollastenothoe minuta* gen. nov., sp. nov., and other Stenothoidae COI sequences available in GenBank. *Iphimedia obesa* (Iphimediidae) and *Gitana sarsi* (Amphilochiidae) were used as outgroups. These sequences attributed to Stenothoidae grouped with *Gitana sarsi* suggesting that these sequences may come from misidentified specimens, but as the corresponding nodes have low ultrafast bootstrap support values (<65%), this grouping is not strongly supported





## Abundance patterns

In total, 1,736 epifaunal individuals were sampled, with amphipods representing a 98.3% of the total epifauna (Table 1); there were 1,721 amphipods belonging to 6 species (Table 1). Significant variation in the total abundance of amphipod was mainly explained by colony size ( $Pseudo-R^2=0.85$ ; Table S1), while the random factor time hardly explained variability ( $Pseudo-R^2=0.13$ ). The highest abundances of amphipods (mean  $\pm$  SE) were recorded in T3 ( $163.3 \pm 36.2$  ind. colony<sup>-1</sup>), relative to T1 and T2 ( $27.6 \pm 8.7$  and  $35.1 \pm 9.4$  ind. colony<sup>-1</sup>, respectively; Fig. 8a; Table S2). *Wollastenothoe minuta* gen. nov., sp. nov., was the most abundant species (Table 1) over time, accounting for 86.6% of amphipods in T1, 59.3% in T2 and 92% in T3 (Fig. 8b). These differences were mostly explained by colony size ( $Pseudo-R^2=0.97$ ; Table S1) and, to a lesser extent, by different sampling times ( $Pseudo-R^2=0.10$ ). A significant positive correlation between the total abundance of amphipods and the size of the coral colonies was found, i.e., the bigger the colonies, the larger the abundances of amphipods (Fig. 8c). A similar pattern was found for *W. minuta* gen. nov., sp. nov. (Fig. 8d). The highest abundances found in T3 (October) coincided with the higher average monthly temperature recorded in our study (Fig. S1).

The new genus and species were found with other amphipod species belonging to five different families: Caprellidae (i.e., *Phthisica marina* Slabber 1769), Pleustidae (Buchholz, 1874), Ischyroceridae Stebbing, 1899 (i.e., *Jassa* Leach, 1814), Lysianassidae (Dana, 1849) and Oedicerotidae (Lilljeborg, 1965).

## Phylogeny

Molecular data were successfully obtained at the two independent loci investigated. The COI sequence (GenBank accession number PP595991) was 658 bp length, and molecular phylogenetic analyses were consistent with the position of the new genus and species within the Stenothoidae family (Fig. 9), confirming its distinctiveness from other genera for which COI sequence data are currently available. The closest sequence (p-distance = 0.25) was from a specimen identified as *Metopa boeckii* G.O. Sars, 1892, but sequences attributed to this species were found at three different places in our Stenothoidae COI tree (with p-distances among them of about 0.25), suggesting that some of these sequences come from misidentified specimens. The 28S sequence fragment (GenBank accession number PP594429) was 1025 bp long—due to the dearth of Stenothoidae 28S sequences currently available in GenBank; no phylogenetic analysis was conducted for this marker.

## Discussion

This is the first study to date describing the temporal patterns of a new genus and species of amphipod associated with a black coral (i.e., *Antipathella wollastoni*). *Wollastenothoe minuta* gen. nov., sp. nov., was the most abundant and recurrent over time amphipod associated with this habitat, and we found that the abundances of this new genus and species were directly related to colony size.

The 46 valid genera of Stenothoidae include around 280 species (Horton et al. 2022), among which the genera *Metopa* Boeck 1871 and *Stenothoe* Dana 1852 are represented by more than 40% of the total species. Among these, 17 genera include only one species, and 10 genera are represented by only 2 species (Horton et al. 2022). *W. minuta* gen. nov., sp. nov., represents the eleventh monotypic genus and the tenth Stenothoid genus in European waters. Its small size (i.e., 1.21–1.45 mm), combined with the difficult accessibility of the mesophotic black coral habitat where the species lives, may explain why this genus had not been yet discovered. Our results suggest a high specificity of *W. minuta* gen. nov., sp. nov., for *A. wollastoni* as a host. To date, studies conducted in other habitats from the Canary Islands such as rhodoliths (Otero-Ferrer et al. 2019; Navarro-Mayoral et al. 2020), seagrasses (i.e., *Cymodocea nodosa*; Navarro-Mayoral et al. 2023), seaweeds (i.e., *Caulerpa prolifera*; Tuya et al. 2014), or sediments (Riera et al. 2012) have not revealed the presence of this genus and species.

