



A review of the Leptostraca of the British Isles with discussion of the genus *Sarsinebalia* Dahl

Edward McCormack¹, Christopher W. Ashelby²
and David McGrath³

¹ Aquafact International Services Ltd., 12, Kilkerrin Park, Liosbaun, Galway, Ireland.
(EMcC) E-mail: eddie@aquafact.ie

² APEM Ltd., Diamond Centre, Works Road, Letchworth Garden City. SG6 1LW.
United Kingdom. (CWA) E-mail: c.ashelby@apemltd.co.uk

³ Department of Life Sciences, Galway-Mayo Institute of Technology, Ireland.
(DMcG) E-mail: dave.mcgrath@gmit.ie

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ABSTRACT

A survey of the Leptostracan fauna of the British Isles collected from routine environmental monitoring samples revealed six species of Nebaliidae to be present in shallow waters. These species were identified as *Nebalia herbstii* Leach, 1814, *Nebalia strausi* Risso, 1826, *Nebalia borealis* Dahl, 1985, *Nebalia kocatasi* Moreira, Koçak and Katagan, 2007, *Nebalia reboredae* Moreira and Urgan, 2009 in Moreira *et al.*, 2009a and *Sarsinebalia urgorrii* Moreira, Gestoso and Troncoso, 2003. The presence of *N. strausi*, *N. kocatasi*, *N. reboredae* and *S. urgorrii* is reported from the British Isles for the first time. Three further species have been previously reported from the waters surrounding Britain and Ireland but were not recorded in the current study. Thus, the number of species recorded in the British Isles now stands at nine and the range of several species is extended northwards from previous records in the Mediterranean and the Iberian Peninsula. The diagnostic characters of *Sarsinebalia* Dahl, 1985 are discussed and it is suggested that a formal reappraisal of the genus be conducted. A key to European Leptostraca is provided based on adult females.

KEY WORDS

Nebaliidae, Ireland, United Kingdom, identification key, new records.

INTRODUCTION

Leptostraca are the only extant members of the marine crustacean subclass Phyllocarida. They possess a movable rostrum, six pairs of pleopods, a pair of uropods and a bivalve carapace covering eight thoracopods. Leptostracans have long been documented from the British Isles and are known from

CORRESPONDING AUTHOR
Edward McCormack
eddie@aquafact.ie

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shallow-and deep-water locations. However, the group is morphologically conservative and the traditionally used identifying characters were inadequate for species separation. Revisions of the group (Dahl, 1985; Moreira *et al.*, 2003; 2007; 2009a; 2009b), including descriptions of several new species, have made it apparent that the list of species reported from the British Isles is inaccurate and the distribution of the previously reported species must be re-evaluated.

Mauchline (1984) lists four species of Leptostraca within the fauna of the British Isles. These include *Nebalia bipes* (Fabricius, 1780), *Sarsinebalia typhlops* (G.O. Sars, 1870), *Nebaliella caboti* Clark, 1932 and *Nebaliopsis typica* G.O. Sars, 1887. *Nebalia bipes* has historically been widely recorded from British and Irish coasts. Tattersall (1911) recorded it from the Clare Island Survey “at low water at spring tides, under stones and seems to prefer the neighbourhood of black, evil-smelling mud”. Fahy (1985) recorded it from the gut contents of sea trout from Mulroy Bay, Co. Donegal. Dahl (1985) provided a revision of the European Leptostraca and demonstrated that *N. bipes* is not a cosmopolitan species recorded throughout western European coastal waters but instead is a boreal, circum-Arctic species known only from Greenland, Arctic North America, and Svalbard to western Norway. Considering Dahl’s (1985) revised distribution of *N. bipes* and his statement that *Nebalia herbstii* Leach, 1814 was the commonest species of *Nebalia* Leach, 1814 of the British Isles and the western coast of France, O’Reilly *et al.* (2001) suggested that it seems probable that most of the British records of *N. bipes* should refer to *N. herbstii*. Correspondingly, it should be considered that all historical identifications of *N. bipes* from the British Isles should be seen as suspect and should be re-examined.

In addition to *N. bipes*, historical records of British and Irish Nebaliidae include *N. herbstii*, *Nebalia borealis* Dahl, 1985, *Nebalia strausi* Risso, 1826 and *Sarsinebalia typhlops*, *Nebaliella caboti* and *Nebaliopsis typica*. *Sarsinebalia typhlops* has previously been recorded (as *Nebalia typhlops*) by Tattersall (1905) off the west coast of Ireland: 60 miles west of Achill Head in 364 m of water and 50 miles off Cleggan Head, Co. Galway in 220 m of water. Linder (1943) recorded *N. typica* from the extreme south-west of the continental slope. Mauchline and Gage (1983) also recorded *S. typhlops* (as *Nebalia*

typhlops), *N. caboti* and *N. typica* at >1500 m from the Rockall Trough. *Nebalia herbstii* is previously recorded from the south-west and western coast of England (Leach, 1814; Dahl, 1985), the Channel Islands, Dublin Bay in the gut of *Gaidropsarus mediterraneus* (Linnaeus, 1758) and off SW Ireland, location not specified (Dahl, 1985). British records of *N. strausi* are confined to the Channel Islands (Dahl, 1985) whilst *N. borealis* has only been reported from Shetland (Dahl, 1985).

The current study examines recent collections of Nebaliidae from inshore and offshore waters around the Irish and British coasts, providing further records for some of the previously known species and demonstrating the occurrence of additional species in these waters.

MATERIAL AND METHODS

Specimens of Nebaliidae were collected from numerous locations during surveys of inshore and offshore waters around the British Isles. The surveys included benthic surveys of Marine Natura 2000 sites, benthic audits of marine fish farms, ecological surveys related to marine aggregate extraction and the oil and gas industry and the U.K.’s Marine Conservation Zone programme. Macrofaunal samples were collected using 0.1 m² Day grabs, 0.1 m² mini-Hamon grabs, dredges and diver-operated cores but did not deliberately target leptostracans. During these surveys macrofaunal samples were fixed in 10% buffered formalin, sieved over either a 0.5 or a 1.0 mm mesh and the residues were sorted under either a Nikon SMZ-10 or Nikon SMZ-645 stereomicroscope into various taxa and transferred to 70% ethanol prior to identification. The leptostracan material was subsequently re-analysed for the current study. All specimens were compared against published descriptions of the species with all diagnostic characters carefully considered. Where available, accompanying habitat and collection data have been included in the material examined; however, since some of the macrofaunal samples were provided by third-party contractors these data have not always been made available. Where grain size analysis was carried out the substrate classification is based on that of Folk (1954). Where this analysis was not carried out the substrate descriptions were based on visual examination of the sediment in the field. In total,

1,251 leptostracan specimens were examined. Sex of a proportion of the material was determined using the relative length of the antennae to the body to provide an indication of the proportion of males to females but this was not conducted for all lots. Voucher specimens have been deposited in the zoological collections of the National Museum of Ireland – Natural History (NMINH) and Oxford University Museum of Natural History (OUMNH.ZC). Specimens that had previously been cited by O'Reilly *et al.* (2001) are housed at SEPA. Irish specimens examined by Juan Moreira, (JM), Universidad Autónoma de Madrid, are retained in his collection. The remaining leptostracan specimens are retained in the collections of the authors (Irish material with Aquafact International Services Ltd. and U.K. material with APEM Ltd.). Line drawings were made using a camera lucida connected to a Nikon YS2-B microscope. Maps are presented for each species discussed. For *Sarsinebalia typhlops*, *Nebaliella caboti* and *Nebaliopsis typica* these are based on the records presented by Tattersall (1905) and Mauchline and Gage (1983) since no material was available to us. For all other species, maps are based only on material reviewed in the present study, given the likelihood of previous misidentifications. Various records of Leptostraca from online datasets and grey literature have not been referenced as confirmation of identifications could not be established.

RESULTS

Family Nebaliidae Samouelle, 1819

Genus *Nebalia* Leach, 1814

Nebalia strausi Risso, 1826

Material examined. Ireland. 1♂, 3♀, Kilkieran Bay, Co. Galway, 53°19.548'N 009°38.9165'W, 7.9 m, sandy gravel, 15.x.2010. 4♂, 4♀, Kingstown Bay, Co. Galway, 53°30.905'N 10°7.6979'W, 10 m, gravelly muddy sand, 16.x.2010. 3♀, Valentia Island, Co. Kerry, 51°53.819'N 10°18.786'W, 4 m, muddy sandy gravel, 16.ix.2010 (NMINH:2016.1.5, 1♀). 1♀, Valentia Island, Co. Kerry, 51°53.2439'N 10°21.948'W, 6 m, maërl, 16.ix.2010 (NMINH:2016.1.4, 1♀). 1♂, 5♀, Ahabeg,

Bantry Bay, Co. Cork, at edge of stocked salmon farm cage located at 51°39.7302'N 009°45.1727'W, 20–23.4 m, mud with broken shell, 4.ix.2012 (JM:2014, 1♂, 4♀). 1♂ adult, Glinsk, Mulroy Bay, Co. Donegal, 55°12.1368'N 007°47.0682'W, 8–15 m, medium sand with both live and dead maërl, 14.viii.2012. 1♂ adult, Millstone, Mulroy Bay, Co. Donegal, 50 m from stocked salmon farm, 55°11.4205'N 007°45.388'W, 5–12.9 m, medium sand with maërl gravel, 15.viii.2012 (JM:2014, 1♂).

British and Irish Distribution. South-west, west, and north of Ireland (Co. Cork, Co. Kerry, Co. Galway and Co. Donegal) and Guernsey (Dahl, 1985) (Fig. 1A).

Distribution beyond the study area. Gulf of Naples, Italy (type locality), Eastern Atlantic, from the north-west coast of France to St. Helena (Dahl, 1985). Western Mediterranean (Dahl, 1985). Eastern Mediterranean (Koçak and Katagan, 2006; Koçak *et al.*, 2007). Concarneau, Brittany, France (J.M.C. Holmes, pers. comm.).

