ZooKeys 787: 135–149 (2018)
doi: 10.3897/zookeys.787.24647
http://zookeys.pensoft.net

CHECKLIST

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A checklist of marine bryozoan taxa in Scottish sea regions

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Academic editor: *D. Gordon* | Received 23 February 2018 | Accepted 27 August 2018 | Published 3 October 2018

http://zoobank.org/85A8A747-5876-4100-89E5-5D172F129BBE

Citation: Rouse S, Loxton J, Jones MES, Porter JS (2018) A checklist of marine bryozoan taxa in Scottish sea regions. ZooKeys 787: 135–149. https://doi.org/10.3897/zookeys.787.24647

Abstract

Contemporary and historical bryozoan records were compiled to provide a comprehensive checklist of species in Scottish waters. The checklist comprises 218 species in 58 families, with representatives from each of the extant bryozoan orders. The fauna was relatively sparse compared to other regions for which bryozoan checklists were available e.g. New Zealand and Australia. Six non-indigenous bryozoan species from the Scottish seas region were included in the checklist. Baseline information on species distributions, such as that presented in this checklist, can be used to monitor and manage the impact of human activities on the marine environment, and ultimately preserve marine biodiversity.

Keywords

Bryozoa, distribution, non-indigenous species, Scotland

Introduction

The phylum Bryozoa comprises approximately 6000 known/described extant species of filter feeding invertebrates that predominantly occur in the marine environment (Gordon and Costello 2016). There are three classes and four orders of extant bryozo-

ans (class Gymnolaemata, orders Cheilostomatida and Ctenostomatida; class Phylactolaemata (freshwater), order Phylactolaemata *incertae sedis*; class Stenolaemata, order Cyclostomatida). The order Cheilostomatida is the most diverse.

All bryozoans are clonal and the colonies can take many different forms including encrusting, erect and arborescent forms (McKinney and Jackson 1991). The majority of bryozoan species have a calcium carbonate skeleton, but there are also a number of chitinous and gelatinous species. Colony growth proceeds via the asexual budding of individual units, called zooids, with sexual reproduction producing free-swimming larvae (McKinney and Jackson 1991). Bryozoan species occur in all major marine habitats, from the Polar regions to the tropics, ranging from the intertidal zone to the deep sea. The vast majority of species live attached to a substrate, which may be rocks, biogenic structures (e.g. coral, shells), algae or man-made debris (Hayward and Ryland 1998).

Bryozoans contribute to ecosystem functioning and services through the provision of three-dimensional structure and habitat for other species, and by serving as a food source for other marine species (Bitschofsky et al. 2011; Lidgard 2008). Bryozoans are also recognized for their potential economic importance due to the pharmaceutical and active compounds that are associated with a number of species. (Narkowicz et al. 2002). Several bryozoan species are recognized as invasive and are potentially harmful to native marine species (O'Brien et al. 2013; Yorke and Metaxas 2011). Despite these ecological and economic roles, knowledge on local bryozoan species and faunistic inventories are often lacking or incomplete (Rouse et al. 2014). Such baseline information on species distributions is required to monitor and manage the impact of human activities on the marine environment, and ultimately preserve marine biodiversity (Powney and Isaac 2015).

Scotland lays claim to one of the largest marine resources in Europe with over 9910 km of mainland coastline, 8092 km of island coastline, and an estimated 88,600 km^2 of territorial seas (Baxter et al. 2011). The west coast of Scotland has numerous exposed islands, high sea cliffs, and fjordic inlets, while the east coast is less variable and dominated by low-lying sedimentary shores. Marine spatial planning has been identified as priority by the Scottish Government (Baxter et al. 2011), and there is a drive towards providing reliable information on species occurrences and distribution. Scotland has historically been the focus of much marine biological research and as such a vast back catalogue of bryozoan records exist (e.g. Norman 1869, Hiscock 1996). These records, however, are often disparate, unreliable and/or difficult to locate. Rouse et al. (2014) analysed records of marine bryozoan from Scotland between 1792 and 2010 to assess spatial and temporal trends in bryozoan diversity. Records were compiled from museum collections, professional/academic surveys, consultancy reports and a citizen science scheme consisting of trained amateurs. Records for which the location was uncertain or not provided, and/or the species seemed likely to be wrong based on its generally accepted distribution (e.g. tropical or Antarctic) were discarded. Other records that had only been documented in Scotland by one source, with an unknown or non-expert identified, were also excluded from the analysis. Approximately 8% of these records were museum collections with associated specimens, 60% from a ten-

year expert survey of the British coastline and 16% from the citizen science scheme, with the latter two relying on identification via optical microscopes. The remaining records were compiled from published manuscripts that used a combination of optical and scanning electron microscopy for identification.

Using these records, Rouse et al. (2014) found bryozoan diversity to be higher on the west coast of Scotland than other regions, but this was largely attributed to a sampling bias towards the west coast. The study also highlighted the lack of a bryozoan species list for Scottish waters. The aim of the present study, therefore, is to combine the data collated by Rouse et al. (2014) with recent bryozoan studies in Scotland to provide to a comprehensive species checklist of marine bryozoan species in the region.

Methods

Study area

The Scottish sea region was defined according to the 'Clean Sea Assessment' in the Scottish Government's Marine Atlas (Baxter et al. 2011). The region constitutes 15 sub-regions covering coastal and offshore areas (Figure 1). Previous sub-divisions of the Scottish seas (e.g., the MNCR regions used by Rouse et al. (2014)) are restricted to coastal areas, and as such have not been selected for use in this checklist. There is no a priori reason to expect that the Scottish sea region would have a distinct fauna, however the region does support a greater range of habitat types than the adjoining English Sea area (Baxter et al. 2011). The north of Scotland also represents a transitional area between arctic and boreal species (Boulton et al. 1991).

Data sources

Historical and contemporary records of bryozoans were obtained from sources including museum collections, literature, and online databases according to the methods of Rouse et al. (2014). These records were supplemented with records from occasional field surveys carried around Scottish harbours and marinas as part of an on-going invasive species survey programme (Collin et al. 2015; Loxton 2014; Nall et al. 2015; Porter et al. 2015; Wasson and De Blauwe 2014). The checklist represents the species known from Scotland up until 2015.