Many species of amphipods live in close association with a wide variety of cnidarians (e.g., sea anemones, gorgonians and corals), through different types of specializations with their hosts (Vader 1983), which vary depending on the family and genus. Amphipods on black corals have been described as opportunistic (Wagner et al. 2012), based on the observations of caprellid amphipods feeding on living tissue of *Antipathes* sp., which led to the death of the entire colony (Tazioli et al. 2007). However, these observations are limited to caprellids and cannot be extended to all amphipods. Furthermore, it is not clear if the cause of death of *Antipathes* sp. is directly linked to the presence of amphipods, or to any previous disturbance. In our study with *A. wollastoni*, we reported a different pattern relative to Tazioli et al. (2007), with large abundances of amphipods that varied over time, while we did not observe any tissue necrosis of colonies throughout the study (almost 1 year). In fact, the most abundant species, *W. minuta* gen. nov., sp. nov., belongs to Stenothoidae, a family that include some species which tends to establish a biological association and display a strongly specificity with their hosts, as it has been observed with hydroids, for example (Vader and Krapp-Schickel 1996). This fact implies that amphipods spend their entire

life cycle on their hosts, where they find shelter and food, such as *Stenothoe brevicornis* with the sea anemone *Actinostola callosa* (Vader 1983). Regarding the relationships between corals and amphipods, multiple ecological roles between them have been reported. *Stenula nordmanni*, for example, was observed in mutualistic relationship with some octocorals (e.g., *Gersemia rubiformis*, Caulier et al. 2021) and *Stenothoe valida* in commensalism with some hydrocorals (e.g., *Millepora complanata*, Lewis 1992). Understanding the interspecific relationships between black corals and amphipods is of great importance, especially in the case of *W. minuta* gen. nov., sp. nov., which was the dominant species over time in all *A. wollastoni* colonies. Regarding their population structure, we did not find any males among the dissected individuals. This result was expected, considering that we dissected 68 specimens out of 1496, and other studies have observed a skewed sex ratio toward females in species of the family Stenothoidae, such as *Stenothoe valida* that exhibited a sex ratio of up to 0.79 for females (Lee and Park 2021).

We found that amphipods were the dominant epifauna on *A. wollastoni* colonies over time, accounting for 98.3% of the total abundances, with *W. minuta* gen. nov., sp. nov., as the most abundant species by far (87.6% of the amphipods). Contrary to our results, the few previous studies on epifauna associated with black corals did not report a dominance of amphipods (Bo et al. 2012; Wagner et al. 2012; Deidun et al. 2015; Matamoros-Calderón et al. 2021), except Love et al. (2007), who reported a dominance of the amphipod *Erichthonius rubricornis* Stimpson 1853 on *Antipathes dendrochristos* Opresko 2005. However, this result was obtained from a single dead coral colony, and it is not easily comparable with our results, as in this case it is not sure if amphipods may be found in living colonies. Moreover, in our study, the abundances of amphipods were consistently large throughout the study, despite some variation among times. We observed the colonization of the near sea bottom by epibionts, such as sponges (e.g., *Axinella* spp.), and the presence of ascidians (e.g., *Stolonica* sp. and *Pycnoclavella* sp.) on the branches of *A. wollastoni*, but in the latter case the presence in the colonies was relatively infrequent or rare. Temporal variation in the abundances of amphipods can be attributed to changes in habitat structure throughout varying time scales, which alter habitat complexity via increased occurrence of epiphytes and associated algae (Jacobucci et al. 2009; Navarro-Mayoral et al. 2020). However, unlike other ecosystem engineers, such as seagrasses (e.g., *Zostera noltii*; Vermaat and Verhagen 1996), the primary habitat generated by *A. wollastoni* is stable over time and does not experience seasonal changes.

Our results showed that variation in amphipod abundances was correlated by the size of the colonies of *A. wollastoni*, with a significant (positive) relationship between

coral colony size and amphipod abundances, both for the entire amphipod assemblage and for *W. minuta* gen. nov., sp. nov. Moreover, there is a colony size influence on the high variability of abundances within the times, especially in T3, where a greater difference in heights between the randomly selected colonies led to larger variations in abundances between replicates. Therefore, this suggests that the presence of amphipods is determined by habitat availability (i.e., colony size). Colonies of *A. wollastoni* dwell on rocky platforms, where they provide three-dimensional complexity to the substratum, offering a variety of microhabitats for several species (Czechowska et al. 2020). When *A. wollastoni* colonies are dense enough, they form a canopy (marine animal forest, sensu Rossi et al. 2017) that gives shelter and protection against strong currents and predators (Buhl-Mortensen et al. 2018). Thus, amphipods can benefit from different habitats provided by black corals, including (1) branches surface, (2) cavities within tissues or skeletons, and (3) free space between branches (Buhl-Mortensen and Mortensen 2004). This is consistent with the relatively large body of research that relates differences in abundances of marine invertebrates, in general, and amphipods in particular, with changes in the availability of habitat (Osman 1977; Aikins and Kikuchi 2001), so a higher abundance is observed in habitats with greater complexity and more available surface. Moreover, at these depths, there is a more limited availability of biogenic habitats compared to shallow waters, e.g., coral reefs, kelp forests, or seagrass meadows (Arfianti and Costello 2020a, b). Thus, the presence of *A. wollastoni* provides a 3-dimensional habitat for many species.