Ecology. Coarse sediments, from gravel to coarse sand at depths of 12.7–15.2 m, Total Organic Matter (%TOM) 0.6–4.9 (Moreira *et al.*, 2009a). Maërl, medium sand to mud at depths of 4–23.4 m, %TOM 2.92–18.93 (present study).

Remarks. *Nebalia strausi* is recorded for the first time from Irish waters. Records of *N. strausi* to date suggest a southerly distribution with the specimens from Mulroy Bay, Co. Donegal, representing the northernmost extent of its range. Features distinguishing *N. strausi* from other species of *Nebalia* within the North-East Atlantic include distally acute denticles on the posterior margin of pleonites 6 and 7, in conjunction with an antennular flagellum with more than 10 articles and the exopod of the 2nd maxilla barely extending past the proximal article of the endopod. However, research (Moreira *et al.*, 2004; Koçak *et al.*, 2010) has shown that specimens of *N. strausi* from different localities can exhibit variation in a number of characters including the shape of the anal scales and the denticles of the posterior border of pleonites 6–7. Koçak *et al.* (2011) suggested that the existence of cryptic species cannot be ruled out for *N. strausi*.

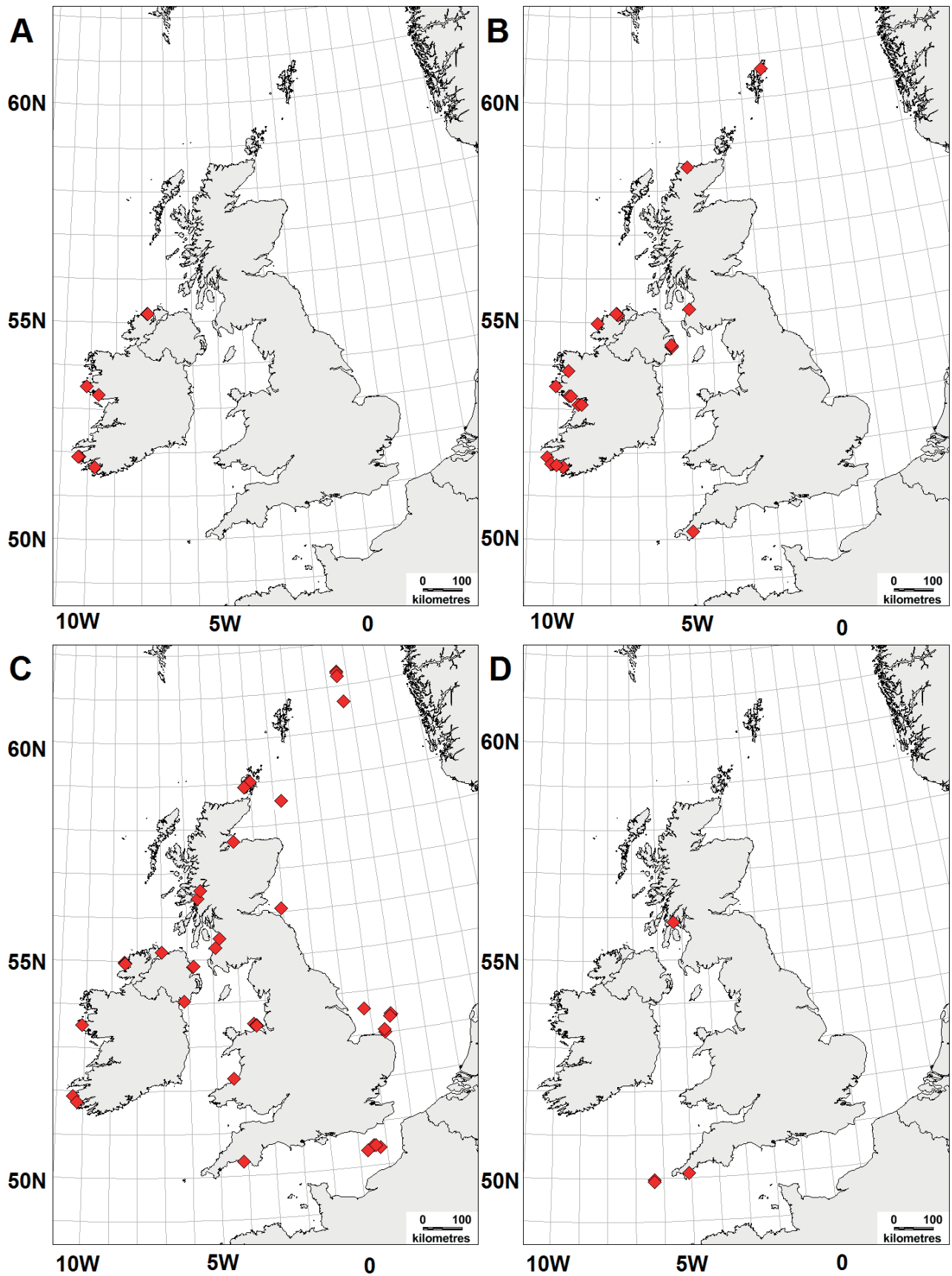


Figure 1. Distribution of Leptostraca in the British Isles: (A) *Nebalia strausi* Risso, 1826; (B) *Nebalia kocatasi* Moreira, Koçak and Katagan, 2007; (C) *Nebalia reboredae* Moreira and Ugorri, 2009 in Moreira *et al.*, 2009a; (D) *Nebalia herbstii* Leach, 1814.

***Nebalia kocatasi* Moreira, Koçak and Katagan, 2007**

Material examined. Ireland. 40♀, 16♂, 52 juveniles, Finavarra, Co. Clare, 53°9.270'N 009°7.059'W, intertidal, semi-exposed shingle, stone and sand beach, 18.ix.2009 (NMINH:2016.1.1, 3♂, 5♀). 5♀, 1♂, Corranroo, Co. Clare, 53°9.033'N 009°0.509'W, intertidal sheltered rocky shore with a muddy substrate, 10.x.2009. 3♀♀, 22♀, 10♂, 19 juveniles, Carna, Co. Galway, 53°18.712'N 009°51.535'W, intertidal, exposed rocky shore with a sandy substrate, 21.ix.2009. 1♀, Aran Island, Co. Donegal, 54°58.2359'N 008°31.0488'W, 5.7 m, sandy gravel, 1.ix.2010. 7♀, 3♂, 17 juveniles, Kilkieran Bay, Co. Galway, 53°17.508'N 009°36.3858'W, 4 m, gravelly muddy sand, 17.x.2010. 22♂, 132♀, 43 juveniles, Kingstown Bay, Co. Galway, 53°30.905'N 10°7.6979'W, 10 m, gravelly muddy sand, 16.x.2010. 6♂, 2♀, 30 juveniles, Kingstown Bay, Co. Galway, 53°30.93'N 10°7.8359'W, 6 m, muddy sandy gravel, 16.x.2010. 4♀, Valentia Island, Co. Kerry, 51°53.418'N 10°21.5879'W, 5 m, muddy sandy gravel, 16.ix.2010. 1♀, Valentia Island, Co. Kerry, 51°53.2439'N 10°21.948'W, 6 m, maërl, 16.ix.2010. 3♂, 18♀, 28 juveniles, Deenish, Kenmare Bay, Co. Cork, at the edge of a stocked salmon farm located at 51°44.364'N 10°12.8189'W, 23.2 m, medium sand with mussel shell, signs of low oxygen/organic enrichment (*Beggiatoa* spp. patches), 13.ix.2012 (NMINH:2016.1.2, 3♂, 1♀, 4 juveniles; JM:2014, 2♂, 5♀, 4 juveniles). 1♂, 3♀, 2 juveniles, Inishfanard, Kenmare Bay, Co. Cork, at the edge of a stocked salmon farm at 51°42.702'N 10°0.4408'W, 20–23 m, muddy sand with shell debris, signs of signs of low oxygen/organic enrichment (*Beggiatoa* spp. patches), 13.ix.2012 (JM:2014, 1♂, 1♀, 2 juveniles). 16♂, 39♀, 59 juveniles, Ahabeg, Bantry Bay Co. Cork, at edge of stocked salmon farm cage located at 51°39.7302'N 009°45.1727'W, 20–23.4 m, mud with shell fragments, 4.ix.2012 (JM:2014, 11♂, 3♀, 3 juveniles). 46♂, 31♀, 34 juveniles, Inishdoonver, Clew Bay, Co. Mayo, at edge of a stocked salmon farm, 53°52.7711'N 009°39.052'W, 21.7 m, cobbles with shell and stone gravel and patches of sand, 20.vii.2012 (JM:2014, 45♂, 30♀, 31 juveniles). 6♂, 10♀, 16 juveniles, Glinsk, Mulroy Bay, Co. Donegal, at edge of a stocked salmon farm located at 55°12.0912'N 007°46.9314'W, 8–13.1 m, medium sand with shell gravel, signs of signs of low