Organization of the checklist

The checklist is arranged phylogenetically for the higher-level taxa, with the families, genera, and species listed alphabetically. Taxonomy was checked against the World Register of Marine Species (Horton et al. 2016), and names that were currently listed as 'ac-

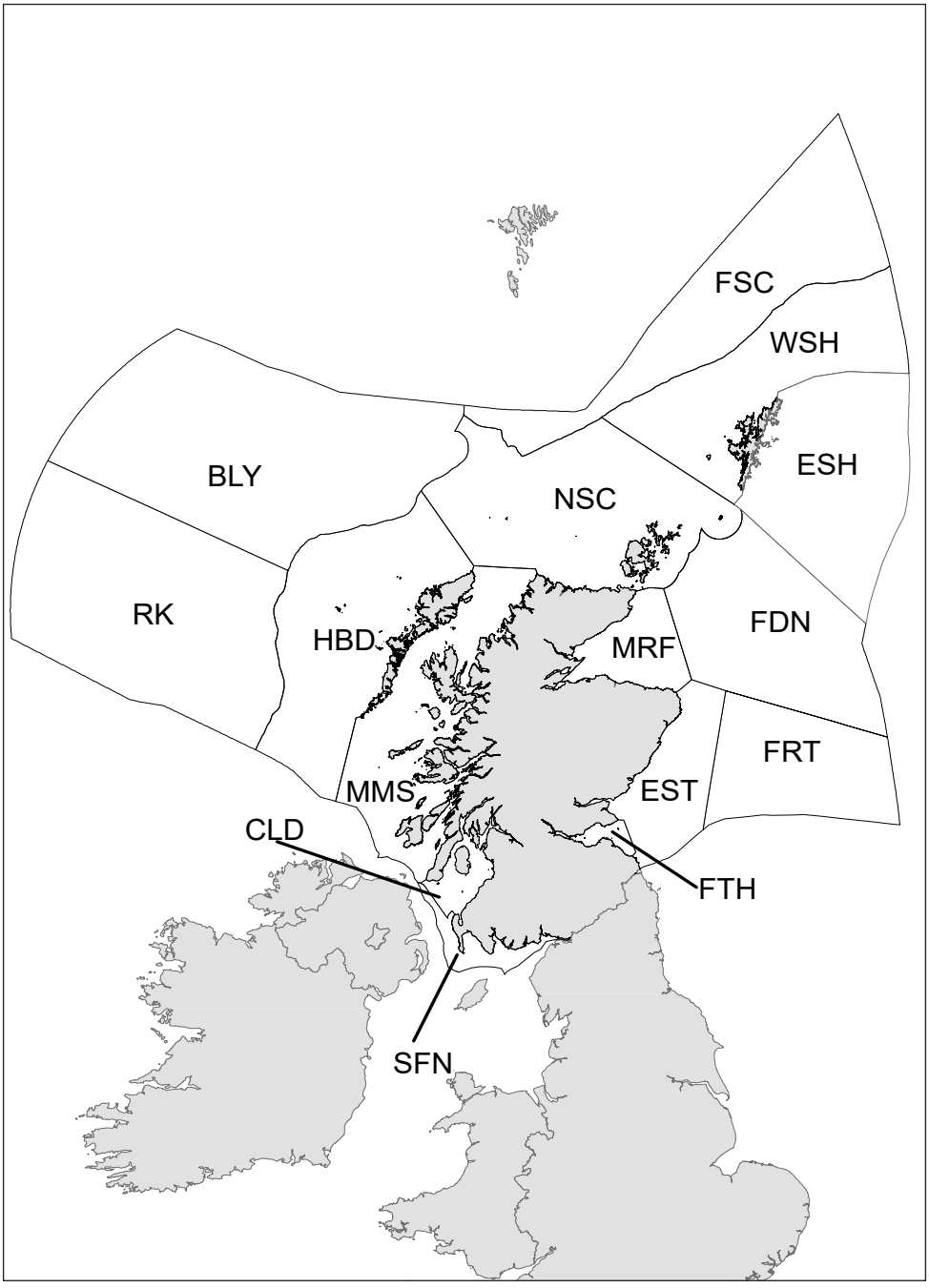

Figure 1. Scottish sea regions. The abbreviations given are used in the checklist. BLY (Bailey), CLD (Clyde), ESH (East Shetland), EST (East Scotland), FDN (Fladen), FRT (Forties), FSC (Faroe-Shetland Channel), FTH (Forth), HBD (Hebrides), MMS (Minches and Malin Sea), MRF (Moray Firth), NSC (North Scotland), RK (Rockall), SFN (Solway Firth and North Channel), WSH (West Shetland).

cepted' are presented. The number in parentheses immediately to the right of the family name indicates the number of associated taxa, and the abbreviations next to each species specify the sub-region from which records originated (see Figure 1 for definitions of abbreviations). Bryozoan non-indigenous species (NIS) are denoted with an asterisk (*) in the checklist. Individual bryozoan records are provided in the Suppl. material 1.

Results

Table 1 shows the checklist of marine Bryozoa from the Scottish sea regions. A total of 218 species are included in the list, belonging to 128 different genera from 58 families. The Scottish records represent approximately 3.7% of the total number of bryozoan species known worldwide (n = 5869) (Bock and Gordon 2013). There are representatives from each of the extant marine bryozoan orders (Cyclostomatida, Ctenostomatida, and Cheilostomatida). The most speciose bryozoan families in Scotland were the Calloporidae (13 species) and the Romancheinidae (13 species), which both contain mainly encrusting species.

Six NIS were identified as part of the Scottish fauna. These were *Bugulina fulva* (Ryland, 1960), *Bugulina simplex* (Hincks, 1886), *Bugula neritina* (Linnaeus, 1758), *Tricellaria inopinata* d'Hondt & Occhipinti Ambrogi, 1985, *Fenestrulina delicia* Winston, Hayward & Craig, 2000, *Schizoporella japonica* Ortmann, 1890. The Clyde subregion contained the greatest number of NIS (all except *B. fulva*).

Table 1. Checklist of marine bryozoan fauna occurring in the Scottish sea region. Species denoted with an asterisk (*) indicate those considered to be non-indigenous within Scotland.