We found that the highest amphipod abundances were recorded in October (T3), which coincided with the highest temperature recorded. Some amphipods in shallow water environments show a turnover (i.e., growth and reproduction), which it is commonly adjusted to seasonal variation in terms of environmental conditions (e.g., temperature, photoperiod) and food resources (e.g., epiphytic biomass for herbivorous amphipods) (Neuparth et al. 2002; Martins et al. 2002; Navarro-Mayoral et al. 2020; Fernandez-Gonzalez et al. 2021). It is known that the temperature-induced changes in amphipod metabolic rates can lead to important physiological constraints to reproduction and determine of life history patterns of amphipods (Sainte-Marie 1991). For example, under laboratory conditions, *Gammarus locusta* showed faster individual growth, anticipated age at maturity, and higher population growth rate at a temperature of 20°C compared to 15°C (Neuparth et al. 2002). In our case, the difference between the minimum and maximum temperatures was 3.9°C and controlled studies would be necessary to know exactly the direct relationship between temperature and the abundances of *W. minuta* gen. nov., sp. nov. Of course, temperature is typically correlated with a range of environmental and

ecological processes. For example, an interesting observation was that the highest abundances of *W. minuta* gen. nov., sp. nov., coincided with a high amount of mucus generated by the colonies (personal observations). Mucus production is a strategy adopted by corals to obtain protection against sedimentation, which also plays a role in the food chain of habitats generated by corals (Galil 1987; Vytöpil and Willis 2001; Wee et al. 2019; Fraser et al. 2020). Thus, mucus can catch detritus and phytoplankton that facilitate the feeding of amphipods, as observed in decapod taxa that feed on particles trapped by coral mucus (Galil 1987). Most of the species of the Stenothoid family are detritivorous and/or carnivorous species (Krapp-Schickel 1993; Moore et al. 1994; Sano et al. 2003; Tandberg et al. 2010; Auster et al. 2011; Vázquez-Luis et al. 2013; Guerra-García et al. 2014; Sedano et al. 2020), and *W. minuta* gen. nov., sp. nov., could take advantage of *A. wollastoni* secretions for feeding. Therefore, the amount of food available in the form of mucus could also be playing a role in the abundance pattern of amphipods, and specially of *W. minuta* gen. nov., sp. nov. However, more studies are needed to clarify the biological associations between deep-sea corals and epifauna, particularly focusing on the relationship between this black coral and this new genus and species of amphipod that dominated the associated epifauna community over time. Overall, this study supports that black coral forests in mesophotic depths have enormous potential for overlooked biodiversity and that much of the associated diversity remains undescribed.

## Conclusions

We here reported patterns in composition and abundances of epifauna associated with *Antipathella wollastoni* over time, showing that amphipods were the dominant group. Our results confirmed that marine animal forests host an important, but somehow unknown, associated biodiversity. The new genus and species of the Stenothoidae family seem to be coral specific, displaying a direct relationship with the availability of habitat generated by the coral host. Our study reinforces the necessity to increase research effort in animal forest to improve management and conservation of these key habitats.

**Acknowledgements** We acknowledge Alvaro Roldán (Liquid Planet) and José Manuel Golderos Tena for their assistance in technical diving.

**Author's contribution** Conceptualization was performed by FOF, LB, SNM; method design by FOF, LB, SNM; investigation by FOF, LB, SNM, LT, FE, RH; analysis by SNM, FT; interpretation of data by SNM, FT, FOF, LB; taxonomy work by BG, SNM, VFG; drawings and taxonomic preparation by BG; DNA extraction, PCR amplification, and

nanopore sequencing by NL; assembly and analysis of DNA sequences by JFF; funding acquisition by FOF, LT, JFF; supervision by FOF, FT; writing—original draft preparation by SNM; writing—review and editing by all authors.

**Funding** Open Access funding provided thanks to the CRUE-CSIC agreement with Springer Nature. This study has been produced with the financial support from the LIFE Programme of the European Union, the French Office for Biodiversity (OFB), and the French Development Agency (AFD) through the LIFE4BEST Programme. The contents of this document are the sole responsibility of B-CHARMED (The Black Coral forests as unexplored Biodiversity Hotspots in the MAcaronesian Region: omplanat functions and sERvices analyzed) project and can under no circumstances be regarded as reflecting the position of the European Union nor of the OFB and AFD. Lucas Terrana was funded by the association Fonds Léopold III pour l'Exploration et la Conservation de la Nature ASBL. DNA sequencing was financed by the Belgian Fond de la Recherche Scientifique—FNRS via "Projet de Recherches" grant no T.00078.23 to Jean-François Flot.

## Declarations

**Conflict of interest** All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript. The contents of this document are the sole responsibility of the authors and can, under no circumstances, be regarded as reflecting the position of the EU, nor of the OFB and AFD.

**Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

## References

- Aikins S, Kikuchi E (2001) Studies on habitat selection by amphipods using artificial substrates within an estuarine environment. *Hydrobiologia* 457(1):77–86. <https://doi.org/10.1023/A:1012261116232>
- Angel, M. V. (1990). Life in the benthic boundary layer: connections to the mid-water and sea floor. *Philosophical Transactions of the Royal Society of London. Series A, Mathematical and Physical Sciences*, 331(1616), 15–28. <https://doi.org/10.1098/rsta.1990.0053>
- Arfianti T, Wilson S, Costello MJ (2018) Progress in the discovery of amphipod crustaceans. *PeerJ* 6:e5187
- Arfianti, T., & Costello, M. J. (2020). The biological, ecological, and ecosystem roles of marine Amphipoda. *Encyclopedia of the World's Biomes*.
- Arfianti T, Costello MJ (2020b) Global biogeography of marine amphipod crustaceans: latitude, regionalization, and beta diversity. *Mar Ecol Prog Ser* 638:83–94



- Auster, P. J., Heinonen, K. B., Watling, L., Parrish-Kuhn, C., Heupel, E., & Lindholm, J. (2011). A rare deepwater anemone and its associates in the Stellwagen Bank National Marine Sanctuary (Gulf of Maine, north-west Atlantic). *Marine Biodiversity Records*, 4. <https://doi.org/10.1017/S175526721100020>
- Barnard, J.L. (1962). Benthic marine Amphipoda of southern California. 3. Families Amphilochidae, Leucothoidae, Stenothoidae, Argissidae, *Hyalidae Pacific Naturalist*, 3(3): 116–163.
- Barnard JL (1972) Gammaridean Amphipoda of Australia, Part I. Smithsonian Contributions to Zoology 103:1–333
- Barnard J.L. & Karaman G.S. (1987). Revisions in classification of gammaridean amphipoda (Crustacea). 3. *Proceedings of the Biological Society of Washington*, 100, 4, 856–875
- Barnard JL, Karaman GS (1991) The families and genera of marine gammaridean Amphipoda (except marine gammaroids). Parts 1 and 2. Records of the Australian Museum, Supplement 13:1–866
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting linear mixed-effects models using lme4. *arXiv preprint arXiv:1406.5823*. <https://doi.org/10.48550/arXiv.1406.5823>
- Bianchi C, Haroun R, Morri C, Wirtz P (2000) The subtidal epibenthic communities off Puerto del Carmen (Lanzarote, Canary Islands). *Arquipélago* 2000(2):145–155
- Bo, M., Lavorato, A., Di Camillo, C. G., Polisenio, A., Baquero, A., Bavestrello, G., ... & Reimer, J. D. (2012). Black coral assemblages from Machalilla National Park (Ecuador). *Pacific Science*, 66(1), 63–81. <https://doi.org/10.2984/66.1.4>
- Bo, M., Cerrano, C., Canese, S., Salvati, E., Angiolillo, M., Santangelo, G., & Bavestrello, G. (2014). The coral assemblages of an off-shore deep Mediterranean rocky bank (NW Sicily, Italy). *Marine Ecology*, 35(3), 332–342. <https://doi.org/10.1111/maec.12089>
- Boeck A (1871) Crustacea Amphipoda borealia et arctica. Forhandlinger I Videnskabs-Selskabet in Christiania 1870:81–280
- Buhl-Mortensen LENE, Mortensen PB (2004) Symbiosis in deep-water corals. *Symbiosis* 37:33–61
- Buhl-Mortensen, L., Vanreusel, A., Gooday, A. J., Levin, L. A., Priede, I. G., Buhl-Mortensen, P., ... & Raes, M. (2010). Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. *Marine Ecology*, 31(1), 21–50. <https://doi.org/10.1111/j.1439-0485.2010.00359.x>
- Buhl-Mortensen, L., Buhl-Mortensen, P., Rungruangsak-Torrissen, K., Schwach, V., Hjort, J., Jakobsen, T., & Toresen, R. (2018). Cold temperate coral habitats. *Corals in a Changing World*, 9. <https://doi.org/10.1007/s10750-014-2116-x>
- Caulier G, Hamel JF, Hendrycks EA, Conlan KE, Mercier A (2021) Mutualistic relationship between the amphipod *Stenula nordmanni* (Stephensen, 1931) and the nephtheid coral *Gersemia rubiformis* (Ehrenberg, 1834). *Symbiosis* 85(1):93–104. <https://doi.org/10.1007/s13199-021-00800-5>
- Chevreux, E. (1900). Amphipodes provenant des campagnes de « l'Hirondelle » 1885–1888. *omplanat des campagnes scientifiques du Prince Albert I de Monaco*. 16: iv + 195 pp.
- Czechowska, K., Feldens, P., Tuya, F., Cosme de Esteban, M., Espino, F., Haroun, R., ... & Otero-Ferrer, F. (2020). Testing side-scan sonar and multibeam echosounder to study black coral gardens: a case study from Macaronesia. *Remote Sensing*, 12(19), 3244. <https://doi.org/10.3390/rs12193244>