oxygen/organic enrichment (small patches of *Beggiatoa* spp.), 14.viii.2013 (JM:2014, 2♂, 4♀, 3 juveniles). 1♀, Glinsk, Mulroy Bay, Co. Donegal, 150 m from edge of stocked salmon farm, 55°12.1368'N 007°47.06819'W, 8–13.1 m, medium sand with live and dead maërl and shell debris, 14.viii.2013 (JM:2014, 1♀). 10♀, 6 juveniles, Millstone, Mulroy Bay, Co. Donegal, at the edge of a stocked salmon farm, 55°11.446'N 007°45.4068'W, 5–12.9 m, medium sand with a shell gravel fraction and maërl debris, 15.viii.2012 (JM:2014, 1♀). 4♂, 7♀, Cranford, Mulroy Bay, Co. Donegal, near edge of a stocked salmon farm, 55°10.4491'N 007°42.1786'W, 5–12.9 m, fine/medium sand with silt and shell debris, sparse patches of bacterial mats (*Beggiatoa* spp.) and feed from salmon farm, 14.viii.2012 (JM:2014, 2♂, 2♀). **Northern Ireland.** 2 specimens, Strangford Lough, 54°27.000'N 005°36.000'W, 19.7 m, mud with shell, 30.v.2012. 1 specimen, Strangford Lough, 54°25.000'N 005°37.480'W, 17.1 m, shelly mud, 30.v.2012 (OUMNH.ZC.2016-01-008, 1 specimen). 2 specimens, Strangford Lough, 54°24.500'N 005°35.400'W, 60.1 m, muddy sand with shell, 31.v.2012. 1 specimen, Strangford Lough, 54°27.730'N 005°36.640'W, 18.8 m, mud with shell, 18.vi.2013. **England.** 1 specimen, Falmouth, Cornwall, 50°93.770'N 005°39.100'W, 4.4 m, clean broken shells/maërl, 01.v.2013. **Scotland.** 9 specimens, Sian Bay, Loch Eriboll, Highlands, 58°31.325'N 004°40.011'W, 20.1 m, sand with shell, 05.xi.2010 (OUMNH.ZC.2016-01-007, 9 specimens). 2 specimens, Sian Bay, Loch Eriboll, Highlands, 58°31.325'N 004°40.011'W, 20.1 m, sand with shell, 05.xi.2010. 1 specimen, south-west Scotland, 55°15.901'N 004°51.197'W, 1.9 m, poorly sorted very coarse sand, 11.vii.2015. 5 specimens, south-west Scotland, 55°16.139'N 004°51.483'W, 11.6 m, poorly sorted very fine gravel, 11.vii.2015. 5 specimens, North Sandwick, Yell, Shetland, 60°39.122'N 000°59.450'W, 15 m, 2003.

British and Irish Distribution. North, west and south-west of Ireland (Co. Donegal, Co. Mayo, Co. Galway, Co. Kerry, Co. Cork), Cornwall, western and northern Scotland, Shetland (Fig. 1B).

Distribution beyond the study area. Izmir Bay, Turkey (type locality). Cyprus and the Aegean Sea to the western Iberian Peninsula and the Canary Islands

(Moreira *et al.*, 2007; Koçak *et al.*, 2011). Based on the previously known distribution and the present records it seems likely that this species is also present along the west coast of France and southern North Sea coasts but this requires confirmation.

Ecology. Gravel to fine sand with mats of *Zostera marina*, at depths of 4.5–13.8 m, %TOM 1.2–4.9 (Moreira *et al.*, 2009a). Cobbles and gravel to mud, at depths of 4–23.2 m, %TOM 0.69–18.93 (present study). Intertidal on semi-exposed and sheltered rocky shores. The study of their distribution relative to aquaculture cages indicates that this species is most abundant at the edges of the cages as distinct from directly beneath them or further out.

Remarks. The specimens examined agree closely with the description and figures given by Moreira *et al.* (2007). A comparison of diagnostic characters of Mediterranean species of *Nebalia* by Koçak and Moreira (2015) highlights useful differences between *N. kocatasi* and other species, in particular the lateral armature of the 3rd article of the antenna (*N. kocatasi* has 3 thin setae and 3 spine-like setae with the proximal spine-like seta smallest (Fig. 5A). *Nebalia kocatasi* is the only species that has been recorded in this study from the intertidal zone. This likely reflects the sampling methodology rather than true habitat preferences. Numerous specimens of *N. kocatasi* from Kenmare, Co. Kerry, and Finavarra, Co. Clare as well as two specimens from Shetland, had epibionts on the pleonites and on the carapace (Fig. 6). These had a total length of 306–392 µm, capsule length of 219–274 µm and stalk length of 86–141 µm (n=15). A study of these by Gregorio Fernandez-Leborans (Universidad Complutense, Madrid) could not determine their identity but concluded they were most likely protozoans. Over 40 species of chonotrich ciliates are known from Nebaliaceans (Fernandez-Leborans, 2001).

***Nebalia reboredae* Moreira and Urgan, 2009 in Moreira *et al.*, 2009a**

Material examined. Ireland. 2♀, Deenish, Kenmare Bay, Co. Kerry, 51°44.364'N 10°12.8189'W, 23.2

m, on medium sand with shell gravel, 13.ix.2012 (NMINH:2016.1.3, 2♀). 3♂, 1♀, Aran Island, Co. Donegal, 54°58.2359'N 008°31.0488'W, 5.7 m, sandy gravel, 1.ix.2010. 2♀, 1 juvenile, Sound of Aran, Co. Donegal, 54°57.4439'N 008°28.6248'W, 5.5 m, gravelly sand, 1.ix.2010. 3♀, 1 juvenile, Sound of Aran, 54°56.562'N 008°28.2629'W, 9.9 m, gravelly sand, 1 September 2010. 12 specimens, Lough Foyle, Co. Donegal, 55°11.510'N 007°00.765'W, 9.5 m, sand with shell, 29.iii.2012. 1 specimen, Lough Foyle, Co. Donegal, 55°11.510'N 007°00.765'W, 15.6 m, sand with shell, 26.vi.2013. 2 juveniles, Kingstown Bay, Co. Galway, 53° 30.9829'N 10°8.22'W, 9.3 m, gravelly sand, 16.x.2010. 3♀, Valentia Island, Co. Kerry, 51° 52.5599'N 10° 24.444'W, 40 m, gravelly sand. **Northern Ireland.** 1♀, NE of Skernaghan Pt, Larne, Co. Antrim, dredge, 54°51.6869'N 005°45.384'W, 25 m, gravel and shell, 15.iv.2010. 5 specimens, Larne Lough, 54°50.352'N 005°47.802'W, 5.7 m, muddy sand, 14.iii.2013. 2 specimens, Carlingford Lough, 54°03.271'N 006°09.058'W, 7 m, muddy sand with shell, 05.vii.2013. **Scotland.** 1 specimen, Oban Bay, 56°24.862'N 005°29.708'W, 37.6 m, gravelly shelly mud, 09.xii.2010. 19 specimens, Kirkwall Bay, 59°02.014'N 002°59.722'W, 13 m, 25.v.2014. 2 specimens, Kirkwall Bay, 59°01.281'N 002°58.329'W, 12 m, 25.v.2014. 1 specimen, St. Abbs, 56°04.500'N 002°05.460'W, 55 m, 02.vi.1986 [specimen previously cited by O'Reilly *et al.* (2001) as *N. herbstii*]. 1 specimen, Ayr Bay, 55°28.570'N 002°41.000'W, 17 m, 08.ix.1989. 1 specimen, Shuna Island, Loch Linnhe, 56°35.570'N 005°22.750'W, 01.vi.1992. 1 specimen, Bring Head, Hoy, Orkney, 58°54.050'N 003°16.191'W, 20 m, sand, 17.xi.2012. 1 specimen, St. Margaret's Hope, Orkney, 15.v.2015. 1 specimen, south-west Scotland, 55°16.121'N 004°51.617'W, 10.6 m, poorly sorted coarse sand, 11.vii.2015. 3 specimens, Moray Firth (Hilton of Cadboll Water Body), 57°38.09'N 003°57.49' W, 19 m, 23.vi.2015. **Wales.** 1 specimen, Cardigan Bay, 52°15.054'N 004°22.582'W, 21.7 m, 2.vii.2014. **England.** 1 specimen, Plymouth Sound, 50°19.933'N 004°09.200'W, 9.6 m, coarse sand, 30.iii.2011. 1 specimen, eastern English Channel, 50°27.845'N 000°32.794'E, 43.7 m, sandy gravel, 2.viii.2014. 1 specimen, eastern English Channel, 50°23.765'N 000°45.489'E, 39.8 m, sandy gravel,

1.viii.2014. 1 specimen, eastern English Channel, 50°26.977'N 000°36.590'E, 46.8 m, gravelly sand, 2.x.2014. 1 specimen, eastern English Channel, 50°21.401'N 000°18.366'E, 43.9 m, sandy gravel, 30.vii.2014. 1 specimen, Cromer Shoals, 52°59.807'N 001°28.649'E, 11.6 m, sand, 12.ix.2014. 1 specimen, Cromer Shoals, 53°04.062'N 001°27.237'E, 10.7 m, mixed sediments, 12.ix.2014. 1 specimen, Liverpool Bay, 53°29.165'N 003°30.429'W, 21.9 m, gravelly sand, 29.x.2014. 2 specimens, Liverpool Bay, 53°26.970'N 003°23.971'W, 16.0 m, gravelly sand, 30.x.2014. 4 specimens, Liverpool Bay, 53°26.038'N 003°24.593'W, 13.8 m, sandy gravel, 30.x.2014. **North Sea.** 5 specimens, Osprey Field, 61°19.530'N 004°32.601'E, 159.9 m, muddy sand, 6.xii.2008. 1 specimen, Dunlin Field, 61°18.115'N 001°32.060'E, 155 m, muddy sand, 11.xi.2009. 1 specimen, Dunlin Field, 61°13.141'N 001°30.927'E, 148.1 m, muddy sand, 08.xi.2009. 2 specimens, Clipper Field, 53°23.826'N 001°47.205'E, 25.1 m, sandy gravel, 27.xii.2008. 2 specimens, Clipper Field, 53°24.179'N 001°46.431'E, 24. m, sandy gravel, 27.xii.2008 (OUMNH.ZC.2016-01-009, 2 specimens). 2 specimens, Dunbar Field, 60°37.700'N 001°39.200'E, 145 m. 6 specimens, Clipper Field, 53°21.452'N 001°44.148'E, 29.9 m, muddy sand, 2.ii.2009. 1 specimen, Juliet Field, 53°35.444'N 000°46.261'E, 33.3 m, sandy gravel, 10.ix.2009.