STENOLAEMATA (30)	
Order Cyclostomatida (30)	**Sub-region**
Family Annectocymidae (2)	
Annectocyma major (Johnston, 1847)	ESH, MMS, RK, WSH
Entalophoroecia deflexa (Couch, 1842)	CLD, HBD, MMS, RK
Family Crisiidae (8)	
Bicrisia abyssicola Kluge,1962	HBD, NCS
Crisia aculeata Hassall,1841	CLD, EST, FTH, HBD, MMS, NCS, WSH
Crisia denticulata (Lamarck, 1816)	CLD, EST, FTH, HBD, MMS, NCS, SFN, WSH
Crisia eburnea (Linnaeus, 1758)	CLD, EST, FTH, HBD, MMS, NCS, SFN, WSH
Crisia ramosa Harmer, 1891	HBD, MMS
Crisidia cornuta (Linnaeus, 1758)	CLD, EST, HBD, MMS, NCS, SFN, WSH
Crisiella producta (Smitt, 1865)	CLD, WSH
Filicrisia geniculata (Milne Edwards, 1838)	CLD, HBD, MMS,
Family Horneridae (1)	
Hornera lichenoides (Linnaeus, 1758)	ESH, FSC, RK, WSH
Family Lichenoporidae (3)	
Coronopora truncata (Fleming, 1828)	MMS, NCS, RK, WSH

Disporella hispida (Fleming, 1828)	CLD, EST, FTH, HBD, MMS, NCS, WSH
Patinella verrucaria (Linnaeus, 1758)	CLD, EST, FTH, MMS, NCS, WSH
Family Oncousoeciidae (2)	
Oncousoecia diastoporides (Norman, 1869)	MRF, WSH
Oncousoecia dilatans (Johnston, 1847)	ESH, MMS, WSH
Family Plagioeciidae (2)	
Diplosolen obelia (Johnston, 1838)	CLD, ESH, HBD, MMS, WSH
Plagioecia patina (Lamarck, 1816)	CLD, EST, HBD, MMS, NCS, WSH
Family Stigmatoechidae (1)	
Stigmatoechos violacea (M.Sars, 1863)	RK, WSH
Family Stomatoporidae (2)	
Stomatopora gingrina Jullien, 1882	RK
Stomatoporina incurvata (Hincks, 1859)	MMS, MRF
Family Terviidae (1)	
Tervia irregularis (Meneghini, 1844)	RK
Family Tubuliporidae (8)	
Exidmonea atlantica (Forbes in Johnston, 1847)	MMS, RK, WSH
Tubulipora aperta Harmer, 1898	EST, FTH, NCS
Tubulipora flabellaris (O. Fabricius, 1780)	CLD
Tubulipora liliacea (Pallas, 1766)	CLD, EST, FTH, FRT, HBD, MMS, MRF, NCS, RK, WSH
Tubulipora lobifera Hastings, 1963	CLD, MMS, MRF, NCS
Tubulipora penicillata (O. Fabricius, 1780)	MMS, MRF
Tubulipora phalangea Couch, 1844	HBD, MMS, NCS, WSH
Tubulipora plumosa Thompson in Harmer, 1898	EST, FTH, MMS, NCS, WSH
GYMNOLAEMATA (189)	
Order Ctenostomatida (27)	
Family Alcyonidiidae (8)	
Alcyonidioides mytili (Dalyell, 1848)	CLD, EST, FTH, HBD, MMS, NCS, SFN, WSH
Alcyonidium albidum Alder, 1857	CLD, EST, FTH, MMS, MRF, NCS, WSH
Alcyonidium diaphanum (Hudson, 1778)	CLD, ESH, EST, FTH, FRT, HBD, MMS, MRF, NCS, RK, SFN, WSH
Alcyonidium gelatinosum (Linnaeus, 1761)	CLD, EST, FTH, FRT, HBD, MMS, MRF, NCS, SFN, WSH
Alcyonidium hirsutum (Fleming, 1828)	CLD, ESH, EST. FTH, HBD, MMS, MRF, NCS, SFN, WSH
Alcyonidium mamillatum Alder, 1857	CLD, EST, MMS, MRF, NCS, SFN
Alcyonidium parasiticum (Fleming, 1828)	CLD, EST, FTH, MMS, MRF, NCS, WSH
Alcyonidium polyoum (Hassall, 1841)	HBD
Family Arachnidiidae (2)	
Arachnidium clavatum Hincks, 1877	CLD, MMS, WSH
Arachnidium fibrosum Hincks, 1880	CLD
Family Buskiidae (1)	
Buskia nitens Alder, 1857	WSH
Family Farrellidae (1)	
Farrella repens (Farre, 1837)	SFN
Family Flustrellidridae (1)	
Flustrellidra hispida (O. Fabricius, 1780)	CLD, EST, FTH, HBD, MMS, MRF, NCS, SFN, WSH
Family Hypophorellidae (1)	
Hypophorella expansa Ehlers, 1876	CLD
Family Nolellidae (3)	