- De Clippele LH, Huvenne VA, Molodtsova TN, Roberts JM (2019) The diversity and ecological role of non-scleractinian corals (Antipatharia and Alcyonacea) on scleractinian cold-water coral mounds. *Front Mar Sci* 6:184. <https://doi.org/10.3389/fmars.2019.00184>
- Deidun, A., Andaloro, F., Bavestrello, G., Canese, S., Consoli, P., Micallef, A., & Bo, M. (2015). First characterisation of a *Leioopathes glaberrima* (Cnidaria: Anthozoa: Antipatharia) forest in Maltese exploited fishing grounds. *Italian Journal of Zoology*, 82(2), 271–280. <https://doi.org/10.1080/11250003.2014.986544>
- Fernandez-Gonzalez V, Navarro-Mayoral S and Sanchez-Jerez P (2021) Connectivity Patterns for Direct Developing Invertebrates in Fragmented Marine Habitats: Fish Farms Fouling as Source Population in the Establishment and Maintenance of Local Metapopulations. *Frontiers in Marine Science*. 8:785260. <https://doi.org/10.3389/fmars.2021.785260>
- Fraser KM, Lefcheck JS, Ling SD, Mellin C, Stuart-Smith RD, Edgar GJ (2020) Production of mobile invertebrate communities on shallow reefs from temperate to tropical seas. *Proc R Soc B* 287(1941):20201798. <https://doi.org/10.1098/rspb.2020.1798>
- Freiwald A, Helge Fosså J, Grehan A, Koslow, T, Roberts JM (2004) Cold-water coral reefs: out of sight - no longer out of mind. UNEP-WCMC Biodiversity Series, 22. Cambridge, UNEP/WCMC. ISBN 92-807-2453-3. 84 pp
- Galil BS (1987) The adaptive functional structure of mucus-gathering setae in trapezid crabs symbiotic with corals. *Symbiosis* 4:75–86
- Gray, D. J. E. (1857). Synopsis of the families and genera of axiferous zoophytes or barked corals. In *Proceedings of the Zoological Society of London* (Vol. 15, No. 1, pp. 278–294). Oxford, UK: Blackwell Publishing Ltd.
- Guerra-García JM, De Figueroa JT, Navarro-Barranco C, Ros M, Sánchez-Moyano JE, Moreira J (2014) Dietary analysis of the marine Amphipoda (Crustacea: Peracarida) from the Iberian Peninsula. *J Sea Res* 85:508–517. <https://doi.org/10.1016/j.seares.2013.08.006>
- 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.
- Hall-Spencer JM, Tasker M (2006) Report of the Working Group on Deep-water Ecology (WGDEC), 4–7 December 2005, Miami. Report of the Working Group on Deep-water Ecology (WGDEC), USA
- Harrison, X. A., Donaldson, L., Correa-Cano, M. E., Evans, J., Fisher, D. N., Goodwin, C. E., ... & Inger, R. (2018). A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ*, 6, e4794. <https://doi.org/10.7717/peerj.4794>
- Havermans C, Smetacek V (2018) Bottom-up and top-down triggers of diversification: A new look at the evolutionary ecology of scavenging amphipods in the deep sea. *Prog Oceanogr* 164:37–51. <https://doi.org/10.1016/j.pocean.2018.04.008>
- Herler J (2007) Microhabitats and ecomorphology of coral-and coral rock-associated gobiid fish (Teleostei: Gobiidae) in the northern Red Sea. *Mar Ecol* 28:82–94. <https://doi.org/10.1111/j.1439-0485.2007.00165.x>
- Hoang DT, Vinh LS, Flouri T, Stamatakis A, von Haeseler A, Minh BQ (2018) MPBoot: fast phylogenetic maximum parsimony tree inference and bootstrap approximation. *BMC Evol Biol* 18:1–11
- Horton, T.; Lowry, J.; De Broyer, C.; Bellan-Santini, D.; Coleman, C.O.; Corbari, L.; Costello, M.J.; Daneliya, M.; Davin, J.-C.; Fišer, C.; Gasca, R.; Grabowski, M.; Guerra-García, J.M.; Hendrycks, E.; Hughes, L.; Jaume, D.; Jazdzewski, K.; Kim, Y.-H.; King, R.; Krapp-Schickel, T.; LeCroy, S.; Lörz, A.-N.; Mamos, T.; Senna, A.R.; Serejo, C.; Sket, B.; Souza-Filho, J.F.; Tandberg, A.H.; Thomas, J.D.; Thurston, M.; Vader, W.; Väinölä, R.; Vonk, R.; White, K.; Zeidler, W. (2022). World Amphipoda Database. Stenothoidae Boeck, 1871. Accessed through: World Register of Marine Species at: <https://www.marinespecies.org/aphia.php?p=taxdetails&id=101409> on 2022-06-15.
- Jacobucci, G. B., Tanaka, M. O., & Leite, F. P. P. (2009). Temporal variation of amphipod assemblages associated with *Sargassum filipendula* (Phaeophyta) and its epiphytes in a subtropical shore. *Aquatic Ecology*, 43(4), 1031–1040. <https://doi.org/10.1007/s10452-009-9230-2>