British and Irish Distribution. West and north-west of Ireland (Co. Kerry, Co. Galway, Co. Donegal) and east of Northern Ireland (Co. Antrim) (Fig. 1C).

Distribution beyond the study area. Ría de Ferrol, Galicia, Spain (type locality). Based on the previously known distribution and the present records it seems likely that this species is also present along the west coast of France and continental southern North Sea coasts but this requires confirmation.

Ecology. Medium sand at depth of 6.4 m, 1.4 % TOM (Moreira *et al.*, 2009a). Gravelly sand at depths of 5.5–40 m, 0.69–3.1% TOM (present study). *Nebalia reboredae* appears to be the European species of *Nebalia* which shows a greater affinity for sandy sediments.

Remarks. The specimens examined agree closely with the description and figures given by Moreira *et al.*

(2009a). Contrary to Dahl's statement that *Nebalia herbstii* is the dominant *Nebalia* species in British waters, *N. reboredae* was the most commonly recorded in this study.

***Nebalia herbstii* Leach, 1814**

Material examined. **Scotland.** 16 specimens, Rubha Stillaig, Loch Fyne, Stn 17:2, 55°51.860'N 005°18.900'W, 08.vi.1999. **England.** 1 specimen, Falmouth, Cornwall, 50°54.740'N 005°54.910'W, 6.8 m, clean shells/maërl, 2.v.2013. 9 specimens, north-east Isles of Scilly, 49°55.289'N 006°19.926'W, 15.9 m, sand, 26.v.2013. 110 specimens, north-east Isles of Scilly, 49°58.125'N 006°19.257'W, 6.1 m, coarse (3–4 cm) gravel with mud and abundant macroalgae, 27.v.2013.

British and Irish Distribution. Shetland, western British Isles (Dahl, 1985), south-west and western coasts of England (Leach, 1814), Loch Fyne, Isles of Scilly, Falmouth (present study) (Fig. 1D).

Distribution beyond the study area. Western France to Spanish border (Walker-Smith and Poore, 2001); northern coast of the Iberian Peninsula (Martínez *et al.*, 2007).

Ecology. Shallow (6.1–15.9 m), near-shore waters over sands, muds, gravels and maërl (present study). Occurring under stones that lay on mud amongst the hollows of the rocks (Leach, 1814).

Remarks. Dahl (1985) believed *N. herbstii* to be the dominant species of the genus in the British Isles. For this reason, many subsequent records of *Nebalia* from the British Isles have been attributed to *N. herbstii*. The material examined in the present study demonstrates that far from being the most common species of the genus it is relatively uncommon, in routine samples at least. Dahl (1985) also believed that the species may well occur around the Iberian Peninsula; however, Moreira *et al.* (2009a) could not confirm the occurrence of *N. herbstii* there. Ledoyer (1997) recorded its presence in the Mediterranean (Corsica and Bonnieu, France). However, Koçak *et al.* (2011) suspect that these specimens may refer to

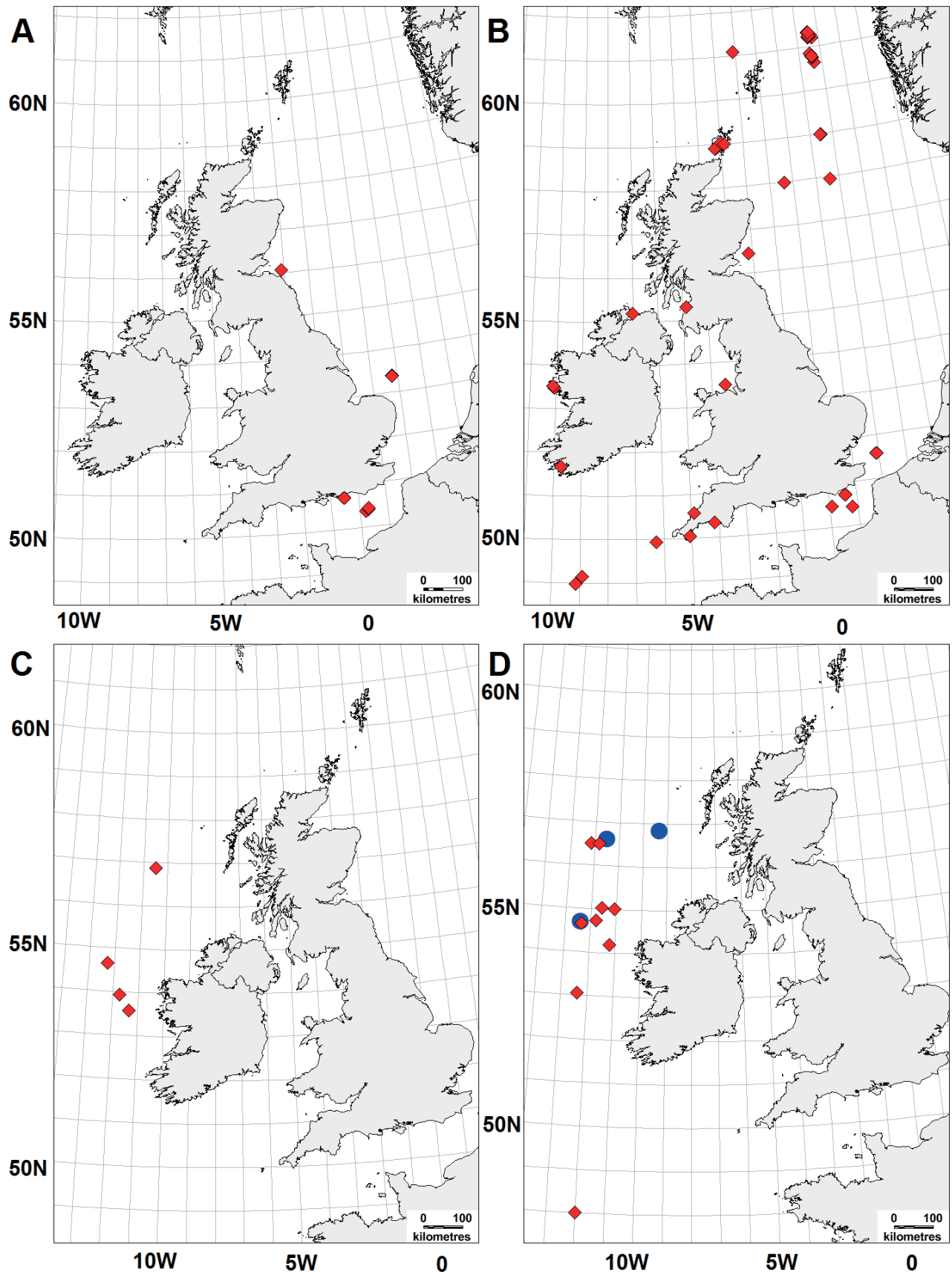


Figure 2. Distribution of Leptostraca in the British Isles: (A) *Nebalia borealis* Dahl, 1985; (B) *Sarsinebalia urgorrhii* Moreira, Gestoso and Troncoso, 2003; (C) *Sarsinebalia typhlops* (G.O. Sars, 1870); (D) *Nebaliella caboti* Clark, 1932 (denoted by blue circles); *Nebaliopsis typica* G.O. Sars, 1887 (red diamonds).

a different species as the dimensions of the maxilla 2 in Ledoyer's specimens differ from that typical of the species [in Dahl's (1985) description the proximal article of the endopod is longer than the distal article, whereas in Ledoyer's specimen they are subequal in length]. Subsequent to Dahl's (1985) revision many of the records that were originally ascribed to *Nebalia bipes* within the British Isles were ascribed to *N. herbstii* but these records should be treated with caution and deposited specimens re-examined in the light of the new records submitted for the British Isles. All 16 specimens of *N. herbstii* from Loch Fyne had epibionts similar to those discussed above for *N. kocatasi*.

Nebalia borealis Dahl, 1985

Material examined. **North Sea.** 1 specimen, Clipper Field, 53°23.071'N 001°47.078'E, 25.9 m, muddy sand, 7.ii.2009 (OUMNH.ZC.2016-01-006, 1 specimen). 1 specimen, Clipper Field, 53°22.121'N 001°46.887'E, 27.1 m, muddy sand, 5.ii.2009. **Scotland.** 1 specimen, St. Abbs, 56°03.440'N 002°07.270'W, 56 m, 30.vi.1987 [specimen previously cited by O'Reilly *et al.* (2001) as *N. herbstii*]. **England.** 1 ♂, eastern English Channel, 50°43.0174'N 0°31.0028'W, 14.7 m, muddy sandy gravel and pebbles, 15.vii.2015. 1 specimen, eastern English Channel, 50°21.968'N 000°12.759'E, 45 m, sandy gravel, 31.vii.2014. 11 specimens, eastern English Channel, 50°23.835'N 000°19.243'E, 48.1 m, sandy gravel, 31.vii.2014. 1 specimen, eastern English Channel, 50°25.786'N 000°18.418'E, 54.1 m, sandy gravel, 7.viii.2014.

British and Irish Distribution. Shetland Islands (Dahl, 1985); North Sea, St. Abbs, Scotland, English Channel (present study) (Fig. 2A).

Distribution beyond the study area. Norway, Sweden (Dahl, 1985).

Ecology. Clay, muddy sands to sandy gravels and rocky bottoms at depths of 14 m to 350 m.

Remarks. The specimens examined here agree well with Dahl's description of the species. One of the specimens cited under the name *N. herbstii* by O'Reilly *et al.* (2001), with the caveat that only specimens for

1989 had been confirmed, was re-examined here and found to be *N. borealis*. This species has a northern distribution and the present records extend the southern range of the species southwards in the British Isles to the central English Channel.