Nolella dilatata (Hincks, 1860)	CLD, FTH, MMS, NCS, WSH
Nolella pusilla (Hincks, 1880)	CLD
Nolella stipata Gosse, 1855	MMS
Family Spathiporidae (1)	
Spathipora sertum Fischer, 1866	WSH
Family Triticellidae (2)	
Triticella flava Dalyell, 1848	CLD, SFN
Triticella pedicellata (Alder, 1857)	CLD
Family Vesiculariidae (6)	
Amathia gracilis (Leidy, 1855)	CLD, FTH, MMS
Amathia gracillima (Hincks, 1877)	MMS
Amathia imbricata (Adams, 1798)	CLD, EST, FTH, HBD, MMS, NCS, SFN
Amathia lendigera (Linnaeus, 1758)	SFN
Amathia pustulosa (Ellis & Solander, 1786)	CLD, MMS, SFN
Vesicularia spinosa (Linnaeus, 1758)	CLD, FTH, MMS, SFN
Family Walkeriidae (1)	
Walkeria uva (Linnaeus, 1758)	CLD, ESH, MMS, NCS
Order Cheilostomatida (160)	
Family Aeteidae (3)	
Aetea anguina (Linnaeus, 1758)	EST, FTH, HBD, MMS, NCS, WSH
Aetea sica (Couch, 1844)	CLD, MMS, NCS
Aetea truncata (Landsborough, 1852)	CLD, MMS, NCS
Family Antroporidae (1)	
Rosseliana rosselii (Audouin, 1826)	ESH, WSH
Family Beaniidae (1)	
Beania mirabilis Johnston, 1840	EST, MMS, NCS
Family Bitectiporidae (7)	
Hippoporina pertusa (Esper, 1796)	CLD, MMS, NCS, SFN, WSH
Pentapora fascialis (Pallas, 1766)	HBD, MMS, SFN
Schizomavella auriculata (Hassall, 1842)	MMS, NCS, SFN, WSH
Schizomavella cornuta (Heller, 1867)	WSH
Schizomavella discoidea (Busk, 1859)	NCS, WSH
Schizomavella hastata (Hincks, 1862)	WSH
Schizomavella linearis (Hassall, 1841)	CLD, EST, FTH, HBD, MMS, MRF, NCS, SFN, WSH
Family Bryocryptellidae (8)	
Marguetta lorea (Alder, 1864)	ESH, WSH
Palmiskenea skenei (Ellis & Solander, 1786)	CLD, EST,MMS, MRF, RK, WSH
Porella alba Nordgaard, 1906	EST, MRF, NCS
Porella compressa (J. Sowerby, 1805)	CLD, HBD, MMS, MRF, NCS, RK, WSH
Porella concinna (Busk, 1854)	CLD, ESH, EST, MMS, MRF, WSH
Porella laevis (Fleming, 1828)	WSH
Porella minuta (Norman, 1868)	MRF, WSH
Porella struma (Norman, 1868)	ESH, WSH
Family Bugulidae (12)	
Bicellariella ciliata (Linnaeus, 1758)	CLD, ESH, EST, FTH, HBD, MMS, NCS, WSH
Bicellarina alderi (Busk, 1859)	MMS, NCS, WSH
Bugulina avicularia (Linnaeus, 1758)	CLD, HBD, MMS, NCS, SFN, WSH
Bugulina calathus (Norman, 1868)	MMS
Bugulina flabellata (Thompson in Gray, 1848)	CLD, ESH, EST, FTH, HBD, MMS, MRF, NCS, RK, SFN, WSH

**Bugulina fulva* (Ryland, 1960)	MMS, NCS
Bugulina turbinata (Alder, 1857)	CLD, FTH, HBD, MMS, NCS, WSH
**Bugulina simplex* (Hincks, 1886)	CLD, ESH, MMS, NCS
**Bugula neritina* (Linnaeus, 1758)	CLD
Crisularia plumosa (Pallas, 1766)	CLD, EST, FTH, HBD, MMS, NCS, SFN
Crisularia purpurotincta (Norman, 1868)	ESH, EST, FTH, HBD, MMS, NCS, WSH
Dendrobeania murrayana (Bean in Johnston, 1847)	ESH, MMS, NCS, WSH
Family Calloporidae (13)	
Alderina imbellis (Hincks, 1860)	MMS, NCS, WSH
Amphiblestrum auritum (Hincks, 1877)	EST, MMS, NCS, WSH
Amphiblestrum flemingii (Busk, 1854)	CLD, EST, FTH, MMS, MRF, NCS, RK, WSH
Amphiblestrum solidum (Packard, 1863)	ESH, MMS, MRF, WSH
Callopora craticula (Alder, 1856)	CLD, MMS, WSH
Callopora dumerilii (Audouin, 1826)	MMS, MRF, NCS, SFN, WSH
Callopora lineata (Linnaeus, 1767)	CLD, EST, FTH, MMS, MRF, NCS, WSH
Callopora rylandi Bobin & Prenant, 1965	EST, FTH, HBD, MMS, NCS
Cauloramphus spiniferum (Johnston, 1832)	EST, MMS, NCS, WSH
Crassimarginatella solidula (Hincks, 1860)	EST, WSH
Megapora ringens (Busk, 1856)	EST, FSC, WSH
Ramphonotus minax (Busk, 1860)	ESH, RK, WSH
Tegella unicornis (Fleming, 1828)	EST, MRF, NCS, WSH
Family Candidae (9)	
Caberea ellisii (Fleming, 1814)	NCS, WSH
Cradoscrupocellaria reptans (Linnaeus, 1758)	CLD, ESH, EST, FTH, HBD, MMS, NCS, SFN, WSH
Notoplites harmeri Ryland, 1963	WSH
Notoplites jeffreysii (Norman, 1863)	ESH, MMS, WSH
Pomocellaria inarmata (O'Donoghue & O'Donoghue, 1926)	FTH, MMS, WSH
Scrupocellaria scruposa (Linnaeus, 1758)	CLD, ESH, EST, FTH, HBD, MMS, NCS, SFN, WSH
**Tricellaria inopinata* d'Hondt & Occhipinti Ambrogi, 1985	CLD, EST, MMS, MRF, NCS
Tricellaria peachii (Busk, 1851)	ESH, EST, MRF, NCS, WSH
Tricellaria ternata (Ellis & Solander, 1786)	ESH, EST, FTH, FRT, HBD, NCS, WSH
Family Cellariidae (4)	
Cellaria fistulosa (Linnaeus, 1758)	CLD, EST, FTH, HBD, MMS, MRF, NCS, SFN, WSH
Cellaria salicornioides Lamouroux, 1816	CLD, MMS, WSH
Cellaria sinuosa (Hassall, 1840)	CLD, EST, HBD, MMS, SFN, WSH
Euginoma vermiformis Jullien, 1883	RK
Family Celleporidae (11)	
Buskea dichotoma (Hincks, 1862)	CLD, EST, MMS, MRF, WSH
Buskea nitida Heller, 1867	CLD, MMS
Cellepora pumicosa (Pallas, 1766)	CLD, ESH, EST, FTH, FRT, HBD, MMS, MRF, NCS, RK, WSH
Celleporina caliciformis (Lamouroux, 1816)	CLD, ESH, FTH, HBD, MRF, MMS, NCS, WSH
Celleporina decipiens Hayward, 1976	HBD
Celleporina pygmaea (Norman, 1868)	FSC, MRF, WSH
Lagenipora lepralioides (Norman, 1868)	ESH, WSH
Omalosecosa ramulosa (Linnaeus, 1767)	CLD, ESH, EST, FTH, HBD, MMS, MRF, NCS, WSH
Palmicellaria elegans Alder, 1864	WSH
Turbicellepora avicularis (Hincks, 1860)	CLD, EST, FRT, HBD, MMS, MRF