- Jiménez Prada P, Hachero Cruzado I, Guerra García JM (2015) Importancia de los anfípodos en la dieta de especies de interés acuícola del litoral andaluz. *Zoologica Baetica* 26:3–29
- Kalyaanamoorthy S, Minh BQ, Wong TK, Von Haeseler A, Jermini LS (2017) ModelFinder: fast model selection for accurate phylogenetic estimates. *Nat Methods* 14(6):587–589
- Karlson K, Bonsdorff E, Rosenberg R (2007) The impact of benthic macrofauna for nutrient fluxes from Baltic Sea sediments. *AMBIO: J Human Env* 36(2):161–167. [https://doi.org/10.1579/0044-7447\(2007\)36\[161:TIOBMF\]2.0.CO;2](https://doi.org/10.1579/0044-7447(2007)36[161:TIOBMF]2.0.CO;2)
- Krapp-Schickel G (1993) Do algal-dwelling amphipods react to the ‘critical zones’ of a coastal slope? *J Nat Hist* 27(4):883–900
- Krapp-Schickel T (2000) *Thaumatesonine stenothoids* (Crustacea, Amphipoda), Part 1. *Mem Mus Vic* 58(1):89–124. <https://doi.org/10.24199/j.mmv.2000.58.5>
- Krapp-Schickel, T. (2006). *Thaumatesonine stenothoids* (Crustacea, Amphipoda). Part 2. *Zootaxa*, 1165(1), 1–31.
- Krapp-Schickel, T. (2011). On the Austral-Antarctic stenothoids *Proboloides*, *Metopoides*, *Torometopa* and *Scaphodactylus* (Crustacea Amphipoda). Part 2: the genus *Proboloides*, with description of two new genera and the transfer of two nominal species to *Metopoides*. *Zookeys*, (86), 11. <https://doi.org/10.3897/zookeys.86.785>
- Krapp-Schickel T (2013) On Austral-Antarctic stenothoids (Amphipoda), part 3: *Torometopa*, *Scaphodactylus*, and two new genera. *Crustaceana* 86(7–8):829–852
- Krapp-Schickel, T. (2015). Minute but constant morphological differences within members of Stenothoidae: The *Stenothoe gallensis* group with four new members, keys to *Stenothoe* worldwide, a new species of *Parametopa* and *Sudanea* n. gen. (Crustacea: Amphipoda). *Journal of natural history*, 49(37–38), 2309–2377. <https://doi.org/10.1080/00222933.2015.1021873>
- Krapp-Schickel T, Vader WJM (2015) Stenothoids living with or on other animals (Crustacea, Amphipoda). *Zoosystematics and Evolution* 91(2):215–246. <https://doi.org/10.3897/zse.91.5715>
- Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. (2017). lmerTest package: tests in linear mixed effects models. *Journal of statistical software*, 82, 1–26. <https://doi.org/10.18637/jss.v082.i13>
- Latreille, P. A. (1806). *Genera crustaceorum et insectorum secundum ordinem naturalem in familias disposita, iconibus exemplisque plurimis explicata*. Amand Koenig, Parisiis et Argentorati (Paris & Strasbourg). 1: xviii + 303 pp., pls. 1–24
- Latreille PA (1816) Amphipoda. In : Nouveau dictionnaire d’Histoire naturelle, appliquée aux Arts, à l’Agriculture, à l’Économie rurale et domestique, à la Médecine, etc. Par une société de Naturalistes et d’Agriculteurs. Vol. 1. 2<sup>nd</sup> Edn. Deterville, Paris, 467–469.
- Lavelle, K.A., 2012. Epifaunal Assemblages on Deep-Water Corals in Roatan, Honduras. Master’s thesis. Texas A&M University–Corpus Christi.
- Lee YJ, Park WG (2021) Population dynamics of *Stenothoe valida* Dana, 1852 (Amphipoda, Stenothoidae) at Cheongsapo beach of Busan. Republic of Korea *Crustaceana* 94(4):413–429
- Lewis JB (1992) Abundance, distribution and behavior of a commensal amphipod *Stenothoe valida* Dana on the hydrocoral *Millepora oplanate* Lamarck. *Bull Mar Sci* 51(2):245–249
- Love MS, Yoklavich MM, Black BA, Andrews AH (2007) Age of black coral (*Antipathes dendrochristos*) colonies, with notes on associated invertebrate species. *Bull Mar Sci* 80(2):391–399
- Lowry JK, Myers AA (2013) A phylogeny and classification of the Senticaudata subord. Nov. (Crustacea: Amphipoda). *Zootaxa* 3610(1): 1–80. <https://doi.org/10.11646/zootaxa.3610.1.1>
- Mann KH, Lazier JR (2013) Dynamics of marine ecosystems: biological-physical interactions in the oceans. Blackwell Scientific Publications, Boston, MA, USA, p 446