Genus *Sarsinebalia* Dahl, 1985

Remarks. Dahl (1985) created the genus *Sarsinebalia* to accommodate *Nebalia typhlops*, and based it on four characters: 1) a complicated rostrum with subterminal spine; 2) the features of the eye; 3) lack of a comb-row on the exopod of the first pleopod; and 4) a short exopod of the 2nd maxilla. Dahl (1985) goes on to state that these features are also present in an undescribed species from the Red Sea [according to Moreira *et al.* (2003) this is corrected to north-west Africa in an unpublished manuscript by Dahl] and two further undescribed species from Australia. Moreira *et al.* (2003) postulate that the north-west African species could be identical to their *Sarsinebalia urgorrii* Moreira, Gestoso and Troncoso, 2003 whilst the identity of the Australian species is unknown as descriptions of these taxa had not appeared at the time of Dahl's death. To date, five species have been ascribed to *Sarsinebalia*: *S. typhlops*, *S. urgorrii*, *Sarsinebalia cristoboi* Moreira, Gestoso and Troncoso, 2003, *Sarsinebalia biscayensis* Ledoyer, 1998, and *Sarsinebalia kunyensis* Ledoyer, 2000. According to Mauchline and Gage (1983) and Dahl (1985), specimens recorded from New Jersey, U.S.A. by Hessler and Sanders (1965) as *Nebalia typhlops occidentalis* Hessler and Sanders, 1965 differ in several significant characters and could represent a further species.

Walker-Smith and Poore (2001) considered *Sarsinebalia* to be a synonym of *Nebalia* but only included the type species *S. typhlops* in their analysis. However, Moreira *et al.* (2003) retained *Sarsinebalia* as valid as some (but not all) of the characters proposed by Dahl (1985) hold between *S. typhlops*, *S. urgorrii* and *S. cristoboi*. However, their study likewise overlooked *S. biscayensis* and *S. kunyensis*. A recent key to worldwide *Nebalia* species (Song and Min, 2016) also did not adopt the synonymy of *Sarsinebalia* suggested by Walker-Smith and Poore (2001).

Since Dahl's (1985) landmark study there have been significant advances in the taxonomy and systematics

of the Leptostraca with around 67% of the currently accepted species having been described since this date with further new species continuing to be described (e.g. Koçak and Moreira, 2015; Song and Min, 2016). Combined with the phylogenetic studies of Olesen (1999) and Walker-Smith and Poore (2001), there is now a greater, if still not complete, understanding of variation in the traditionally used diagnostic characters across the Leptostraca. Many of Dahl's diagnostic characters for *Sarsinebalia* no longer stand up to scrutiny and now appear to be more indicative of species- rather than genus-level differences. These are discussed in turn here.

1) Complicated rostrum with subterminal spine. All species of *Nebalia* have a rostral keel (Walker-Smith and Poore, 2001) so in this respect the rostrum of *Sarsinebalia* species is no more complex. The subterminal spine is present in *Sarsinebalia* and the undescribed *Nebalia* sp. B of Walker-Smith and Poore (2001) as well as the less closely related genera of the Paranebaliidae. Additionally, *S. biscayensis* has a reduced spine (see Ledoyer, 1998), and some mature males of *S. typhlops* are also noted by Dahl (1985) as having a reduced spine.

2) Features of the eye. Of the five nominal species, only *S. typhlops* (and possibly the undescribed species of Dahl, 1985) has the 'squarish' eye shape described by Dahl (1985). The eyes of *S. urgorrii* and *S. cristoboi* are of a similar but not identical shape, whilst *S. biscayensis* has long slender eyes (see Ledoyer, 1998) and *S. kunyensis* appears to have rounded eyes (see Ledoyer, 2000). Eye shape is exceptionally variable in other *Nebalia* (even as far as being bi-lobed – see Walker-Smith and Poore, 2001) so a 'squarish' eye seems not to be too unusual and certainly within the range of variation covered by other *Nebalia*. In addition, Hessler (1984) illustrated significant developmental changes in the shape and armature of the eye of *Dahlella caldariensis* Hessler, 1984. Pigment is absent in *S. biscayensis*, *S. kunyensis* and *S. typhlops* but present in the *S. urgorrii* and *S. cristoboi* (but also seems to fade after long-term storage in alcohol, in *S. urgorrii* at least). As a general rule within the Crustacea, there is a tendency towards unpigmented eyes in deeper water species which may explain its absence in *S. biscayensis*, *S. kunyensis* and *S. typhlops* which are found deeper than *S. urgorrii* and *S. cristoboi*. Ommatidia are absent in *S. typhlops* and

S. biscayensis but present in the other three species (also absent in unrelated *Speonebalia* Bowman, Yager and Iliffe, 1985, *Nebaliella* Thiele, 1904, and *Dahlella* Hessler, 1984).

3) Lack of a comb-row on the exopod of the first pleopod. A comb-row is absent in *S. typhlops*, *S. urgorrii* and *S. cristoboi* but present in both *S. biscayensis* and *S. kunyensis*. The length of the comb-row appears to be diagnostic (at least partially so) at a species level in *Nebalia* (see Walker-Smith and Poore, 2001) and the complete absence of a comb-row could just represent the extreme of this variation.

4) A short exopod of the 2nd maxilla. Only *S. typhlops* and *S. biscayensis* have an unusually short exopod on maxilla 2, whereas the other species have an exopod longer than the first segment of the endopod. In *S. kunyensis* and *S. biscayensis* the division between the two endopod segments is indistinct but the length of the exopod relative to the overall endopod can be used.

Based on this, the only character that is consistent between all 5 species of *Sarsinebalia* is the presence of a subterminal rostral spine. As already mentioned this spine occurs elsewhere in the Paranebaliidae and in Walker-Smith and Poore's (2001) *Nebalia* sp. B and so is not unique to *Sarsinebalia*. A formal reappraisal of *Sarsinebalia* is outside of the scope of the current study and should await examination of material of the currently included species as it is conceivable that other, as yet un-investigated, characters may unite all or some of the species currently assigned to the genus. Molecular methods may also help resolve the status of the genus. Until such time we continue to use *Sarsinebalia* here in accordance with Moreira *et al.* (2003).

***Sarsinebalia urgorrii* Moreira, Gestoso and Troncoso, 2003**

Material examined. Ireland. 1♀, Mannin Bay, Co. Galway, 53°28.3919'N 10°5.118'W, 9.9 m, sand, 16.x.2010. 2♂, 37♀ and 8 juveniles, Kingstown Bay, Co. Galway, 53°30.9829'N 10°8.22'W, 9.3 m, gravelly sand, 16.x.2010. 1♀, Ahabeg, Bantry Bay, Co. Cork, under a cage at stocked salmon farm located at 51°39.7302'N 009°45.1727'W, 20–24.5 m, mud interspersed with shelly sand, 29.viii.2013. 16♀, Ahabeg, Bantry Bay, Co. Cork, near edge of stocked salmon farm located

at 51°39.7302'N 009°45.1727'W, 20–24.5 m, shelly gravel, 29.viii.2013 (NMINH:2016.1.6, 2♀). 2 specimens, Lough Foyle, Co. Donegal, 55°11.510'N 007°00.765'W, 9.5 m, sand with shell, 29.iii.2012. 3 specimens, Lough Foyle, 55°11.510'N 007°00.765'W, 15.6 m, sand with shell, 26.vi.2013. **North Sea.** 9 specimens, Osprey Field, 61°19.530'N 001°32.601'E, 159.9 m, muddy sand, 6.xii.2008. 1 specimen, Osprey Field, 61°19.249'N 001°34.643'E, 159.5 m, muddy sand, 7.xii.2008. 2 specimens, Osprey Field, 61°20.318'N 001°31.633'E, 160.1 m, muddy sand, 7.xii.2008. 2 specimens, Osprey Field, 61°19.257'N 001°34.653'E, 158.6 m, muddy sand, 7.xii.2008. 1 specimen, Osprey Field, 61°19.102'N 001°32.295'E, 159.1 m, muddy sand, 6.xii.2008. 1 specimen, Osprey Field, 61°18.626'N 001°30.998'E, 157.6 m, muddy sand, 4.xii.2008. 2 specimens, Dunlin Field, 61°12.819'N 001°30.926'E, 149.09 m, muddy sand, 9.xi.2009. 1 specimen, Dunlin Field, 61°12.151'N 001°41.738'E, 145.8 m, muddy sand, 11.xi.2009. 1 specimen, Dunlin Field, 61°15.547'N 001°39.227'E, 151.5 m, muddy sand, 11.xi.2009 (OUMNH.ZC.2016-01-012, 1 specimen). 1 specimen, Dunlin Field, 61°16.961'N 001°33.856'E, 153.2 m, muddy sand, 11.xi.2009. 1 specimen, Dunlin Field, 61°12.911'N 001°30.772'E, 148.45 m, muddy sand, 9.xi.2009. 1 specimen, Dunlin Field, 61°12.908'N 001°30.776'E, 148.39 m, slightly gravelly muddy sand, 9.xi.2009. 1 specimen, Dunlin Field, 61°12.921'N 001°30.438'E, 148.9 m, muddy sand, 9.xi.2009. 1 specimen, Dunlin Field, 61°13.140'N 001°30.883'E, 148.4 m, muddy sand, 8.xi.2009. 1 specimen, Dunlin Field, 61°15.052'N 001°33.887'E, 149.9 m, slightly gravelly muddy sand, 8.xi.2009. 2 specimens, Dunlin Field, 61°14.780'N 001°33.292'E, 149.1 m, slightly gravelly muddy sand, 8.xi.2009. 1 specimen, Dunlin Field, 60°46.631'N 001°33.047'E, 141.4 m, muddy sand, 20.v.2010. 1 specimen, Glenlivet Field, 61°04.600'N 002°05.420'W, 435 m. 1 specimen, Staffa Field, 60°44.490'N 001°35.349'E, 135.5 m, muddy sand, 17.ix.2009. 2 specimens, Staffa Field, 60°49.431'N 001°30.370'E, 134.9 m, muddy sand, 20.v.2010. 3 specimens, Staffa Field, 60°47.964'N 001°31.698'E, 138.7 m, muddy sand, 20.v.2010. 1 specimen, Staffa Field, 60°44.405'N 001°34.707'E, 138.6 m, muddy sand, 16.v.2010. 2 specimens, Staffa Field, 60°45.327'N 001°34.281'E, 139.3 m, muddy sand, 17.v.2010. 1 specimen, Staffa Field, 60°47.964'N