Turbicellepora boreale Hayward & Hansen, 1999	RK
Family Chaperiidae (1)	
Larnacicus corniger (Busk, 1859)	FSC, RK, WSH
Family Chorizoporidae (1)	
Chorizopora brongniartii (Audouin, 1826)	EST, MMS, NCS, SFN, WSH
Family Cribrilinidae (7)	
Collarina balzaci (Audouin, 1826)	CLD, MMS, WSH
Cribrilina annulata (O. Fabricius, 1780)	CLD, EST, FTH, MMS, NCS, WSH
Cribrilina cryptooecium Norman, 1903	EST, MMS, MRF, NCS, WSH
Cribrilina punctata (Hassall, 1841)	CLD, EST, FTH, MMS, MRF, NCS, WSH
Membraniporella nitida (Johnston, 1838)	CLD, EST, FTH, HBD, MMS, NCS, WSH
Puellina innominata (Couch, 1844)	CLD
Puellina venusta (Canu & Bassler, 1925)	CLD, WSH
Family Cryptosulidae (1)	
Cryptosula pallasiana (Moll, 1803)	CLD, MMS, MRF, NCS, WSH
Family Doryporellidae (1)	
Doryporellina reticulata (Ryland, 1963)	RK
Family Electridae (7)	
Aspidelectra melolontha (Landsborough, 1852)	NCS
Conopeum reticulum (Linnaeus, 1767)	CLD, EST, FTH, FRT, MMS, NCS, MRF
Conopeum seurati (Canu, 1928)	NCS
Einhornia crustulenta (Pallas, 1766)	NCS
Electra monostachys (Busk, 1854)	MMS, NCS, SFN
Electra pilosa (Linnaeus, 1767)	CLD, ESH, EST, FTH, HBD, MMS, MRF, NCS, RK, SFN, WSH
Pyripora catenularia (Fleming, 1828)	CLD, FRT, MMS, NCS, SFN, WSH
Family Escharinidae (5)	
Escharina alderi (Busk, 1856)	FSC, MMS, RK, WSH
Escharina dutertrei haywardi Zabala, Maluquer & Harmelin, 1993	FSC, WSH
Escharina johnstoni (Quelch, 1884)	CLD, MMS
Herentia hyndmanni (Johnston, 1847)	NCS, WSH
Phaeostachys spinifera (Johnston, 1847)	FTH, MMS, NCS, WSH
Family Eucrateidae (1)	
Eucratea loricata (Linnaeus, 1758)	CLD, ESH, EST, FTH, HBD, MMS, MRF, NCS, SFN, WSH
Family Exechonellidae (1)	
Anarthropora monodon (Busk, 1860)	FSC, WSH
Family Exochellidae (2)	
Escharoides coccinea (Abildgaard, 1806)	CLD, EST, FTH, HBD, MMS, MRF, NCS, WSH
Escharoides mamillata (Wood, 1844)	EST, MMS, NCS, WSH
Family Flustridae (7)	
Carbasea carbasea (Ellis & Solander, 1786)	EST, FTH, HBD, WSH
Chartella barleei (Busk, 1860)	ESH, NCS, WSH
Chartella papyracea (Ellis & Solander, 1786)	CLD, HBD, MMS
Flustra foliacea (Linnaeus, 1758)	CLD, ESH, EST, FTH, FRT, HBD, MMS, MRF, NCS, SFN, WSH
Hincksina flustroides (Hincks, 1877)	HBD
Sarsiflustra abyssicola (Sars G.O., 1872)	WSH
Securiflustra securifrons (Pallas, 1766)	CLD, ESH, EST, FTH, FRT, HBD, MMS, MRF, NCS, SFN, WSH
Family Haplopomidae (4)	

Haplopoma graniferum (Johnston, 1847)	CLD, FTH, NCS, WSH
Haplopoma impressum (Audouin, 1826)	CLD, MMS, NCS, WSH
Haplopoma planum Ryland, 1963	ESH, WSH
Haplopoma sciaphilum Silén & Harmelin, 1976	HBD
Family Hippoporidridae (2)	
Hippoporella hippopus (Smitt, 1867)	MRF
Hippoporidra lusitania Taylor & Cook, 1981	WSH
Family Hippothoidae (4)	
Celleporella hyalina (Linnaeus, 1767)	CLD, EST, FTH, HBD, MMS, MRF, NCS, WSH
Haplota clavata (Hincks, 1857)	CLD
Hippothoa divaricata Lamouroux, 1821	CLD, EST, NCS
Hippothoa flagellum Manzoni, 1870	CLD, MMS, NCS
Family Lacernidae (1)	
Cylindroporella tubulosa (Norman, 1868)	HBD, MRF, NCS, WSH
Family Membraniporidae (1)	
Membranipora membranacea (Linnaeus, 1767)	ESH, EST, FTH, HBD, MMS, MRF, NCS, RK, SFN, WSH
Family Microporellidae (3)	
Fenestrulina delicia Winston, Hayward & Craig, 2000	CLD, WSH
Fenestrulina malusii (Audouin, 1826)	CLD, EST, HBD, MMS, MRF, NCS, SFN, WSH
Microporella ciliata (Pallas, 1766)	CLD, EST, FTH, MMS, NCS, SFN, WSH
Family Microporidae (3)	
Micropora coriacea (Johnston, 1847)	CLD
Micropora normani Levinsen, 1909	WSH
Mollia multijuncta (Waters, 1879)	WSH
Family Phidoloporidae (5)	
Reteporella beaniana (King, 1846)	MMS, NCS, RK, WSH
Reteporella incognita Hayward & Ryland, 1996	RK, WSH
Reteporella watersi (Nordgaard, 1907)	WSH
Rhynchozoon bispinosum (Johnston, 1847)	WSH
Schizotheca fissa (Busk, 1856)	MMS
Family Romancheinidae (13)	
Arctonula arctica (M. Sars, 1851)	EST, WSH
Escharella abyssicola (Norman, 1869)	FSC, WSH
Escharella immersa (Fleming, 1828)	CLD, EST, MMS, MRF, NCS, WSH
Escharella labiosa (Busk, 1856)	HBD, MMS
Escharella laqueata (Norman, 1864)	MMS, WSH
Escharella octodentata (Hincks, 1880)	FSC, RK, WSH
Escharella variolosa (Johnston, 1838)	CLD, EST, MMS, MRF, WSH
Escharella ventricosa (Hassall, 1842)	CLD, EST, FTH, MMS, MRF, NCS, WSH
Hemicyclopora polita (Norman, 1864)	ESH, MMS, WSH
Neolagenipora collaris (Norman, 1867)	MMS, MRF, NCS, WSH
Neolagenipora eximia (Hincks, 1860)	WSH
Ragionula rosacea (Busk, 1856)	CLD, NCS, WSH
Temachia microstoma (Norman, 1864)	ESH, WSH
Family Schizoporellidae (6)	
Schizoporella cornualis Hayward & Ryland, 1995	MMS