- Marin, I. N., & Sinelnikov, S. Y. (2017). Amphipod assemblage found on sublittoral hydroids in the White Sea with the special remarks to symbiotic association of stenothoid *Metopa alderi* with hydroid *Tubularia larynx*. *Ukrainian Journal of Ecology*, 7(4), 473–479. [https://doi.org/10.15421/2017\\_146](https://doi.org/10.15421/2017_146)
- Martins I, Maranhão P, Marques JC (2002) Modelling the effects of salinity variation on *Echinogammarus marinus* Leach (Amphipoda, Gammaridae) density and biomass in the Mondego estuary (Western Portugal). *Ecol Model* 152(2–3):247–260. [https://doi.org/10.1016/S0304-3800\(02\)00012-1](https://doi.org/10.1016/S0304-3800(02)00012-1)
- Matamoros-Calderón, W., Lara, M., & Breedy, O. (2021). Bosques de coral negro del Área de Conservación Guanacaste, Costa Rica: especies y distribución. *Revista de Biología Tropical*, 69, 208–218. <https://doi.org/10.15517/rbt.v69is2.48317>
- Minh, B. Q., Schmidt, H. A., Chernomor, O., Schrempf, D., Woodhams, M. D., Von Haeseler, A., & Lanfear, R. (2020). IQ-TREE 2: new models and efficient methods for phylogenetic inference in the genomic era. *Molecular Biology and Evolution*, 37(5), 1530–1534.
- Molodtsova T, Opresko D (2023) World List of Antipatharia. Antipatharia. World Register of Marine Species, Accessed through
- Moore, P. G., Rainbow, P. S., & Vader, W. (1994). On the feeding and comparative biology of iron in coelenterate-associated gammaridean Amphipoda (Crustacea) from N. Norway. *Journal of experimental marine biology and ecology*, 178(2), 205–231.
- Navarro-Mayoral S, Fernandez-Gonzalez V, Otero-Ferrer F, Tuya F (2020) Spatio-temporal variability of amphipod assemblages associated with rhodolith seabeds. *Mar Freshw Res* 72(1):76–83. <https://doi.org/10.1071/MF19360>
- Navarro-Mayoral, S., Tuya, F., Prado, P., Marco-Méndez, C., Fernandez-Gonzalez, V., Fernández-Torquemada, Y., ... & Martínez-Crego, B. (2023). Drivers of variation in seagrass-associated amphipods across biogeographical areas. *Marine Environmental Research*, 186, 105918.
- Neuparth T, Costa FO, Costa MH (2002) Effects of temperature and salinity on life history of the marine amphipod *Gammarus locusta*. Implications for Ecotoxicological Testing *Ecotoxicology* 11(1):61–73. <https://doi.org/10.1023/a:1013797130740>
- Orejas C, Gori A, Iacono CL, Puig P, Gili JM, Dale MR (2009) Cold-water corals in the Cap de Creus canyon, northwestern Mediterranean: spatial distribution, density and anthropogenic impact. *Mar Ecol Prog Ser* 397:37–51. <https://doi.org/10.3354/meps08314>
- Osman RW (1977) The establishment and development of a marine epifaunal community. *Ecol Monogr* 47(1):37–63
- Otero-Ferrer, F., Mannarà, E., Cosme, M., Falace, A., Montiel-Nelson, J. A., Espino, F., & Tuya, F. (2019). Early-faunal colonization patterns of discrete habitat units: A case study with rhodolith-associated vagile macrofauna. *Estuarine, Coastal and Shelf Science*, 218, 9–22. <https://doi.org/10.1016/j.ecss.2018.11.020>
- Ren X, Huang L (1991) Studies on gammaridea and caprellidea (Crustacea: Amphipoda) from the northwest waters off the Antarctic Peninsula. *Studia Marina Sinica* 32(10):185–323
- Riera R, Tuya F, Ramos E, Rodríguez M, Monterroso Ó (2012) Variability of macrofaunal assemblages on the surroundings of a brine disposal. *Desalination* 291:94–100. <https://doi.org/10.1016/j.desal.2012.02.003>
- Rossi, S., Bramanti, L., Gori, A., & Orejas, C. (2017). An overview of the animal forests of the world. *Marine animal forests: the ecology of benthic biodiversity hotspots*, 1–28. [https://doi.org/10.1007/978-3-319-17001-5\\_1-1](https://doi.org/10.1007/978-3-319-17001-5_1-1)
- RStudio Team. (2022). RStudio: Integrated development for R. RStudio, PBC.
- Ruffo S (1998) The amphipoda of the Mediterranean. *Memoires De L’institut Oceanographique De Monaco* 13:959
- Sainte-Marie B (1991) A review of the reproductive bionomics of aquatic gammaridean amphipods: variation of life history traits