001°31.697'E, 138.7 m, slightly gravelly muddy sand, 20.v.2010 (OUMNH.ZC.2016-01-011, 1 specimen). 1 specimen, Staffa Field, 60°46.631'N 001°33.047'E, 141.4 m, muddy sand, 20.v.2010. 1 specimen, Staffa Field, 60°50.390'N 001°29.613'E, 134.4 m, slightly gravelly muddy sand, 20.v.2010. 7 specimens, Staffa Field, 60°50.390'N 001°29.612'E, 134.35 m, slightly gravelly muddy sand, 20.v.2010. 1 specimen, Staffa Field, 60°49.431'N 001°30.370'E, 134.9 m, slightly gravelly muddy sand, 20.v.2010. 1 specimen, Staffa Field, 60°47.964'N 001°31.698'E, 138.7 m, slightly gravelly muddy sand, 20.v.2010. 7 specimens, Dunbar Field, 60°37.700'N 001°39.200'E, 145 m. 2 specimens, Braemar Field, 58°58.991'N 001°27.840'E, 118 m, sandy mud, 21.xi.2012. 1 specimen, Braemar Field, 58°58.360'N 001°26.961'E, 124 m, MDAC mud and shell, 21.xi.2012. 1 specimen, Goldeneye Field, 57°58.921'N 000°23.452'W, 122 m, muddy sand, 15.i.2010. 1 specimen, Nelson Field, 57°56.500'N 001°36.683'E, 95 m, muddy sand, 12.xii.2013. **Scotland.** 1 specimen, Bring Head, Hoy, Orkney, 58°53.702'N 003°15.115'W, 23 m, sand, 17.i.2012 (OUMNH.ZC.2016-01-010). 1 specimen, Bring Head, Hoy, Orkney, 58°54.050'N 003°16.191'W, 20 m, sand, 17.i.2012. 1 specimen, Bring Head, Hoy, Orkney, 58°53.702'N 003°15.115'W, 23 m, sand, 17.i.2012. 1 specimen, Bring Head, Hoy, Orkney, 58°53.765'N 003°15.115'W, 21.8 m, sand, 19.ix.2013. 1 specimen, Bring Head, Hoy, Orkney, 58°54.050'N 003°16.191'W, 19 m, sand, 19.ix.2013. 1 specimen, Kirkwall Bay, Orkney, 59°00.864'N 002°57.872'W, 11 m, 25.v.2014. 5 specimens, Kirkwall Bay, Orkney, 59°02.014'N 002°59.722'W, 13 m, 25.v.2014. 1 specimen, Kirkwall Bay, Orkney, 58°59.729'N 002°49.951'W, 19 m, 25.v.2014. 3 specimens, Bell Rock, 56°27.000'N 002°10.000'W, 53 m, 24.iv.1989 [specimen previously cited by O'Reilly *et al.* (2001) as *S. typhlops*]. 1 specimen, Girvan Mains, 55°15.780'N 004°51.790'W, 30.viii.2000. **England.** 1 specimen, Plymouth Sound, 50°20.333'N 004°10.567'W, 6.3 m, coarse sand, 30.iii.2011. 1 specimen, Padstow, Cornwall, 50°34.263'N 004°57.480'W, 11.9 m, sand with shell, 12.iii.2013. 2 specimens, Lizard Peninsula, Cornwall, 50°02.550'N 005°03.998'W, 10.5 m, muddy coarse sand, 13.vii.2014. 1 specimen, north-east Isles of Scilly, 49°56.194'N 006°16.593'W, 18.8 m, fine sand, 26.v.2013. 1 specimen, South West Deeps rMCZ,

48°58.885'N 009°08.731'W, 161 m, sand, 17.v.2013. 1 specimen, South West Deeps rMCZ, 49°08.603'N 008°54.977'W, 154 m, muddy sand, 13.v.2013. 1 specimen, eastern English Channel, 50°43.7117'N 0°34.5528'E, 24.5 m, sandy gravel, 7.vi.2015. 1 specimen, eastern English Channel, 50°26.046'N 000°48.017'E, 44.1 m, gravelly sand, 1.viii.2014. 1 specimen, eastern English Channel, 50°29.212'N 000°04.533'E, 56.8 m, gravelly sand, 4.viii.2014. 1 specimen, South Falls Disposal Ground, Outer Thames, 51°34.3416'N 1°58.3548'E, 49 m, muddy sand with clay, 2.xi.2014. 1 specimen, Liverpool Bay, 53°28.641'N 003°29.659'W, sandy gravel, 29.x.2014.

British and Irish Distribution. North, west and south-west Ireland (Co. Donegal, Co. Galway and Co. Cork), North Sea, Orkney Islands, Firth of Clyde, English Channel, Cornwall, Isles of Scilly, South West Deeps (Fig. 2B).

Distribution beyond the study area. Galicia, NW Iberian Peninsula (Moreira *et al.*, 2003; 2009a). Based on the previously known distribution and the present records it seems likely that this species is also present along the west coast of France and continental southern North Sea coasts but this requires confirmation.

Ecology. Coarse sandy sediments, from very coarse sand to medium sand, at depths of 12.7–20 m, 1.4–3.7% TOM (Moreira *et al.*, 2009a). Coarse shelly gravel to mud at depths 9.3–435 m, 9.03–14.73% TOM (present study).

Remarks. Based on the current records, *S. urgorrii* is the dominant species of *Sarsinebalia* in shallow British and Irish waters. The pigmentation of the eyes was variable in the present material ranging from dark to orange and occasionally being almost completely absent; when this was the case externally visible ommatidia were still evident. The examined material generally agreed with the description of Moreira *et al.* (2003) but in one female from the English Channel six spines were noted on the distolateral border of the sixth pleopod rather than four as stated in the diagnosis provided by Moreira *et al.* (2003). All other characters agreed well with *S. urgorrii*.

***Sarsinebalia typhlops* (G.O. Sars, 1870)**

Material examined. None.

British and Irish Distribution. Rockall Trough, 1990–2900 m (Mauchline and Gage, 1983), west of Ireland (Tattersall, 1905) (Fig. 2C).

Distribution beyond the study area. Widespread; Red Sea, Lofoten Is. (Norway), Messina, Bay of Naples (Italy), North America from Davis Strait to New Jersey, Australia (Walker-Smith and Poore, 2001). Records should be examined as it is possible that some may refer to undescribed species.

Remarks. Previous British and Irish records of *S. typhlops* require confirmation in light of the present study where only *S. urgorrii* was recorded amongst abundant material from shallow waters (much of which was originally identified as *S. typhlops* following Mauchline, 1984). It is likely that *S. typhlops* is restricted to deeper waters in the area (Mauchline and Gage, 1983).

Genus *Nebaliella* Thiele, 1904

***Nebaliella caboti* Clark, 1932**

Material examined. None.

British and Irish Distribution. Rockall Trough, 1390–2900 m (Mauchline and Gage, 1983) (Fig. 2D).

Distribution beyond the study area. Cabot Strait, eastern Canada at 378 m (type locality – Clark, 1932), off New Jersey, U.S.A., 2085 m (Hessler and Sanders, 1965).

Remarks. Although Mauchline and Gage (1983) referred their specimens to *N. caboti* they did so with some reservation given the uncertainty surrounding the systematics of *Nebaliella* at that time and stated that comparative studies should be made of all *Nebaliella* species to help resolve these issues. Such a study was conducted by Walker-Smith (1998) who reviewed Mauchline and Gage's (1983) record accepting their identification in addition to providing other characters

useful for separating *N. caboti* from its congeners.

Family Nebaliopsididae Hessler, 1984

Genus *Nebaliopsis* G.O. Sars, 1887

Nebaliopsis typica G.O. Sars, 1887

Material examined. None.

British and Irish Distribution. South-west British Isles (Linder, 1943), Rockall Trough (Mauchline and Gage, 1983) (Fig. 2D).

Distribution beyond the study area. Described from the South Pacific midway between New Zealand and Chile (Sars, 1887). Considered to be near cosmopolitan between the latitudes 50°N and 50°S (Mauchline, 1984). West and south-east coast of South America, near Falkland Is., off coast of Ghana, Ivory Coast, south-west Indian Ocean, South Pacific, Scotia Sea (Walker-Smith and Poore, 2001).

DISCUSSION

Prior to the present study, five species of Leptostraca were recorded from the British Isles. These are *Nebalia herbstii*, *Nebalia borealis*, *Sarsinebalia typhlops*, *Nebaliella caboti* and *Nebaliopsis typica*. In light of the present research, the number of leptostracan species recorded in the British Isles is nine, as outlined above. These records provide further evidence to support Dahl's (1985) removal of *N. bipes* from the British species list and demonstrate that, despite the previous works, the leptostracan fauna of the British Isles was poorly known.

Our records indicate that the dominant species in shallow, offshore waters of the British Isles are *N. reboredae* and *S. urgorrhii*, neither of which has previously been formally reported for the region. Many of the current records are from routine monitoring projects, in coastal and offshore waters and collected using grab

samplers, dredges and diver cores. The distributions presented here are therefore influenced to a degree by the sampling methods, sampling intensity, target habitats and the drivers of these surveys. For example, we have few records from intertidal areas (the exception being *N. kocatasi* as outlined above) and comparatively few from very shallow near-shore locations. It is possible that targeted sampling for leptostracans using other methods such as light traps may yield further records of species new to the area and provide a better understanding of the distribution of each species in the region.