Schizoporella dunkeri (Reuss, 1848)	MMS, NCS, WSH
**Schizoporella japonica* Ortmann, 1890	CLD, ESH, EST, MMS, MRF, NCS, WSH
Schizoporella patula Hayward & Ryland, 1995	ESH, FSC, NCS, WSH
Schizoporella umbonata O'Donoghue & O'Donoghue, 1926	WSH
Schizoporella unicornis (Johnston in Wood, 1844)	CLD, HBD, MMS, MRF, NCS, WSH
Family Scrupariidae (2)	
Scruparia ambigua (d'Orbigny, 1841)	EST, HBD
Scruparia chelata (Linnaeus, 1758)	CLD, EST, FTH, HBD, MMS, NCS, WSH
Family Setosellidae (1)	
Setosella vulnerata (Busk, 1860)	ESH, WSH
Family Smittinidae (8)	
Parasmittina trispinosa (Johnston, 1838)	CLD, ESH, EST, FTH, HBD, MMS, MRF, NCS, RK, SFN, WSH
Phylactella labrosa (Busk, 1854)	MRF, NCS, WSH
Pseudoflustra virgula Hayward, 1994	FSC
Smittina bella (Busk, 1860)	CLD, EST, WSH
Smittina crystallina (Norman, 1867)	MMS, MRF, NCS, WSH
Smittoidea amplissima Hayward, 1979	WSH
Smittoidea marmorea (Hincks, 1877)	EST, FTH, MMS, NCS, WSH
Smittoidea reticulata (MacGillivray, 1842)	CLD, EST, FTH, MMS, MRF, NCS, WSH
Family Stomachetosellidae (3)	
Stomachetosella normani Hayward, 1994	WSH
Stomacrustula cruenta (Busk, 1854)	CLD, ESH, WSH
Stomacrustula sinuosa (Busk, 1860)	CLD, MMS, WSH
Family Tessaradomidae (1)	
Tessaradoma boreale (Busk, 1860)	HBD, RK, WSH
Family Umbonulidae (1)	
Oshurkovia littoralis (Hastings, 1944)	CLD, ESH, EST, FTH, HBD, MMS, MRF, NCS SFN, WSH

Discussion

The Scottish sea regions contain 218 bryozoan species with representatives from each of the extant bryozoan orders. Based on the checklist, it can be concluded that Scotland has fewer bryozoan species than New Zealand (n = 953), Australia (n = 886), and the Mediterranean (n = 556) (Gordon 1999; Gordon et al. 2010; Rosso and Di Martino 2016). Given Scotland's location within a single biogeographical region, this relative lack of species is as expected (Baxter et al. 2011). When coastline length is accounted for, Scotland has approximately half the number of species per km (0.01) as Australia (0.02 species/km) and approximately six times fewer than New Zealand (0.06 species/km). The proportion of ctenostomes in Scotland (12% of total species) is greater than the global average (~5%) (Bock and Gordon 2013), and greater than the proportion of ctenostomes reported from New Zealand (5%), Australia (4%), Argentina (4%) and the Mediterranean (10%) (Gappa 2000; Gordon 1999; Rosso and Di Martino 2016). Only the bryozoan fauna of Brazil has a greater percentage (26.2%) of ctenostomes. Previously, higher incidences of ctenostomes (and/or cyclostomes) have been attributed to the results

of focused taxonomic efforts in certain regions (Gappa 2000; Rosso 2003). Rosso and Di Martino (2016), however, suggested that the abundance of ctenostomes in the Mediterranean could also reflect the availability of high-energy algal and seagrass dominated habitats, for which the flexible uncalcified ctenostome colony forms are well adapted to exploit. Scotland, and the Scottish west coast in particular, has a high abundance and diversity of algae and algal dominated habitats (Smale et al. 2013), which may explain the high number of ctenostomes found in the study region.

As with other benthic marine invertebrates in Scotland, the bryozoan fauna includes NIS (Nall et al. 2015). The presence of all but one NIS within the Clyde Sea region most likely represents the fact that the area is both a well-studied region and the location of a significant number of ports. As global shipping and aquaculture increase, along with climate change, it is expected that the number of invasive or non-indigenous bryozoans in the Scottish sea regions will increase in the future (Stretaris et al. 2005).

The estimate of bryozoan species number in Scotland, presented here, is likely to be conservative, since much of the offshore shelf areas and seamounts have not been fully explored. Estimates of the global number of bryozoan species yet to be discovered range from 2800–5200 (Appeltans et al. 2012). Given that the Scottish bryozoan fauna currently constitutes 3.7% of global bryozoan species richness, and assuming that this proportion will remain constant, it could be expected that there are approximately 104–192 bryozoan species in Scotland yet to be discovered.

Acknowledgements

This study received funding from the UK research council knowledge exchange fellowship [NE/P006566/2], a NERC MSc bursary and EOL Rubenstein Fellowship. The authors would like to thank the numerous people who collected the bryozoan records used in this study.