- with latitude, depth, salinity and superfamily. *Hydrobiologia* 223(1):189–227. <https://doi.org/10.1007/BF00047641>
- Sano M, Omori M, Taniguchi K (2003) Predator-prey systems of drifting seaweed communities off the Tohoku coast, northern Japan, as determined by feeding habit analysis of phytal animals. *Fish Sci* 69(2):260–268
- Schellenberg, A., (1931). Gammariden und Caprelliden des Magellangebietes, Sudgeorgiens und der Westantarktis. *Further Zoological Results of the Swedish Antarctic Expedition, 1901–1903* 2(6): 1–290.
- Sedano F, de Figueroa JT, Navarro-Barranco C, Ortega E, Guerra-García JM, Espinosa F (2020) Do artificial structures cause shifts in epifaunal communities and trophic guilds across different spatial scales? *Marine Env Res* 158:104998
- Spalding M, Ravilious C, Green EP (2001) World Atlas of coral reefs. Univ of California Press.
- Stebbing, T. R. R. (1888). Report on the Amphipoda collected by HMS Challenger during the years 1873–1876. *Report on the Scientific Results of the Voyage of HMS Challenger during the Years 1873–1876, Zoology*, 29, pls-I.
- Tandberg AHS, Vader W, Berge J (2010) Studies on the association of *Metopa glacialis* (Amphipoda, Crustacea) and *Musculus discors* (Mollusca, Mytilidae). *Polar Biol* 33:1407–1418
- Tamura K, Stecher G, Kumar S (2021) MEGA11: molecular evolutionary genetics analysis version 11. *Mol Biol Evol* 38(7):3022–3027
- Tazioli S, Bo M, Boyer M, Rotinsulu H, Bavestrello G (2007) Ecological observations of some common antipatharian corals in the marine park of Bunaken (North Sulawesi, Indonesia). *Zoological Studies* 46(2):227–241
- Tuya F, Png-Gonzalez L, Riera R, Haroun R, Espino F (2014) Ecological structure and function differ between habitats dominated by seagrasses and green seaweeds. *Mar Environ Res* 98:1–13. <https://doi.org/10.1016/j.marenvres.2014.03.015>
- Tuya, F., Aguilar, R., Espino, F., Bosch, N. E., Meyers, E. K., Jiménez-Alvarado, D., ... & Haroun, R. (2021). Differences in the occurrence and abundance of batoids across an oceanic archipelago using complementary data sources: Implications for conservation. *Ecology and Evolution*, 11(23), 16704–16715. <https://doi.org/10.1002/ece3.8290>
- Vader W (1983) Associations between amphipods (Crustacea: Amphipoda) and sea anemones (Anthozoa, Actiniaria). *Memoirs of the Australian Museum* 18:141–153
- Vader, W., & Krapp-Schickel, G. (1996). Redescription and biology of *Stenothoe brevicornis* Sars (Amphipoda: Crustacea), an obligate associate of the sea anemone *Actinostola callosa* (Verrill). *Journal of Natural History*, 30(1), 51–66. <https://doi-org.bibproxy.ulpgc.es/https://doi.org/10.1080/00222939600770041>
- Vázquez-Luis, M., Sanchez-Jerez, P., & Bayle-Sempere, J. T. (2013). Does the invasion of *Caulerpa racemosa* var. *cylindracea* affect the feeding habits of amphipods (Crustacea: Amphipoda)? *Journal of the Marine Biological Association of the United Kingdom*, 93(1), 87–94.
- Vermaat, J. E., & Verhagen, F. C. (1996). Seasonal variation in the intertidal seagrass *Zostera noltii* Hornem.: coupling demographic and physiological patterns. *Aquatic Botany*, 52(4), 259–281.
- Vytopil, E., & Willis, B. (2001). Epifaunal community structure in *Acropora* spp. (Scleractinia) on the Great Barrier Reef: implications of coral morphology and habitat complexity. *Coral Reefs*, 20(3), 281–288. <https://doi.org/10.1007/s003380100172>
- Wagner D, Luck DG, Toonen RJ (2012) The biology and ecology of black corals (Cnidaria: Anthozoa: Hexacorallia: Antipatharia). *Adv Mar Biol* 63:67–132. <https://doi.org/10.1016/B978-0-12-394282-1.00002-8>
- Wee, S. Y. C., Sam, S. Q., Sim, W. T., Ng, C. S. L., Taira, D., Afiq-Rosli, L., ... & Chou, L. M. (2019). The role of in situ coral nurseries in supporting mobile invertebrate epifauna. *Journal for Nature Conservation*, 50, 125710. <https://doi.org/10.1016/j.jnc.2019.125710>

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.