Historically, the distribution and identity of leptostracans in European waters has been problematic, although several recent studies beginning with Dahl (1985) have contributed greatly to our understanding of the group in Europe. In order to help clarify species ranges and consistently identify specimens a key to the currently described Leptostraca of Europe is provided below. Given the highly conservative morphology of leptostracans, it is likely that molecular studies will demonstrate that some of the currently accepted species in fact represent species complexes, particularly for some of the more wide-ranging species. Furthermore, as new species continue to be described and further works are likely to provide insights into variability of character states, this key should be regarded as provisional rather than definitive at this stage and identifications should be carefully compared with original descriptions where possible. Several studies, most notably that of Olesen and Walossek (2000), have discussed ontogenetic changes in some taxonomically important characters such as antennae, maxillae and pleopods. Males for some species are unknown or poorly described. The key is therefore based on adult females and using this key for males or immature specimens could result in incorrect identifications. Staining specimens in Methyl Green improves the visibility of certain characters and may aid in the accurate identification of specimens. In particular it makes it possible to discern the relative lengths of the articles of the second maxilla without dissection.

Key to the adult females of leptostracan species from European waters

1. Caudal furcae leaf-like, broadest midway; rostral plate small
..... Nebaliopsididae; *Nebaliopsis typica* G.O. Sars, 1887
- 1'. Caudal furcae tapering evenly to a point; rostral point well developed [Nebaliidae] 2

2. Rostrum with ventral keel longer than rostral flange; thoracopods 2–5 without epipods; eye modified into leaf-like appendage; molar with accessory spine *Nebaliella caboti* Clark, 1932
- 2'. Rostrum with keel shorter than rostral flange (Fig. 4A, B); thoracopods 2–5 with epipod that is longer than exopod; eye of different form; molar without accessory spine **3**
3. Rostrum with small subterminal spine (may be difficult to discern) (Fig. 4B) [*Sarsinebalia*] **4**
- 3'. Rostrum lacking subterminal spine (Fig. 4A) [*Nebalia**] **7**
4. Dorsal denticles of pleonites 6–7 with distally acute denticles; exopod of pleopod 1 with a spine row of about 12 spines with simple apices; antennule peduncle article 4 without spine; subterminal spine of rostrum small *Sarsinebalia biscayensis* Ledoyer, 1998
- 4'. Dorsal denticles of pleonites 6–7 with distally rounded denticles; exopod of pleopod 1 without spine row; antennule peduncle article 4 with spine; subterminal spine of rostrum well developed (may be reduced in adult males) **5**
5. Eye lacking pigment and externally discernable visual elements; exopod of maxilla 2 shorter than first article of endopod *Sarsinebalia typhlops* (G.O. Sars, 1870)
- 5'. Eye provided with pigment and ommatidia (although colour may have faded following preservation in alcohol); exopod of maxilla 2 longer than first article of endopod **6**
6. Supraorbital scale surpassing distal end of eye; antennal flagellum with thin long setae; pleonite 4 posterior border with acute denticles *S. cristoboi* Moreira *et al.*, 2003
- 6'. Supraorbital scale not surpassing distal end of eye; antennal flagellum with short spine-like setae; pleonite 4 posterior lateral border with distally rounded to pointed denticles *S. urgorrhii* Moreira *et al.*, 2003
7. Pleonites 6–7 provided with distally acute denticles (Fig. 3A, D) **8**
- 7'. Pleonites 6–7 provided with denticles of a different shape (Fig. 3A, C) **10**
8. Antennular flagellum with more than 10 articles; antennular scale more than twice as long as wide **9**
- 8'. Antennular flagellum with up to 7 articles; antennular scale twice as long as wide
..... *Nebalia troncosoi* Moreira *et al.*, 2003
9. Terminal dorsal spine of peduncle of pleopod 1 reaching nearly to end of spine row; exopod of 2nd maxilla extends past proximal article of endopod *Nebalia borealis* Dahl, 1985
- 9'. Terminal dorsal spine of peduncle of pleopod 1 reaching at most to centre of spine row; exopod of 2nd maxilla barely extends past proximal article of endopod *Nebalia strausi* Risso, 1826
10. Eyes pigmented **11**
- 10'. Eyes lacking pigment *Nebalia abyssicola* Ledoyer, 1997
11. Proximal article of the endopod of 2nd maxilla longer than distal article [Fig. 4D ($a > b$)] **12**
- 11'. Proximal article of the endopod of 2nd maxilla of equal length to the distal article [Fig. 4E ($a' = b'$)]; lateral external armature of the antenna, article 3, consists of 3 thin setae and three spine-like setae (Fig. 5A, shaded); proximal spine-like seta (Fig. 5A, arrowed, shaded) shorter than other two
..... *Nebalia kocatasi* Moreira *et al.*, 2007
12. Exopod of 2nd maxilla extends past the proximal article of the endopod (Fig. 4D) **13**
- 12'. Exopod of 2nd maxilla does not extend past the proximal article of the endopod ... *Nebalia clausi* Dahl, 1985
13. Antennular flagellum with more than 10 articles; antennule peduncle article 4 with three or more distal thick spines **14**
- 13'. Antennular flagellum with less than 10 articles; antennule peduncle article 4 with one distal thick spine (Fig. 3B) **15**
14. Anal scale with point lying over mid-line of the scale (Fig. 5B); (endopod of thoracopods 2–7 in prae-ovigerous females extend well past exopod); distal article of mandible palp with parallel margins (Fig. 5E) ...
..... *Nebalia herbstii* Leach, 1814
- 14'. Anal scale with point lying closer to medial margin (Fig. 5C); (endopod of thoracopods 2–7 in prae-ovigerous females reaching only level with or just past exopod); distal article of mandible palp with margins diverging (Fig. 5D) *Nebalia bipes* (Fabricius, 1780)

15. Pleopod 4 protopod without serrations along posterior border
 *Nebalia reboredae* Moreira and Urgorri, 2009 in Moreira *et al.*, 2009a
- 15'. Pleopod 4 protopod with 4 serrations along posterior border (as in Fig. 4C); lateral external armature of the antenna, article 3, consists of 3 thin setae and 3 spine-like setae (spine-like setae of equal length)
 *Nebalia mediterranea* Koçak and Moreira, 2015

* A further species, *Nebalia biarticulata* Ledoyer, 1997, has been described from the Mediterranean French coast. In the original description of the species, Ledoyer (1997) stated that all the specimens are presumed to be male, due to the length of the antennae in relation to the body. No additional specimens of this species have been reported upon since its discovery and the female is unknown. It is possible that it represents the male of one of the other species known from the Mediterranean region and that the two have not yet been linked but since no confirmed females are known it is omitted from this key. The species is characterised by possessing a biarticulate pleopod 6. According to the most recent diagnosis of *Nebalia* (Walker-Smith and Poore, 2001) this character should exclude *N. biarticulata* from the genus *Nebalia* in which the sixth pleopod is uniarticulate. A biarticulate sixth pleopod is otherwise found in *Nebaliopsis* (Nebaliopsidae), *Speonebalia* and *Nebaliella* (both Nebaliidae). A re-examination of this species may prove worthwhile.

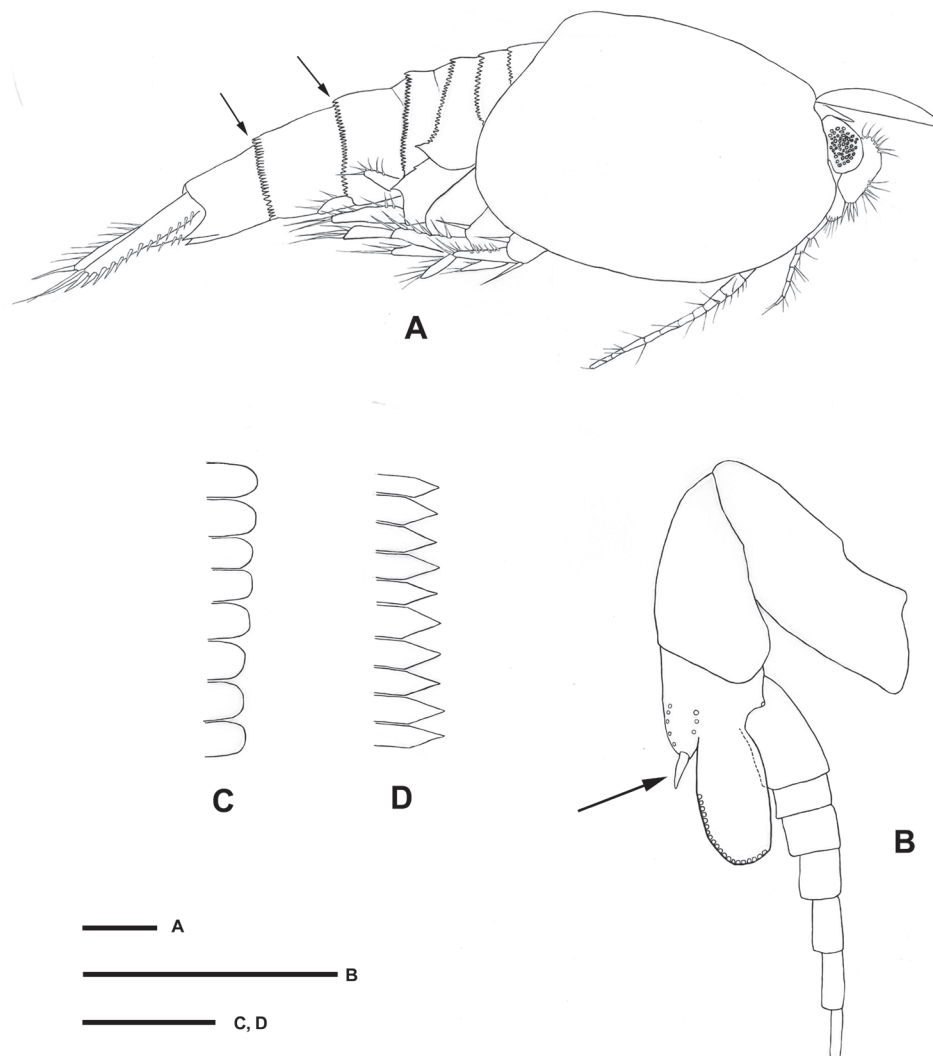


Figure 3. (A) *Nebalia kocatasi* female habitus (position of denticles on posterior margin of pleonite 6 and 7 arrowed); (B) *N. reboredae* antennule (antennule peduncle article 4 with one thick spine arrowed, setae omitted); (C) *N. kocatasi* denticles at posterior margin of pleonite 7; (D) *N. strausi* denticles at posterior margin of pleonite 7. Scale bars: A, 0.5 mm; B–D 0.1 mm.