References

Appeltans W, Ahyong Shane T, Anderson G, Angel Martin V, Artois T, Bailly N, Bamber R, Barber A, Bartsch I, Berta A, Błażewicz-Paszkowycz M, Bock P, Boxshall G, Boyko Christopher B, Brandão Simone N, Bray Rod A, Bruce Niel L, Cairns Stephen D, Chan T-Y, Cheng L, Collins Allen G, Cribb T, Curini-Galletti M, Dahdouh-Guebas F, Davie Peter JF, Dawson Michael N, De Clerck O, Decock W, De Grave S, de Voogd Nicole J, Domning Daryl P, Emig Christian C, Erséus C, Eschmeyer W, Fauchald K, Fautin Daphne G, Feist Stephen W, Fransen Charles HJM, Furuya H, Garcia-Alvarez O, Gerken S, Gibson D, Gittenberger A, Gofas S, Gómez-Daglio L, Gordon Dennis P, Guiry Michael D, Hernandez F, Hoeksema Bert W, Hopcroft Russell R, Jaume D, Kirk P, Koedam N, Koenemann S, Kolb Jürgen B, Kristensen Reinhardt M, Kroh A, Lambert G, Lazarus David B, Lemaitre R, Longshaw M, Lowry J, Macpherson E, Madin Laurence P, Mah C, Mapstone G, McLaughlin Patsy A, Mees J, Meland K, Messing Charles G, Mills Claudia E, Molodtsova Tina N, Mooi R, Neuhaus B,

Ng Peter KL, Nielsen C, Norenburg J, Opresko Dennis M, Osawa M, Paulay G, Perrin W, Pilger John F, Poore Gary CB, Pugh P, Read Geoffrey B, Reimer James D, Rius M, Rocha Rosana M, Saiz-Salinas José I, Scarabino V, Schierwater B, Schmidt-Rhaesa A, Schnabel Kareen E, Schotte M, Schuchert P, Schwabe E, Segers H, Self-Sullivan C, Shenkar N, Siegel V, Sterrer W, Stöhr S, Swalla B, Tasker Mark L, Thuesen Erik V, Timm T, Todaro MA, Turon X, Tyler S, Uetz P, van der Land J, Vanhoorne B, van Ofwegen Leen P, van Soest Rob WM, Vanaverbeke J, Walker-Smith G, Walter TC, Warren A, Williams Gary C, Wilson Simon P, Costello Mark J (2012) The magnitude of global marine species diversity. Current Biology 22: 2189–2202. https://doi.org/10.1016/j.cub.2012.09.036

Baxter JM, Boyd IL, Cox M, Donald AE, S.J M, Miles H, Miller B, Moffat CF (2011) Scotland's Marine Atlas: Information for the National Marine Plan. Marine Scotland, Edinburgh, 191 pp.

Bitschofsky F, Forster S, Scholz J (2011) Regional and temporal changes in epizoobiontic bryozoan-communities of Flustra foliacea (Linnaeus, 1758) and implications for North Sea ecology. Estuarine, Coastal and Shelf Science 91: 423–433. https://doi.org/10.1016/j.ecss.2010.11.004

Bock PE, Gordon DP (2013) Phylum Bryozoa Ehrenberg, 1831. In: Zhang Z-Q (Ed.) Animal biodiversity: an outline of higher-level classification and survey of taxonomic richness (Addenda 2013). Zootaxa 3703: 67–74.

Boulton G, Peacock J, Sutherland D (1991) Quaternary. In: Trewin NH (Ed.) Geology of Scotland, 503–543.

Collin SB, Tweddle JF, Shucksmith RJ (2015) Rapid assessment of marine non-native species in the Shetland Islands, Scotland. BioInvasions Records 4: 147–155. https://doi.org/10.3391/bir.2015.4.3.01

Gappa JL (2000) Species richness of marine Bryozoa in the continental shelf and slope off Argentina (south-west Atlantic). Diversity and Distributions 6: 15–27. https://doi.org/10.1046/j.1472-4642.2000.00067.x

Gordon D, Costello MJ (2016) Bryozoa - not a minor phylum. New Zealand Science Review 73: 63–66.

Gordon DP (1999) Bryozoan diversity in New Zealand and Australia. In: Ponder W, Lunney D (Eds) The other 99% The conservation and biodiversity of invertebrates. Transactions of the Royal Zoological Sociert of New South Wales, Mosman. doi: https://doi.org/10.7882/RZSNSW.1999.033 https://doi.org/10.7882/RZSNSW.1999.033

Gordon DP, Beaumont J, MacDiarmid A, Robertson DA, Ahyong ST (2010) Marine Biodiversity of Aotearoa, New Zealand. PLoS ONE 5: e10905. https://doi.org/10.1371/journal.pone.0010905

Hayward P, Ryland J (1998) Cheilostomatous Bryozoa. Part 1. Aeteoidea—Cribrilinoidea. Synopses of the British fauna. Field Studies Council, Shrewsbury, 366 pp.

Hiscock K (1996) Marine nature conservation review: rationale and methods. Joint Nature Conservation Committee, Peterborough, 54 pp.

Horton T, Kroh A, Bailly N, Boury-Esnault N, Nunes Brandão SN, Costello MJ, Gofas S, Hernandez F, Mees J, Paulay G, Poore G, Rosenberg G, Stöhr S, Decock W, Dekeyzer S, Vandepitte L, Vanhoorne B, Vranken S, Adams MJ, Adlard R, Adriaens P, Agatha S, Ahn KJ, Ahyong S, Alvarez B, Anderson G, Angel M, Arango C, Artois T, Atkinson S, Barber A, Bartsch I, Bellan-Santini D, Berta A, Bieler R, Błażewicz M, Bock P, Böttger-Schnack