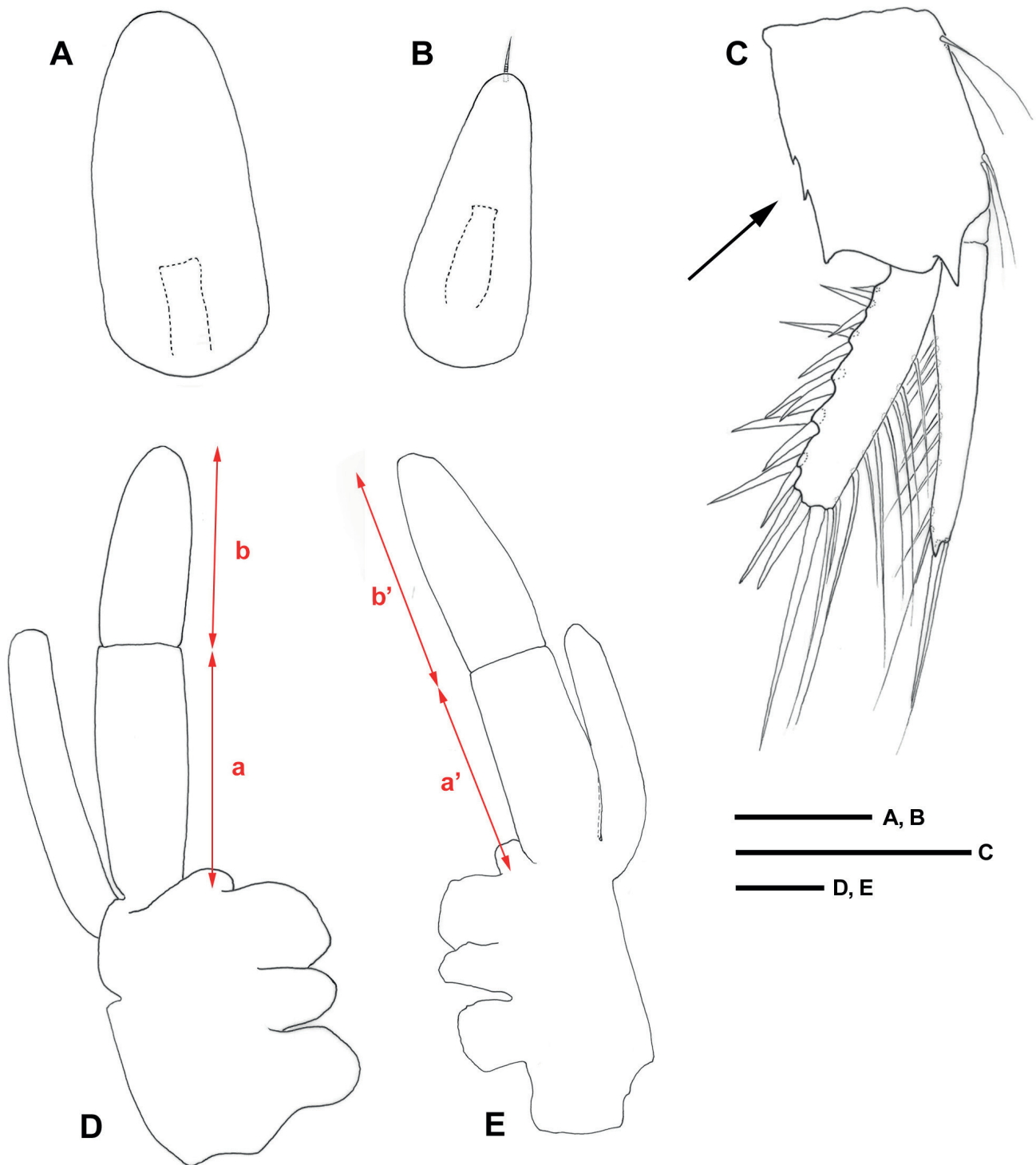


Figure 4. (A) *Nebalia kocatasi* rostrum, dorsal view (ventral rostral keel outlined); (B) *Sarsinebalia urgorrhii* rostrum, dorsal view (ventral rostral keel outlined); (C) *N. kocatasi* pleopod 4 (serrated margin arrowed); (D) *N. reboredae* maxilla 2 (length of $a > b$, setae omitted); (E) *N. kocatasi* maxilla 2 (length of $a' = b'$, setae omitted). Scale bars: A, B, D, E, 0.1 mm; C 0.5 mm.

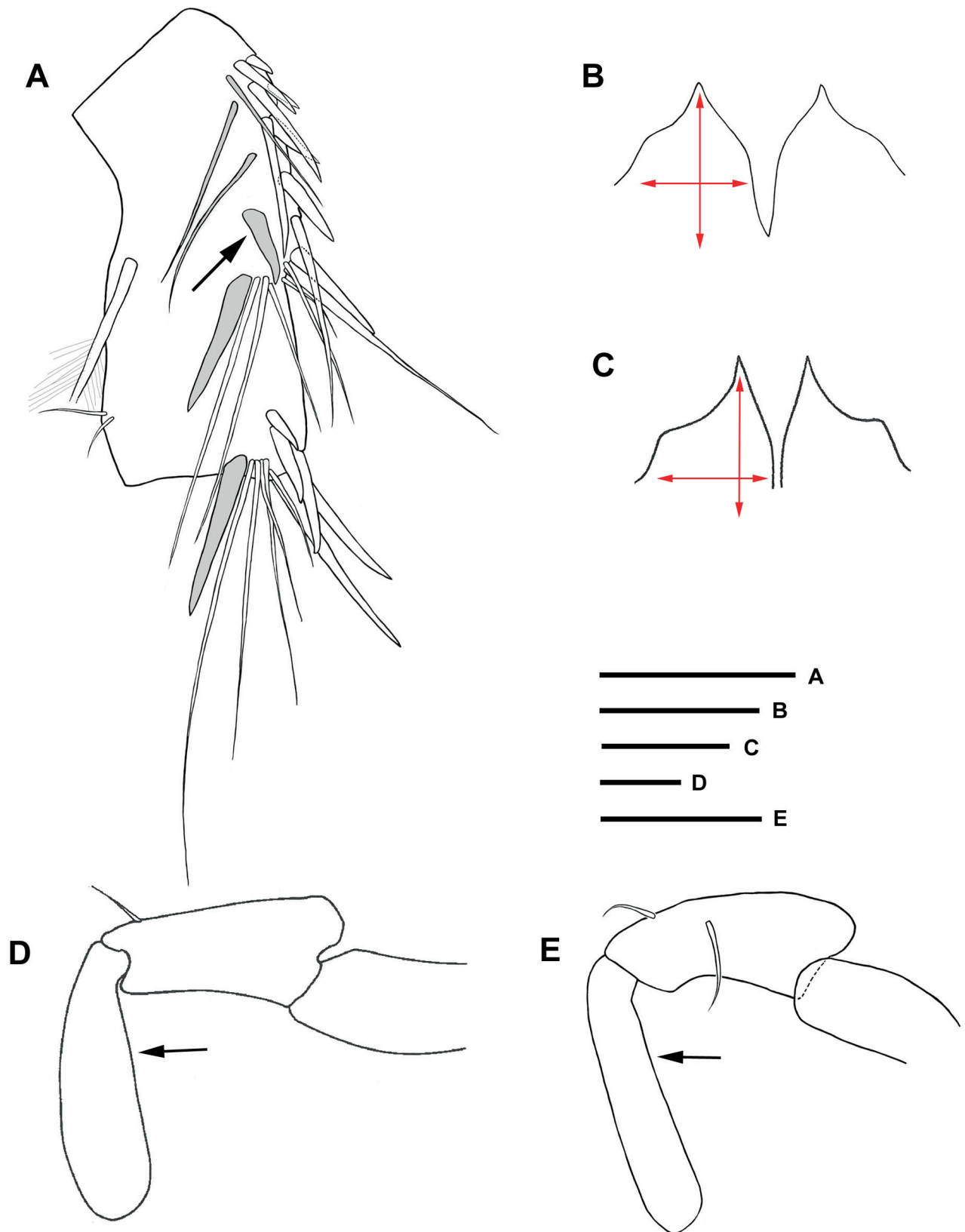


Figure 5. (A) *Nebalia kocatasi* female antenna, article 3, external side, lateral view. Lateral spine-like setae shaded, short proximal spine-like seta arrowed (setae of internal side omitted); (B) *N. herbstii* anal scales; (C) *N. bipes* anal scales (illustration from Dahl, 1985); (D) *N. bipes* mandibular palp, distal article arrowed (illustration from Dahl, 1985); (E) *N. herbstii* mandibular palp, distal article arrowed. Scale bars: A, B, D, 0.2 mm; C, 0.1 mm; E, 0.5mm.



Figure 6. Unidentified epibiont detached from the carapace of *Nebalia kocatasi* sampled from Shetland Isles, 2003 (image courtesy of G. Fernandez-Leborans).

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