R, Bouchet P, Boyko CB, Bray R, Bruce NL, Cairns S, Campinas Bezerra TN, Cárdenas P, Carstens E, Cedhagen T, Chan BK, Chan TY, Cheng L, Churchill M, Coleman CO, Collins AG, Crandall KA, Cribb T, Dahdouh-Guebas F, Daly M, Daneliya M, Dauvin JC, Davie P, De Grave S, de Mazancourt V, Defaye D, d'Hondt JL, Dijkstra H, Dohrmann M, Dolan J, Downey R, Drapun I, Eisendle-Flöckner U, Eitel M, Encarnação SCd, Epler J, Ewers-Saucedo C, Faber M, Feist S, Finn J, Fišer C, Fonseca G, Fordyce E, Foster W, Frank JH, Fransen C, Furuya H, Galea H, Garcia-Alvarez O, Gasca R, Gaviria-Melo S, Gerken S, Gheerardyn H, Gibson D, Gil J, Gittenberger A, Glasby C, Glover A, Gordon D, Grabowski M, Gravili C, Guerra-García JM, Guidetti R, Guilini K, Guiry MD, Hajdu E, Hallermann J, Hayward B, Hendrycks E, Herrera Bachiller A, Ho Js, Høeg J, Holovachov O, Hooper J, Hughes L, Hummon W, Hyzny M, Iseto T, Ivanenko S, Iwataki M, Jarms G, Jaume D, Jazdzewski K, Kaminski M, Karanovic I, Kim YH, King R, Kirk PM, Kolb J, Kotov A, Krapp-Schickel T, Kremenetskaia A, Kristensen R, Kullander S, La Perna R, Lambert G, Lazarus D, LeCroy S, Leduc D, Lefkowitz EJ, Lemaitre R, Lörz AN, Lowry J, Macpherson E, Madin L, Mah C, Mamos T, Manconi R, Mapstone G, Marshall B, Marshall DJ, McInnes S, Meidla T, Meland K, Merrin K, Messing C, Miljutin D, Mills C, Mokievsky V, Molodtsova T, Monniot F, Mooi R, Morandini AC, Moreira da Rocha R, Moretzsohn F, Mortelmans J, Mortimer J, Musco L, Neubauer TA, Neuhaus B, Ng P, Nielsen C, Nishikawa T, Norenburg J, O'Hara T, Okahashi H, Opresko D, Osawa M, Ota Y, Parker A, Patterson D, Paxton H, Perrier V, Perrin W, Petrescu I, Picton B, Pilger JF, Pisera A, Polhemus D, Pugh P, Reimer JD, Reuscher M, Rius M, Rützler K, Rzhavsky A, Saiz-Salinas J, Santos S, Sartori AF, Satoh A, Schatz H, Schierwater B, Schmidt-Rhaesa A, Schneider S, Schönberg C, Schuchert P, Self-Sullivan C, Senna AR, Serejo C, Shamsi S, Sharma J, Shenkar N, Sicinski J, Siegel V, Sierwald P, Sinniger F, Sivell D, Sket B, Smit H, Smol N, Souza-Filho JF, Stampar SN, Sterrer W, Stienen E, Strand M, Suárez-Morales E, Summers M, Suttle C, Swalla BJ, Taiti S, Tandberg AH, Tang D, Tasker M, Taylor J, Tchesunov A, ten Hove H, ter Poorten JJ, Thomas J, Thuesen EV, Thurston M, Thuy B, Timi JT, Timm T, Todaro A, Turon X, Tyler S, Uetz P, Utevsky S, Vacelet J, Vader W, Väinölä R, van der Meij SE, van Soest R, Van Syoc R, Venekey V, Vonk R, Vos C, Walker-Smith G, Walter TC, Watling L, Whipps C, White K, Williams G, Wilson R, Wyatt N, Wylezich C, Yasuhara M, Zanol J, Zeidler W (2016) World Register of Marine Species (WoRMS). WoRMS Editorial Board.

Lidgard S (2008) Predation on marine bryozoan colonies: taxa, traits and trophic groups. Marine Ecology Progress Series 359: 117–131. https://doi.org/10.3354/meps07322

Loxton JL (2014) Investigations into the Skeletal Mineralogy of Temperate and Polar Bryozoans. PhD Thesis. UK: Heriot Watt University.

McKinney FK, Jackson JBC (1991) Bryozoan Evolution. University of Chicago Press, Chicago, 238 pp.

Nall CR, Guerin AJ, Cook EJ (2015) Rapid assessment of marine non-native species in northern Scotland and a synthesis of existing Scottish records. Aquatic Invasions 10: 107–121. https://doi.org/10.3391/ai.2015.10.1.11

Narkowicz CK, Blackman AJ, Lacey E, Gill JH, Heiland K (2002) Convolutindole A and convolutamine H, new nematocidal brominated alkaloids from the marine bryozoan

Amathia convoluta. Journal of natural products 65: 938–941. https://doi.org/10.1021/np010574x

Norman AM (1869) Shetland final dredging report. Part II. On the Crustacea, Tunicata, Polyzoa, Echinodermata, Actinozoa, Hydrozoa, and Porifera. Report of the British Association for the Advancement of Science 38: 247–336.

O'Brien JM, Krumhansl KA, Scheibling RE (2013) Invasive bryozoan alters interaction between a native grazer and its algal food. Journal of the Marine Biological Association of the United Kingdom 93: 1393–1400. https://doi.org/10.1017/S0025315412001683

Porter JS, Spencer Jones ME, Kuklinski P, Rouse S (2015) First records of marine invasive non-native Bryozoa in Norwegian coastal waters from Bergen to Trondheim. Bioinvasions Rec 4: 157–169. https://doi.org/10.3391/bir.2015.4.3.02

Powney G, Isaac N (2015) Beyond maps: A review of the applications of biological records. Bioloigcal Journal of the Linnean Society 115: 532–542. https://doi.org/10.1111/bij.12517

Rosso A (2003) Bryozoan diversity in the Mediterranean Sea. Biogeographia 24: 219–238. https://doi.org/10.12681/mms.1706

Rosso A, Di Martino E (2016) Bryozoan diversity in the Mediterranean Sea: an update. Mediterranea Marine Science 17: 567–607. https://doi.org/10.12681/mms.1706

Rouse S, Spencer Jones ME, Porter JS (2014) Spatial and temporal patterns of bryozoan distribution and diversity in the Scottish sea regions. Marine Ecology 35: 85–102. https://doi.org/10.1111/maec.12088

Smale DA, Burrows MT, Moore P, O'Connor N, Hawkins SJ (2013) Threats and knowledge gaps for ecosystem services provided by kelp forests: a northeast Atlantic perspective. Ecology and Evolution 3: 4016–4038. https://doi.org/10.1002/ece3.774

Stretaris N, Zenetos A, Papthanassiou E (2005) Globalisation in marine ecosystems: the story of non-indigenous marine species across European seas. Oceanography and Marine Biology: An Annual Review 43: 419–453.

Wasson B, De Blauwe H (2014) Two new records of cheilostome Bryozoa from British waters. Marine Biodiversity Records 7: e123. https://doi.org/10.1017/S1755267214001213

Yorke AF, Metaxas A (2011) Interactions between an invasive and a native bryozoan (*Membranipora membranacea* and *Electra pilosa*) species on kelp and Fucus substrates in Nova Scotia, Canada. Marine Biology 158: 2299. https://doi.org/10.1007/s00227-011-1734-3

Supplementary material 1

Scottish bryozoan records

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Data type: occurence

Link: https://doi.org/10.3897/zookeys.787.24647.suppl1